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**Assessment of individual personality and the effect of personality traits on
discrimination learning in Nigerian dwarf goats (*Capra aegagrus hircus*)**

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Thesis



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Chapter 1: General Introduction

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General Introduction



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1.1. The concept of personality

Measuring and understanding personality in animals is a rising scientific field. Much research has been conducted to assess distinctive individual differences in behaviour in a large number of species in the past few decades, and increasing numbers of studies include farm animals. The assessment and understanding of personality in farm animals is of growing scientific and practical interest, because even the consumer of farm animal products and society itself show higher interest about the animal's welfare during a farm animal's lifetime. In farm animals, understanding individual differences in personality and its relation to behavioural, cognitive, and physiological traits has gained increased attention for welfare purposes. Personality and its relationship to other traits and cognitive abilities may have an impact on economic factors as farm animals such as pigs, cattle, chicken and horses must cope with numerous challenging situations, automatic systems and different husbandry practises during their lifetime (reviewed by Finkemeier et al., 2018). To date, the five domains model by Mellor et al. (2020) is one of the most important concepts in animal welfare research. It describes: 1. Nutrition. 2. Physical Environment. 3. Health. 4. Behavioural interactions. 5. Mental state (Mellor et al., 2020). The first three domains focus on the physical well-being of an animal, while the fourth describes the brain processing of each sensory input (e.g. the environment, interactions with other animals, conspecifics, or humans) leading to a behavioural reaction. The fifth domain describes the associated effects elicited by external stimuli (also processed in the brain) leading to an

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individual perception of a situation and leading to a reaction, e.g. fear. Negative or positive affective experiences in human-animal interactions can be gentle handling (no responses of fear, positive) or very strong restraint (extreme responses of fear, negative) (Mellor et al., 2020). These five domains encompass the mental and physical well-being of animals. To measure the mental and physical well-being of an animal we need to understand the underlying mechanisms of personality and the relationships to other traits and cognitive abilities. This is one of the most important tools to improve farm animal welfare as the results can help to adjust management and housing conditions, veterinary interventions, and many other challenges of a farm animal's lifetime.

1.1.1 Personality

In human personality research, the term personality is used to describe a distinctive and relatively stable set of mental traits that describe the organism's behaviour, which is explained with the "Five-Factor Model of Personality". The five factors describing human personality are extraversion, agreeableness, conscientiousness, neuroticism, and openness (John & Srivastava, 1999). Goldberg (1993) describes which traits define each factor – extraversion (or surgency) comprises traits like talkativeness, assertiveness and activity levels on one end of the spectrum and silence, passivity and reserve on the other end; agreeableness (or pleasantness) includes traits like kindness, trust and warmth and the opposite traits of hostility, selfishness and distrust; conscientiousness (or dependability) comprises traits like organization, thoroughness and reliability from beginning of the spectrum and carelessness, negligence and unreliability on the other end; neuroticism (or emotional stability) includes traits like nervousness,

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moodiness and temperamentality; and openness to experience (or intellect) describes traits like imagination, curiosity and creativity on one end of the spectrum and shallowness and imperceptiveness to the end of the spectrum. As the result of questionnaires, the five factors have been identified in humans, with extraversion and neuroticism as the first two factors identified (McCrae & John, 1992). Openness was the third factor identified and later agreeableness and conscientiousness were the last factors included in human personality research (McCrae & John, 1992). With the help of questionnaires, researchers are able to assess individual human personalities and generate individual personality profiles. Personality traits are often assumed to be acquired patterns of thought and behaviour that might be found in organisms with sophisticated cognitive systems (McCrae et al., 2000). Furthermore, the environment also has an influence on personality factors because the adaptations of the organism to the environment are always involved in their expression, but the results of studies have shown a consistent pattern of stability of personality over time and contexts (reviewed by McCrae et al., 2000). Sex seems to have an influence on personality factors as well. Schmitt et al. (2008) describe in their review that studies have reported women as having higher levels of neuroticism, extraversion, agreeableness, and conscientiousness than men. On the other hand, men tend to be more assertive and risk-taking than women. These sex differences can already be detected in early childhood and remain constant across adulthood (Schmitt et al., 2008).

1.1.2 Temperament

The term temperament in human psychology research is closely related to personality. Temperament is defined as the inherited, early appearing tendencies

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that continue throughout life and serve as the foundation for personality (Buss, 1995; Goldsmith et al., 1987; Gosling, 2001) because temperament is observable in infants and is tied to basic psychological processes (McCrae et al., 2000; Rothbart et al., 2000). According to Buss (1987), the term temperament is used to reflect genetic behavioural differences, while the term personality, which is based on temperament, seems to be used to reflect non-genetic differences. Mason (1984) defined temperament as “the individual’s basic stance towards environmental changes and challenges”. Rothbart et al. (2000) suggested that understanding temperament is central for the understanding of personality because it influences and is influenced by the experiences of each individual and because one of its outcomes is the adult personality. However, most theorists assume that temperament provides the starting place for personality development (reviewed by McCrae et al., 2000). Rothbart et al. (2000) also noted significant similarities between temperamental dispositions and several of the “Big Five” factors. Zentner & Bates (2008) reviewed nine temperamental factors that can be found in children: (a) activity level, (b) rhythmicity (regularity), (c) approach/withdrawal, (d) adaptability, (e) sensory threshold, (f) intensity of reaction, (g) quality of mood, (h) distractibility, and (i) attention span/persistence. What distinguishes these factors from personality factors seems to be their formal or stylistic nature, which means that they refer to the “how” of behaviour (e.g., the behavioural style), whereas personality factors refer to the “what” (abilities) and the “why” (motivation) of behaviour (Thomas & Chess, 1977). Therefore, temperament provides process-oriented models by establishing links between individual differences in behaviour and their psychological and biological substrates in

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humans as well as in non-human animals, while personality provides subject-oriented models (Rothbart et al., 2000).

1.1.3 Coping Style

Coping is a very broad and a multidimensional concept with a long and complex history. In human psychological research, coping refers to intentional cognitive or behavioural attempts by the individual to manage a stressor (Affleck & Tennen, 1996). Lazarus (1993) has emphasized coping as a key concept for research on adaptation and health. Because coping is a behavioural reaction to aversive situations that induce several physiological stress reactions (Wechsler, 1995), individual ways of dealing with stress have an enormous impact on human health (Henry & Stephens, 1977). Lazarus (1993) suggests to differentiate between two approaches to coping, one that treats coping as a personality characteristic (style) and another that refers to the efforts to manage stress (process). Whereas the process approach primarily addresses the behavioural and physiological mechanisms involved in the adaptational response to stress, coping style rather seems to describe a personal or individual consistency in this response. According to Koolhaas et al. (1999), a coping style can be defined as a coherent set of behavioural and physiological stress responses that is shaped by evolution, is consistent over time and is characteristic to a certain group of individuals.

There are some indications that coping and personality are substantially related (Carver & Connor-Smith, 2010), and that coping can be classified into a variety of different types or styles. Lazarus and Folkman (1984) address two types of coping style: the problem-focused style and the emotion-focused style. While the first refers to the attempt to solve the problem that causes the stressful situation, the

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second deals with the way of decreasing the emotional feelings caused by the problem without concentrating on the problem itself (Lazarus & Folkman, 1984). The problem-focused style includes subscales such as “accepting responsibility”, “planful problem solving” and “self-controlling”, whereas the subscales of the emotion-focused style are “seeking social support”, “confrontive coping” and “escape-avoidance” (Lazarus & Folkman, 1984). Another possibility is the classification of coping into an “approach-avoidance” category. This category classifies behaviour and cognitive abilities that are used by the individual to face the problem (approach) or to divert the individual’s attention away (avoidance) from the problem (Moos, 1993). Moreover, further ways to group coping responses are discussed that focus on different questions about responses to stress (Carver & Connor-Smith, 2010).

1.1.4 Animal Personality

The five personality factors derived from human psychology (extraversion, neuroticism, agreeableness, openness, and conscientiousness) have been investigated also in animals, whereas researchers found equivalent five personality factors that proved to be more suitable to measure individual differences in animals: exploration, activity, aggressiveness, sociability, and boldness (Verbeek et al., 1996; Réale et al., 2007; Guenther et al., 2014b). Personality in animals is defined as a correlated set of individual behavioural and physiological traits that are consistent over time and across contexts (Koolhaas et al., 1999; Réale et al., 2007). In animal personality research, the term temperament is closely related to personality and matches the definition found in human personality research and is also defined as inherited, early-appearing

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tendencies that continue throughout life and that serve as the foundation for personality (McCrae et al., 2000). Both terms are often used as synonyms (Réale et al., 2007), while other researchers argue the term temperament is simply used to avoid the use of the term personality as it might be associated with anthropomorphism (Jones & Gosling, 2005). Another term often used in animal personality research is “behavioural syndromes”. Behavioural syndromes are defined as a suite of correlated behaviours reflecting an individual’s consistency in behaviour across multiple situations (Sih et al., 2004). While a behavioural syndrome can be exhibited by a population or a species, individuals have a behavioural type within a populations’ behavioural syndrome (Sih et al., 2004). The concept of animal coping is based on the animal’s reaction to its environment with respect to reducing effects of aversive stimuli (e.g., fight or flight response, approach or avoidance, boldness or shyness) (Cannon, 1929; Wechsler, 1995; Koolhaas et al., 1999; Korte et al., 2005).

All these terms, especially personality, temperament and coping are also used in farm animal personality research. But the terminology and definitions are often confusing as the different terms and concepts are often used synonymously to explain individual differences in farm animal species. Therefore, the second chapter of my thesis specifically deals with the different definitions used in animal personality research, how these are used in farm animal personality research and how individual differences in personality in farm animals can be properly measured in the future.

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1.2. The Relationship between Personality and Cognitive Performance especially Learning in (Farm) Animals

Cognition is defined as all mental processes on the basis of brain capacity and functionality such as attention, thinking processes, expectation, problem solving including perception, decision making, memory and learning (Shettleworth, 2001, 2010; Dukas, 2004; Weinandy, 2006). Learning comprises an individual's ability of behavioural adjustment due to changing environmental conditions due to perception, processing and storing information (Tembrock, 1978; Wat et al., 2020). For instance, being able to remember food patches and to adjust foraging behaviour in case of food patch depletion can be crucial in the context of survival for any animal (Shettleworth, 2010). Individual differences in personality can lead to individual differences in the ability to adjust individual behaviour explaining individual differences in learning performance and/or cognitive capacities in general (Carere & Locurto, 2011). Going further, Sih & Del Guidice (2012) already postulated that individual differences in personality can be functionally related to individual differences in cognitive abilities as both are supposed to share the same risk-reward trade-offs. Numerous studies with different species were able to find relationships between certain personality traits and cognitive capacities and/or learning in the last decade (please see Dougherty & Guillette, 2018 for a detailed meta-analysis). For instance, boldness in female guppies was related to speed accuracy in a spatial associative learning task: bold female guppies learned the task faster and were more accurate than shy female guppies (Trompf & Brown, 2014). Shy three spined sticklebacks showed more flexibility in response speed in a social foraging task (Harcourt et al., 2010). In wild cavies the personality trait boldness was also correlated to learning speed: bold cavies

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learned an associative learning task more quickly than shy cavies (Guenther et al., 2014a). Personality traits such as boldness and exploration seem to have the strongest relationship to individual learning success as bold and explorative animals seem to form routines in stable environmental conditions – shy and less explorative animals perform better in changing environmental conditions as they show more flexible individual behaviour (Guillette et al., 2011). Recently, Goulet et al. (2018) postulated that cognitive capacities should be more incorporated in the “Pace-of-Life-Syndrom” (POLS) framework as it already comprises behavioural and physiological traits. The authors also suggest that certain behavioural types can lead to a certain cognitive style. For instance, a lizard scoring high on activity, exploration and boldness is categorized as fast behavioural type, having a high thermal physiological trait (here body temperature) is predicted to learn a novel task faster at the cost of accuracy, while a lizard scoring low on activity, exploration and boldness is categorized as slow behavioural type with a low thermal physiological trait would be more attentive and flexible to external cues, but being more accurate resulting in a slower learning rate (Goulet et al., 2018).

In farm animal species, the research about relationships between personality traits and cognitive abilities has gained more interest in the last decade. These relationships together with a certain awareness about housing and management conditions lead to a certain societal discussion about the welfare status of farm animals. These relationships are also so seen to be related to a certain product quality and therefore, became even more significant in politics (Nawroth et al., 2019). Studies investigating the impact of farm animal personality on cognitive

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capacities are quite scarce but the few I found show remarkable results across all farm animal species. For instance, in horses, the personality trait fearfulness (measured in a novel object test by measuring the number of contacts with the object) influences extinction and working memory performance according to the state of stress: fearful horses showed better performance under controlled conditions (less contacts in comparison to fearless horses) and worse performance under stressful conditions (decrease of the number of contacts in comparison to prior measurement) and were more resistant to extinction in a backward task (the handler teaches the horse to be led with a lunge and to walk forwards or move backwards) than fearless horses, which were more resistant to extinction in an active avoidance test (the test horses had to learn to actively avoid compressed puffs of air by crossing a yellow crossbar during the sound of a door bell (Valenchon et al., 2013)). In calves, personality has been shown to affect learning as well: calves with a higher activity showed less feeding apparatus visits during the training of an operant conditioning task (Webb et al., 2015). In goats, personality traits like exploration and sociability were related to cognitive performance, learning style and learning flexibility: less explorative goats performed better on a non-associative cognitive task, and less sociable goats performed better compared to more sociable goats in a visual discrimination task (Nawroth et al., 2017). In pigs, fearfulness towards humans and locomotion activity were linked with learning performance in relation to task complexity (Brajon et al., 2016) and in chicken, learning speed in reversal tasks was associated with individual variation in exploration: more explorative chicks learned the reversal task faster than less explorative ones (Zidar et al., 2018).

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All these results show a high interest and species- and/or even context-related differences in the relationship between personality traits and cognitive capacities in nonhuman animals as well as in farm animal species. Therefore, chapter three of my thesis deals first with species-related personality traits in farm animals, especially in dwarf goats, while chapter four addresses the relationship between the defined personality traits and the cognitive capacities of dwarf goats.

1.3. Small Ruminants – Why using dwarf goats to study individual differences in behaviour, physiology, and cognition?

The right choice of the study species is crucial for the planning and the execution of the experiments and the interpretation of the results. This raises the question, why using dwarf goats to investigate about the relationship between personality, especially personality traits and cognitive capacities. The majority of the worldwide goat population remains under extensive use, but there is a steady increase in high production and commercial systems, particularly in the dairy sector (reviewed by Zobel & Nawroth, 2020). According the FAO (2018) the world goat population surpasses 1 billion. Goats are able to survive in many regions and under challenging environmental conditions because of their complex foraging and social skills, as they are highly dynamic in social settings and they have sophisticated cognitive capacities (reviewed by Zobel & Nawroth, 2020). Feral goats live in groups with a fission-fusion dynamic in stable dominance hierarchies with different group sizes from 2 to 100 (reviewed by Zobel & Nawroth, 2020). Goats are able to identify individuals using acoustic (Poindron et al., 2003; Briefer & McElligott, 2012) as well as visual (Keil et al., 2012; Langbein et al., 2023) cues. Goat groups often live in steep, rocky, and often

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nutritionally challenging terrain (Zobel et al., 2019) and preferentially browse on grasses, herbs and shrubbery (reviewed by Zobel & Nawroth, 2020). Although domestic goats appear to be less selective than feral and wild goats (Aldezabal & Garin, 2000), they are highly flexible in what they eat and learn where preferential plant species are located (Provenza et al., 1994). Such capacities in adapting to harsh foraging and environmental conditions have resulted in the expression of distinct cognitive capacities shown in numerous experiments conducted under laboratory settings (reviewed by Zobel & Nawroth, 2020). Using an automated learning device which presented artificial symbols via a screen, dwarf goats could show that they have clear categorization capacities (Meyer et al., 2012). Furthermore, goats were able to remember a navigational route for over 3 months (Langbein, 2012) and vocalisations of offspring for at least one year (Briefer et al., 2012, 2014), suggesting high capacities in retaining spatial information. Another skill that goats possess is object permanence: They followed the trajectory of the non- visible reward, which was hidden in full sight in one of two opaque containers and then switched in position. After the switch, most goats chose the correct container with moderate to high success (Nawroth et al., 2015). Individual differences in behaviour and personality are often neglected as goats in commercial systems are often treated as herds (reviewed by Zobel & Nawroth, 2020). Therefore, investigating individual differences in personality are of great importance especially for welfare purposes. Research about personality in goats is quite scarce. To date, only one study was able to categorize two of the five accepted personality traits in animal personality research – sociability and exploration (Nawroth et al., 2017). Another study could show that goats seek cognitive challenges (Langbein et al., 2009), known as the concept of contra-

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freeloading, where learning has an intrinsic value (Osborne, 1977; Franks, 2019). According to Hagen & Broom (2004), successfully coping with a cognitive challenge could have intrinsic reinforcing properties. Another study already showed that at least structural enrichment appeared to improve the goat's ability to solve a visual discrimination task (Oesterwind et al., 2016). In the same study, goats that performed the cognitive task showed also a bolder response towards novel items. Regarding the mentioned studies and results, further investigating individual differences in personality and the relationship to cognitive capacities is a logical consequence to understand underlying mechanisms in this species and next, to improve their housing, management conditions and welfare.

1.4. Hypotheses and goal of the thesis

The concept of personality is a broad field in (farm) animal research as well as in human psychology research. Many studies already have shown remarkable results about factors, traits, individual behavioural expression, and inter- and/or intra-related links to other effects affecting individual expression as well. The following figure (Figure 1) roughly describes the concept of personality as the whole concept for sure comprises many more components that need further investigation. Personality comprises individual temperament and individual coping. Temperament and individual coping are also related as temperament can explain individual coping and in turn individual coping can explain individual temperament (reviewed by Finkemeier et al., 2018). Personality is stable over time and context and is described by different personality traits and/or factors. The 5-factor-model is one of the more prominent models, but more factors e.g. in primates, are discussed (reviewed by Finkemeier et al. 2018). Both parts, stability

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over time and contexts and personality traits, describe individuality on a continuum. This continuum explains individual variation of behavioural expression. Behavioural expression on the population level can lead to behavioural syndromes, when different behaviours are correlated and these correlations are consistent in multiple situations (Sih et al., 2004). Some personality traits can correlate with and/or can have an effect on physiological and cognitive traits. Individual experience over life-time and/or environmental conditions, can also have an effect on individual coping and influence personality, physiological and cognitive traits, which in turn influence individual variation of the behavioural expression (reviewed by Finkemeier et al., 2018). The effect of individual experience over life-time and/or environmental conditions can be seen as equivalent to the description of Mellor et al. (2020) fifth domain “Mental State” which considers external circumstances and the individual perception (negative or positive) of those.

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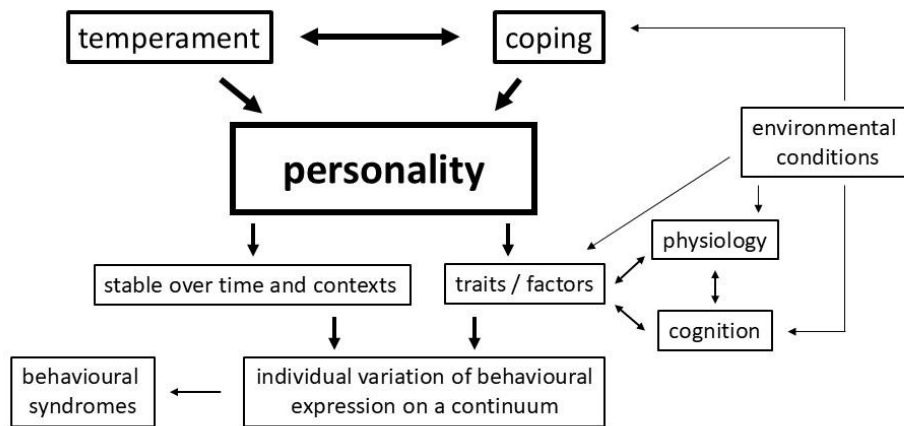


Figure 1: The concept of personality. The arrows describe relationships between components and parts of the personality concept. This is a small part of the whole concept as the whole personality concept comprises surely more components that need further investigation.

Considering the complexity of the personality concept, one of the main goals of this thesis is to investigate how personality is expressed, in which form it is related to physiology and cognition in farm animals on the example of dwarf goats. Personality traits are often assumed to be acquired patterns of thought and behaviour that might be found in organisms with sophisticated cognitive systems, as results of studies with humans have shown a consistent pattern of stability of personality over time and contexts (reviewed by McCrae et al., 2000). Terms explaining different aspects of personality, especially “personality”,

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“temperament” and “coping” are also used in farm animal personality research. Therefore, the second chapter of my thesis specifically deals with the different definitions used in animal personality research, how these are used in farm animal personality research as the terminology and definitions are often confusing and the different terms and concepts are often used synonymously to explain individual differences in farm animal species, while studies in different mammals, birds, and other taxa widely use the term personality to describe between-individual consistency in behavioural variation. In farm animal research the terms temperament and coping style are predominantly used, probably because personality might be associated with anthropomorphism. The mentioned chapter deals also with how individual differences in personality in farm animal can be properly measured in the future and how these findings can lead to a better understanding of what farm animal welfare is and how personality can be considered to improve welfare in farm animals.

Goats are able to survive in many regions and challenging environmental conditions because of their complex foraging and social skills, and are known to have sophisticated cognitive capacities (reviewed by Zobel & Nawroth, 2020). Research about personality in goats is quite scarce. To date, only one study was able to categorize two of the five accepted personality traits in animal personality research – sociability and exploration (Nawroth et al., 2017). Therefore, the third chapter of my thesis deals with the investigation of personality traits in this species. Specifically, the investigation of other personality traits than sociability and exploration up to the formation of behavioural syndromes, to correlations with physiological traits and dominance hierarchy.

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As goats have sophisticated cognitive capacities, already shown in numerous studies (reviewed by Zobel & Nawroth, 2020), the fourth chapter of this thesis deals with the relationship of cognitive capacities and personality trait in dwarf goats. Many research with different species has already been done, but results were quite divers and somehow species-related as some studies found relationships, while others did not.

Considering all the mentioned aspects this thesis addresses three main hypotheses:

1. I expect that goats show different personality traits, based on measuring behaviours in repeatedly conducted open-field and novel-object tests and analysing these behaviours with a principal component analysis.
2. I expect that the personality traits in goats are correlated with physiological traits and dominance hierarchy, based on heart rate variability measurement and weight, direct observations of dyadic agonistic interactions and a limited access test, and behaviour measured in a social separation test.
3. I also expect the personality traits of the goats to be related to their cognitive abilities, especially in learning and reversal learning in a visual discrimination task. I expect that bold goats will learn a visual discrimination task faster than shy goats, while shy goats will perform better in reversal learning.

**Chapter 2 – Personality Research in Mammalian Farm Animals:
Concepts, Measures, and Relationship to Welfare**

Chapter TWO:

**Personality Research in Mammalian Farm
Animals: Concepts, Measures, and Relationship to
Welfare**



Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

This chapter is redrawn from *Frontiers in Veterinary Science*: "Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare".

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Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

2.1 Abstract

Measuring and understanding personality in animals is a rising scientific field. Much research has been conducted to assess distinctive individual differences in behavior in a large number of species in the past few decades, and increasing numbers of studies include farm animals. Nevertheless, the terminology and definitions used in this broad scientific field are often confusing because different concepts and methods are used to explain often synonymously applied terms, such as personality, temperament and coping style. In the present review we give a comprehensive overview of the concepts and terms currently used in animal personality research and critically reveal how they are defined and what they measure. First, we shortly introduce concepts describing human personality and how these concepts are used to explain animal personality. Second, we present which concepts, methods and measures are applied in farm animal personality research and show that the terminology used seems to be somehow species-related. Finally, we discuss some findings on the possible impact of personality on the welfare of farm animals. The assessment of personality in farm animals is of growing scientific and practical interest. Differences in theoretical frameworks and methodological approaches may also entail the diverse use of the different concepts between basic and applied research approaches. We conclude that more consistency is needed in using different theoretical concepts, terms and measures, especially in farm animal personality research. The terms coping style and temperament, which are used in different ways, should not be examined as independent concepts, but rather should be considered as different aspects of the whole personality concept. Farm animal personality should be increasingly

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considered for the improvement of animal housing, management, breeding and welfare.

Keywords

Personality, temperament, coping style, welfare, farm animals

2.2 Introduction

Measuring animal personality has become quite important in the past few decades, but many studies use different concepts and terminology to explain individual differences in behavior and physiology. Nevertheless, studies on farm animals do measure personality traits with methods that have been used to assess animal behavior. It must be born in mind that the concepts and terms such as personality, temperament, coping style used in animal personality research have their origin in human personality research.

In human personality research, the term personality is used to describe a distinctive and relatively stable set of mental traits that explain the organism's behavior, and the concept of personality is explained with the "Five-Factor Model of Personality". The five factors describing human personality are extraversion, agreeableness, conscientiousness, neuroticism, and openness (1). Goldberg (2) describes which traits define each factor – extraversion (or surgency) comprises traits like talkativeness, assertiveness and activity levels on one end of the spectrum and silence, passivity and reserve on the other end; agreeableness (or pleasantness) includes traits like kindness, trust and warmth and the opposite traits of hostility, selfishness and distrust; conscientiousness (or dependability)

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comprises traits like organization, thoroughness and reliability on one end of the spectrum and carelessness, negligence and unreliability on the other end; neuroticism (or emotional stability) includes traits like nervousness, moodiness and temperamentality; and openness to experience (or intellect) describes traits like imagination, curiosity and creativity on one end of the spectrum and shallowness and imperceptiveness on the other end.

The term temperament in human psychology research is closely related to personality. Temperament is defined as the inherited, early appearing tendencies that continue throughout life and serve as the foundation for personality (3-5) because temperament is observable in infants and is tied to basic psychological processes (6, 7). According to Buss (8), the term temperament is used to reflect genetic behavioral differences, while the term personality, which is based on temperament, seems to be used to reflect non-genetic differences. Rothbart et al. (7) suggested that understanding temperament is central to understanding personality because it influences and is influenced by the experiences of each individual and because one of its outcomes is the adult personality. However, most theorists assume that temperament provides the starting place for personality development [reviewed by McCrae et al. (6)]. Temperament provides process-oriented models by establishing links between individual differences in behavior and their psychological and biological substrates in humans as well as in non-human animals, while personality provides subject-oriented models (7).

Coping is a very broad and a multidimensional concept with a long and complex history. In human psychology research, coping strategies refer to intentional cognitive or behavioral attempts by the individual to manage a stressor (9).

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Lazarus (10) has emphasized coping as a key concept for research on adaptation and health. Because coping is a behavioral reaction to aversive situations that induce several physiological stress reactions (11), individual ways of dealing with stress have an enormous impact on human health (12). Lazarus (10) suggests to differentiate between two approaches to coping, one that treats coping as a personality characteristic (style) and another that refers to the efforts to manage stress (process). Whereas the process approach primarily addresses the behavioral and physiological mechanisms involved in the adaptational response to stress, coping style rather seems to describe a personal or individual consistency in this response. The classification of coping into an “approach-avoidance” category can also be found in animal personality research. This category classifies behavior and cognitive abilities that are used by the individual to face the problem (approach) or to divert the individual’s attention away (avoidance) from the problem (13).

Aim of the present review was to give a comprehensive overview how these concepts and terms, which have their origin in human psychology, are currently used in animal and especially farm animal personality research and to critically reveal how they are defined and what they measure. To obtain an overview of published studies in selected mammalian farm animal species we carried out a systematic literature search using the Web of Science (state December 2017) with keywords including the respective animal species (cattle, goat, sheep, horse, pig) and different synonyms applied in personality research (temperament, personality, coping). Then we exemplarily assessed the found studies within the context of terms and methodological approaches in general personality research. Finally, we

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discuss some findings on the possible impact of personality on the welfare of farm animals to especially highlight a future direction of personality research.

2.3 General Concepts and Terms in Animal Personality

2.3.1 Personality

In animal personality research, many terms are used to explain individual differences in behaviour, besides personality itself [e.g., behavioural syndromes (14) and coping style (15, 16)]. Definitions of the different terms used in animal personality research are shown in Table 1: Personality is defined as a correlated set of individual behavioural and physiological traits that are consistent over time and contexts (15, 17).

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Table 1: Different personality-related terms in alphabetical order used to describe individual differences in animal behaviour and their definitions.

Personality-related term	Definition	References
Behavioural Response	behavioural response to handling	(132)
Behavioural Syndrome	a suite of correlated behaviours reflecting an individual's consistency in behaviour across multiple situations; a population or species can exhibit a behavioural syndrome; within the syndrome, individuals have a behavioural type	(14)
Coping Personality Type	coping strategies that may reflect different personality types	(42)
Coping Style	based on the animal's reaction to its environment with respect to reducing effects of aversive stimuli: - fight or flight response - approach or avoidance - boldness or shyness	(11, 15, 16, 62)
Emotional Reactivity	social reactivity (i.e., active vs. passive strategy); exploratory activity; reactivity to humans	(133)
Identity Profiles	describe individuality, personality and their relationship with certain morphological traits of the animals; four groups of similar animals: aggressive, affiliative, passive, avoiders	(134)
Individual Differences in Behaviour	individual variation; intra-animal repeatability; the relationships between different test situations and the frequency distributions of various measures of behaviour; consistency of individual variability	(76, 135-137)
Temperament	inherited, early appearing tendencies that continue throughout life and serve as the foundation for personality; observable in infants and animals and tied to basic psychological processes	(3, 4-6)
Personality	a correlated set of individual behavioural and physiological traits that are consistent over time and contexts	(15, 26, 33, 32)

Personality may explain individual differences in dominance rank, coping, cognitive abilities and physiology. At least one of the five factors which are used

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to describe human personality (i.e., extraversion, neuroticism, agreeableness, openness and conscientiousness) has been investigated in many different species. The most commonly measured personality factors in animal personality research are exploration, activity, aggressiveness, sociability, and boldness (17-19). Exploration seems to resemble the human factor openness, aggressiveness seems to resemble agreeableness, and sociability seems to resemble extraversion, while boldness and activity seem to be combined in the human factor neuroticism [reviewed by Gosling and John (20)]. According to Gosling and John (20), the human factor conscientiousness can only be found in chimpanzees and gorillas. Figure 1 shows the five personality factors in humans and how they describe the personality type of two imaginary individuals [adapted from (21)] and the equivalent personality factors found in animals. While individual A scores highly in exploration (openness), sociability (extraversion) and aggressiveness (agreeableness), individual B scores highly on boldness and activity (neuroticism) and, if this individual is a human, in conscientiousness (Fig. 1). A discussed factor in animals is the dominance factor that seems to be defined by boldness, physical aggression and low levels of fearfulness (20). In humans, these traits seem to be related to extraversion because humans participate in multiple dominance hierarchies that are less clearly defined and involve widely divergent skills (20). This means that species not only differ in the type of relevant factors, but also in the number of such factors (22): While chimpanzees share a common six-factor structure, including dominance, extraversion, agreeableness, conscientiousness, neuroticism, and openness (23), mountain gorillas seem to have only four personality factors: dominance, openness, sociability and proto-agreeableness

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(24). As in human personality research, sex differences can be found in the expression of animal personality traits. For example, hyena (*Crocuta crocuta*) males are more fearful and nervous than females. This effect seems to be influenced by the social organization. In hyenas, the dominance rank is transmitted through a matrilineal system, and females are larger than males. Sex differences in personality seem to be related to the ecological niches occupied by the two sexes [reviewed by Gosling and John (20)].

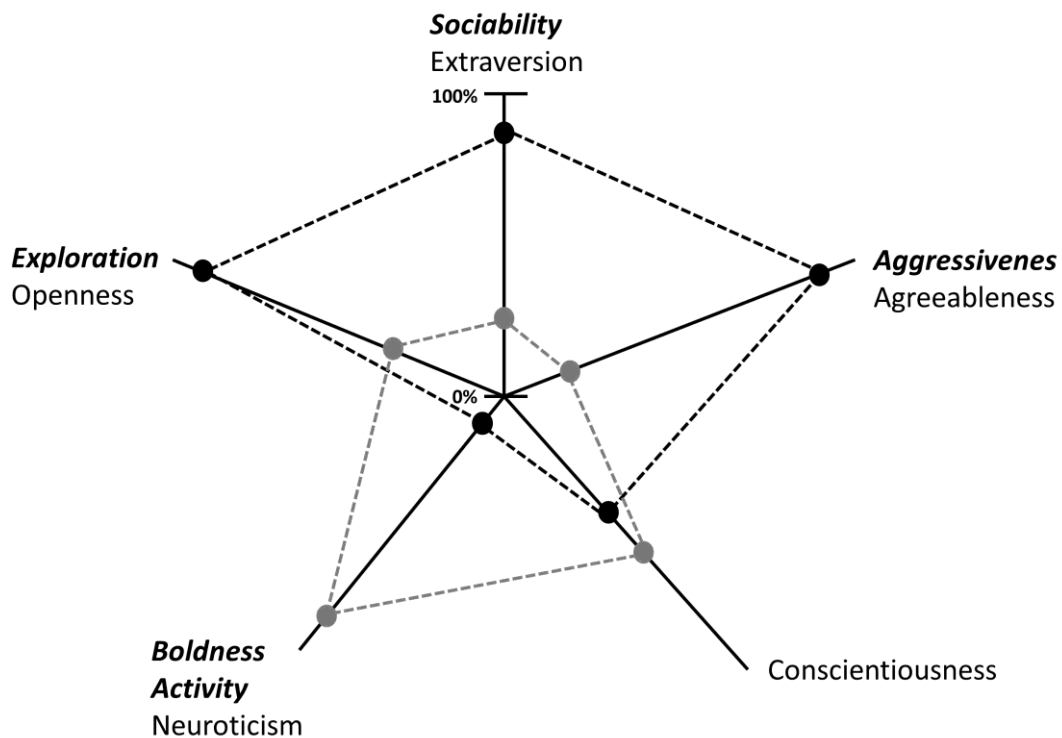


Figure 1: The five personality factors in humans and how they describe the personality type of two imaginary individuals [adapted from (21)]. The equivalent personality factors described in animals are written in bold and italics. Scores are given from zero to 100 in percentages. For example, Individual A (black dashed lines and points) scored high in

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openness, extraversion and agreeableness, while Individual B (grey dashed lines and points) scored high on neuroticism and conscientiousness.

David and Dall (25) state in their review that most of the confusion about terminology in animal personality studies is due to two main concepts, which can also be used complementarily: the intra-individual variability and the life-history approach. The first concept tries to explain the occurrence of between-individual differences in the consistency of any behaviour (22), which means that studies employing this concept focus on the consistency and flexibility of behavioural expression. The second concept focuses only on boldness-like behaviours, which means that studies using this concept concentrate on the individual average behaviour and the between-individual relationships between life history and behaviour (25). One approach using both concepts is the pace-of-life syndrome (POLS) [reviewed by Réale et al. (26)]. This concept includes the idea that between-individual differences in behaviour are associated with individual variations in life-history traits [e.g., habitat use, predation avoidance, dispersal and/or social behaviour (14, 27-29)] because both may contribute to evolutionary trade-offs and may have co-evolved. And physiological traits that differ between individuals, such as growth, metabolic rate, reproductive value and hormone levels have also become important for animal personality research (29, 30-32) because they can be influenced by genetic predispositions and early environmental effects (33, 34).

Another important aspect of personality research in animals is that despite the consistency of some factors, others seem to be plastic and help the organism adapt to changing environments. This aspect is termed behavioural and/or physiological

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plasticity (34). Responsiveness to environmental conditions may span from short-term (phenotypic flexibility) to long-term effects (35), and the early environment an individual experiences contributes to between-individual differences in life histories and personality factors (30, 36). For example, in coral reef fish, individual scores on activity, boldness and aggressiveness increased from 2.5- to six-fold when induced by an increase in water temperature, indicating individual coping abilities and/or behavioural plasticity (37). Moreover, photoperiodic changes influenced fearlessness, the stress response, the timing of maturation and resting metabolic rate (RMR) in wild caviars (*Cavia aperea*) and showed differences between sexes (38, 39). Behavioural and physiological plasticity is an important factor for the survival of an organism. Even if most of the personality factors proved to be consistent over time and contexts, factors like resting metabolic rate and fearlessness were not consistent in caviars, whereas exploration and boldness were consistent regardless of the photoperiodic treatment (38). One might argue that factors such as resting metabolic rate and fearlessness should not count as personality factors. However, an example in the European mink (*Mustela lutreola*) showed that traits that describe factors like boldness and exploration can change between seasons but that these changes remain consistent over time (40), which matches the definition of a personality factor. These examples indicate that the plasticity and consistency of personality factors are not exact opposites and indicate interesting asymmetries in the adjustments of personality factors that seem somehow species-related.

In farm animal studies, the term personality is scarcely used, even if the methods employed (e.g., repeated measurements) and measured variables (e.g., curiosity)

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can be described as personality factors. In those studies, the term temperament is used as an equivalent to the term personality. This could be due to the fact that farm animals are used to get meat, milk and other products and that it is easier to consume farm animal products when scientists do not attribute human-like characteristics to explain individual differences in farm animal behaviour. Table 2 lists selected studies assessing personality factors using different experimental designs in mammalian farm animals (Table 2a: cattle; Table 2b: goats; Table 2c: sheep; Table 2d: horses; Table 2e: pigs) and the behavioural tests used. Some of these studies only measured and/or analysed a small aspect of personality, measured just one or two personality traits or are examples of the very beginning of farm animal personality research, while other studies, shown in this table, show consistency and/or cross-context correlations between traits. One can see that the use of a certain personality-related term is dependent on the species studied. In cattle, the term temperament is mostly used to explain individual differences in behaviour, while in pigs, the term coping style is mainly used (Table 2a + 2e). In horses and more recent farm animal personality studies, one can find the term personality as well (e.g., (41, 42)) (Table 2d).

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Table 2: Selected studies assessing personality factors using different experimental designs in mammalian farm animals **(A)**: cattle; **(B)**: goats; **(C)**: sheep; **(D)**: horses; **(E)**: pigs. The column “Personality-related term used” refers to the term the studies used to explain their results. The column “Test” refers to the behavioural tests used, while the column “Measures” refers to the measured variables.

Table 2 (A): Cattle (*Bos taurus*)

Personality-related term used	Test	Measures	Study
Behavioural Response	Docility Test	aggressiveness against the handler, running time and number of escapes per minute of test period in presence or absence of the handler	(132)
Individual Differences in Behaviour	Human Approach Test; Lateralisation Test; Novel Human Test; Novel Object Test; Open Field Test; Surprise Test; Temperament Score	behavioural response when a human approaches the cow; the side the animal uses to avoid an obstacle; behavioural response towards an unknown human; behavioural response towards an unknown object; activity and exploration behaviour in an unknown arena; latency to start eating again after encountering a blast of air; chute score, velocity exit, pen score, flight speed	(135, 136)
Temperament	Combined Social Isolation and Open Field Test; Docility Test; Handling Test; Human Approach Test; Novel Human Test; Novel Object Test; Open Field Test; Social Isolation Test; Temperament Score	activity and exploration behaviour in an unknown arena and activity during social isolation; aggressiveness against the handler, running time and number of escapes per minute of test period in presence or absence of the handler; touching the cow from head to tail; behavioural response when a human approaches the cow; behavioural response towards an unknown human; behavioural response towards an unknown object; activity and exploration behaviour in an unknown arena; activity and exploration behaviour during social isolation; chute score, velocity exit, pen score, flight speed	(44, 57, 59, 61, 79, 92, 122, 125, 126, 138-140)

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Table 2 (B): Goats (*Capra hircus*)

Personality-related term used	Test	Measures	Study
Identity Profiles	Behavioural Observation	direct observation during milking and/or over a certain period of time	(134)
Temperament	Behavioural Observation; Novel Human Test	direct observation during milking and/or over a certain period of time; behavioural response towards an unknown human	(141,142)
Personality	Novel Object Test; Social Isolation Test	behavioural response towards an unknown object; call, activity and exploration behaviour during social isolation	(143)

Table 2 (C): Sheep (*Ovis aries*)

Personality-related term used	Test	Measures	Study
Emotional Reactivity	Human Approach Test; Open Field Test; Social Isolation Test	behavioural response when a human approaches the sheep; activity and exploration behaviour in an unknown arena; activity and exploration behaviour during social isolation	(133)
Temperament	Novel Object Test; Open Field Test; Social Isolation Test	behavioural response towards an unknown object; activity and exploration behaviour in an unknown arena; activity and exploration behaviour during social isolation	(48, 128, 144, 145)
Personality	Open Field Test	activity and exploration behaviour in an unknown arena	(46)

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Table 2 (D): Horses (*Equus caballus*)

Personality-related term used	Test	Measures	Study
Coping Type	Behaviour After Reintroduction in a Group; Novel Object Test; Open Field Test; Owner Ratings; Water Spray Test	expression of submissive or dominant behaviour towards conspecifics; behavioural response towards an unknown object; activity and exploration behaviour in an unknown arena; questionnaire about the expression of certain behaviours; scoring of the horse's reaction to a spray of water	(146)
Temperament	Behaviour After Reintroduction in a Group; Behavioural Observation; Handling Test; Horse Personality Questionnaire (HPQ); Novel Human Test; Novel Object Test; Open Field Test; Owner Ratings; Social Isolation Test; Surprise Test; Water Spray Test	expression of submissive or dominant behaviour towards conspecifics; expression of behaviours in the home pen; latency to allow the human to touch the leg about three times; questionnaire about 43 behaviourally defined adjectives; behavioural response towards an unknown human; behavioural response towards an unknown object; activity and exploration behaviour in an unknown arena; questionnaire about the expression of certain behaviours; activity and exploration behaviour during social isolation; latency to start eating again after opening an umbrella; scoring of the horse's reaction to a spray of water	(93, 124, 146-149)
Personality	Handling Test, Horse Personality Questionnaire (HPQ); Novel Human Test; Novel Object Test; Owner Ratings	latency to allow the human to touch the leg about three times of the horse; questionnaire about 43 behaviourally defined adjectives; behavioural response towards an unknown human; behavioural response towards an unknown object; questionnaire about the expression of certain behaviours	(41, 45, 88, 150-158)

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Table 2 (E): Pigs (*Sus scrofa*)

Personality-related term used	Test	Measures	Study
Coping Personality Type	Backtest	number of escape attempts, latency to first escape attempt	(42)
Coping Type	Backtest; Behavioural Observation; Combined Open Field and Novel Object Test; Human Approach Test; Novel Object Test; Resident-Intruder Test; Social Support Test	number of escape attempts, latency to first escape attempt; expression of behaviours in the home pen; activity and exploration behaviour in an unknown arena with an unknown object; behavioural response when a human approaches the pig; behavioural response towards an unknown object; latency to attack a conspecific, number and duration of fights, lesion score; socio-positive behaviour towards a conspecific	(78, 81, 82, 98, 159-163)
Individual differences in behaviour	Backtest; Combined Open Field and Novel Object Test; Human Approach Test; Novel Object Test; Open Door Test	number of escape attempts, latency to first escape attempt; activity and exploration behaviour in an unknown arena with an unknown object; behavioural response when a human approaches the pig; behavioural response towards an unknown object; latency to leave the home pen	(77, 137)
Temperament	Human Approach Test; Novel Object Test; Open Door Test	behavioural response when a human approaches the pig; behavioural response towards an unknown object; latency to leave the home pen	(91)
Personality	Backtest; Open Field Test	number of escape attempts, latency to first escape attempt; activity and exploration behaviour in an unknown arena	(164)

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In most of the farm animal studies investigating temperament, different personality factors can be found (e.g., curiosity shown in the general response to unfamiliar humans or the exit from a restraint device (43, 44)). These can be considered as personality factors when they are measured in at least two different time periods of an animals' life. Like in other taxa, some farm animal studies can show that the personality factor boldness is related to other investigated behavioural traits. Boldness was found to be related to reactivity to humans in horses (45), cattle (44) and sheep (46): Individuals that interacted more with a novel stimulus were more interested in novel humans as well. In sheep, bold individuals proved to be more explorative and the distance between individuals while grazing was greater than in shy individuals (46). Moreover, the personality factor activity proved to be related to boldness and reactivity to humans in sheep: More active sheep seem to be bolder and more reactive to humans than shy sheep (47, 48). Calves can be categorized in four different personality types based on a combination of behavioural and heart rate variability (HRV) data (44).

2.3.2 Temperament

In animal personality research, the term temperament is closely related to personality. Temperament often matches the definition found in human personality research and is defined as inherited, early-appearing tendencies that continue throughout life and that serve as the foundation for personality (6) (Table 1). Since the distinction of both terms by definition is often vague, some animal researchers simply treat them as synonyms (17), while others argue that the term temperament is used simply to avoid using the term personality with regard to

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animals, which might be associated with anthropomorphism by some ethologists (49). While temperament is assumed to be based on early, stable predispositions in the emotional and behavioural responses of an individual like boldness, aggressiveness and pleasantness, personality is often reserved for patterns of reflection and reaction to environmental circumstances acquired during a lifetime in organisms with sophisticated cognitive capacities. The behavioural factors that are the focus of research on animal temperament in many different species are reactivity, fearfulness, sociability, responsiveness, and aggression. Temperament in non-human animals is often described on a one-dimensional scale using expressions such as “proactive vs. reactive”, “aggressive vs. nonaggressive”, “bold vs. shy”, etc. (50, 51). The actual theoretical frameworks on temperament in non-human animals argue for scoring reactions in more than one dimension to reflect the entire nature of temperament (17, 52). A multivariate approach has been used by Meager et al. (53) to investigate whether distinct temperaments are present in Atlantic cod (*Gadus morhua*). Their results refer to the multidimensionality of animal temperament and provide a clear indication that two distinct behavioural phenotypes are evident in fish. A study in non-human primates has shown that temperament, based on a factor analysis including behaviour in different dimensions in yearling rhesus monkeys (*Macaca mulatta*), seems to be an important factor in an individual’s ability to select friends and is related to later variations in the animals’ social networks (54). The subjects preferred peers that had similar temperament scores to their own even after accounting for sex, rank and kinship. This example shows that the definition of temperament from the human domain can be used for nonhuman animals as well.

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Foyer et al. (55) investigated the impact of the level of maternal care in dogs on the offspring's behaviour at approximately 18 months of age. The authors conducted a set of temperament tests to score the behaviour of the dogs in different factors, such as sociability and fearfulness. The study showed that the level of maternal care differed consistently and that it has a significant impact on the adult temperament of the offspring, mainly in terms of sociability and dominance. The responses of cats across different behavioural factors were assessed to calculate a feline temperament profile (56). Later, the reactions of the cats in a 3-min stress test were measured. The authors did not find correlations between temperament scores and measures of behavioural and adrenocortical responses in the stress test. However, many studies concerning individual differences in animal behaviour do not make the distinction between temperament and personality consistently, which makes it more difficult to understand the results with regard to temperament and/or personality.

In many farm animal studies, the term temperament is used as an equivalent to the term personality, which also can be seen in Table 2. General responses to unfamiliar humans or situations are quite important for handling, management and selective breeding (48). And traits such as fearfulness, happiness, alertness and docility (57-59) can be considered to describe temperament when measured during the juvenile period of an animal and/or once in an animal's life. Animals that are more likely to cope with handling procedures are considered to have a "good" temperament (57) and dairy temperament (generally defined as the animal's response to milking) has been included in the breeding objectives of some countries [reviewed by Gibbons (60)]. Furthermore, high reactive bulls

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(reactivity was measured with a temperament score) had a greater rectal temperature and a higher cortisol and epinephrine concentration prior to and after transportation than low reactive bulls (61). As these examples measure personality, because measured in adult animals, these examples show how complex it is to describe individual personality in animals and that temperament reflects a sub-aspect of the whole concept of animal personality.

2.3.3 Coping Style

The concept of coping styles has also been used in the past few decades to better understand animal personality and is based on the animal's reaction to its environment with respect to reducing the effect of aversive stimuli (16, 62) (Table 1). Like in humans, animals show individual differences in coping with different environmental changes, confirming that personality and coping style are closely linked (11, 15, 16, 62, 63; but see Zidar et al. (64) for an example of a missing relationship in the red jungle fowl). According to the boldness-shyness continuum, animals can be categorized into three sub-groups based on their risk-taking behaviour: bold, intermediate and shy (63) or proactive, intermediate and reactive based on the animal's reaction to its environment with regard to altering the effect of aversive stimuli (fight/flight response) (11, 15, 16, 62). Proactive individuals are considered to be more aggressive towards conspecifics, show more dominant behaviour, and are considered more explorative, bold and active. Moreover, they respond with a strong sympathetic activation and an increase in noradrenergic stimulation when confronted with a challenging situation, while reactive animals are considered the opposite behavioural phenotype, with

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behaviour that is more submissive, less explorative and less active and responding with a strong hypothalamic-pituitary-adrenocortical reactivity towards challenging situations (19, 65-68).

Figure 2 shows a possible multidimensional approach to describing the five basic factors in animal personality research applied to the concept of animal coping style using an example of two imaginary animals. In addition, there is a potential sixth factor, dominance. There is an ongoing discussion as to whether dominance is a factor by itself or just a social outcome, and it also represents other species-related factors that are often missed in measurements (49, 22). Considering the description of proactive and reactive individuals above, the animal that scores low on the aggressiveness, activity and sociability axes would be described as being more peaceful, inactive and highly social and would represent a reactive coping style. The animal that scores high on the boldness, exploration and aggressiveness axes would be described as being more aggressive, explorative and bold and would be considered as a proactive individual. Intermediate individuals would express behaviour described by a mixture of the scores on the factors resulting in individual differences on a continuum.

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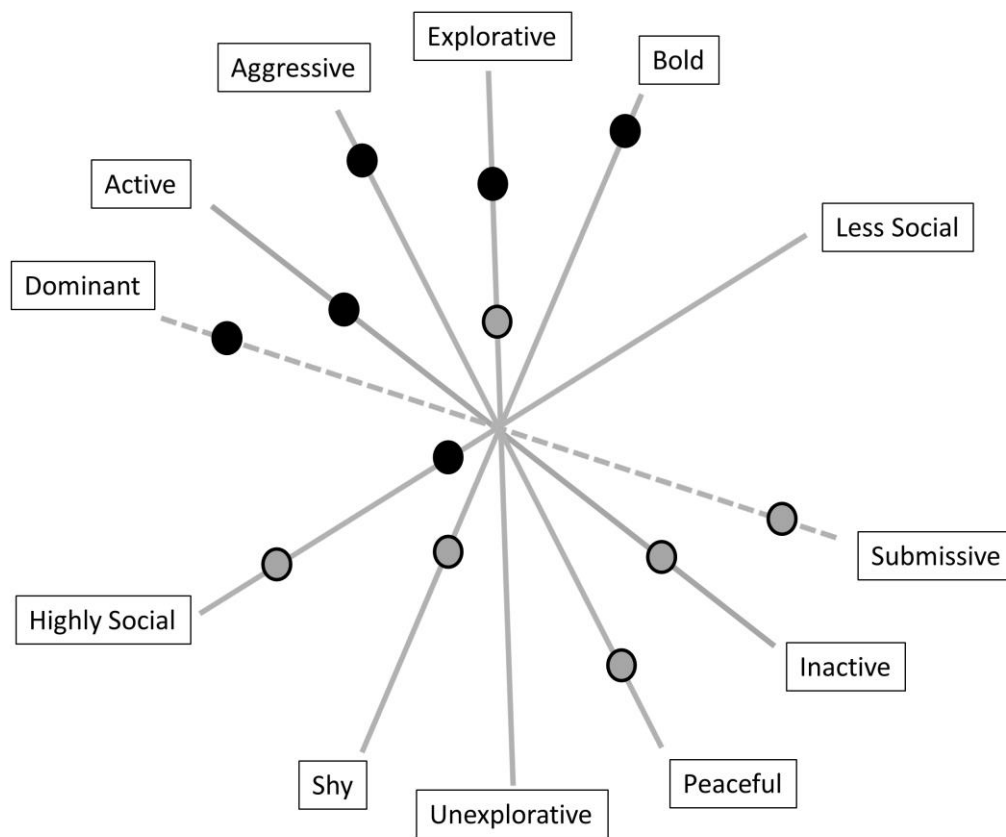


Figure 2: The five basic factors in animal personality research (bold lines) that can also be used to describe coping style. The dominance factor is presented in dashed lines because there are insufficient data to consider it as a fully accepted sixth factor in animal personality. The dots represent two imaginary animals with different coping styles. The animal behaving as described by the black-grey dots would represent a reactive copper, while the animal behaving as described by the black dots would be considered as a proactive individual. Intermediate individuals would express behaviour described by a mixture of scores on the factors resulting in individual differences along a continuum.

Some factors show only low inter-correlations and are relatively independent from one another, which means that they must not co-occur [reviewed by Uher (69)].

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Each factor summarizes the shared variation of diverse inter-correlating traits. The rank-orders of the same individuals on the same factor can vary considerably across different situations. An individual can have different scores on each factor [reviewed by Uher (69)]. The individual-oriented perspective (like in humans and shown in Fig. 1) can also be applied to the analyses of multiple individuals such that individuals sharing a similar profile can be grouped statistically into configurational types. Such groups represent distinct and discontinuous categories of prototypes (e.g. proactive, intermediate and reactive) [reviewed by Uher (69)]. According to Koolhaas (70), proactive individuals perform better under highly predictable conditions, while reactive individuals perform better under variable and unpredictable environmental conditions. Proactive individuals also grow faster and have a higher RMR, which they can afford due to their higher rates of food acquisition. When food is abundant, proactive individuals may perform better than reactive individuals [reviewed by Careau et al. (71)]. Many studies have shown that different coping styles correlate with dominance rank, cognitive abilities and physiological measures [e.g., immunology (70)]. In fish, bold female guppies (*Poecilia reticulata*) learned a task more quickly than shy females (72), and in zebra finches (*Taeniopygia guttata*), more active birds were faster at solving a task, while less active individuals needed longer or did not solve the task at all, which indicates that higher activity may lead to routine-forming behaviour instead of being attentive to external cues (73). Proactive Senegalese sole (*Solea senegalensis*) juveniles exhibited a shorter feeding latency, a higher duration of escape attempts and a lower cortisol level than reactive individuals (74). An example in mammals revealed that different coping styles in wild alpine marmots

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(*Marmota marmota*) are accompanied by different baseline and stress-induced plasma oxidative statuses (32). In male rainbowfish (*Melanotaenia duboulayi*), personality factors like aggression, activity and boldness covaried with the male's position in the hierarchy, directly influencing their reproductive success (75). Moreover, an example of spiders living in colonies showed that individuals with different coping styles do different tasks. While aggressive spiders perform prey capture and colony defence, less aggressive spiders perform brood care (76).

Farm animal research on coping styles became more and more important because the coping style covers the aspect of an animal's skill in coping with environmental challenges. Farm animals like pigs (*Sus scrofa*), cattle (*Bos taurus*) and horses (*Equus caballus*) have to cope with numerous challenging situations (e.g., regrouping, housing, management) and technical material during their lives. Therefore, investigating their coping strategies and cognitive abilities appears to be a very important research topic, because like temperament, it reflects sub-aspects of the whole concept of animal personality. Aggression, boldness and exploration seem to be related to results in backtests that determine the specific coping-type in pigs assessed by the early escape behaviour of piglets: Proactive pigs proved to be more aggressive, explorative and bolder than reactive pigs (77, 78). Recently, a number of studies were conducted to investigate the impact of different coping styles on psychophysiological measures and molecular correlates later in life. Reactive cows can be distinguished by their baseline HRV (79) and pigs characterized as belonging to different coping styles differed in their general autonomic reaction (e.g. HR, HRV) and in their affective appraisal in relation to common husbandry-related situations like feeding or human handling (80),

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indicating personality-dependent emotional assessment of environmental situations. There is also evidence that individual coping styles of pigs are reflected in their immune responses indicating that proactive pigs might favour molecular pathways enabling a more effective strategy for defence and recovery than in reactive pigs (81, 82). Moreover, a recently conducted genome-wide association study revealed that hypothalamic genes known to be involved in pathways regarding the immune system, telomere function signalling, neurotransmitter receptors as well as circadian rhythms were differently expressed in pigs with different coping styles (83).

2.4 Measures and Methods in Farm Animal Personality Research

Personality, temperament and/or coping style and how they are interrelated with a diversity of other external or internal stimuli are investigated using different experimental setups. The main problem is to know exactly which personality factor or variable is being investigated using a certain experimental design (e.g., tests of exploration in an open field, test of boldness in investigating a novel object). Murphy et al. (84) identify in their review the most important aspects of experiments used to investigate farm animal personality. A test should be ecologically valid and the animal should be able to display its natural emotion-related behaviours. Since emotions have recently been discussed to be a personality factor by itself (see below [reviewed by Koolhaas et al. (85)]), tests should be sensitive enough to capture slight differences in levels of emotional arousal (bodily activation or excitation, the first dimension of emotion) or valence

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(negative or positive, the second dimension of emotion) (86, 87), which is important for longitudinal studies. Furthermore, the test itself and the variables measured should be standardized to allow for comparisons between studies (84). In his review, Gosling (3) describes the variables that can be used to analyse personality factors: i) reactivity, emotionality, fearfulness: e.g., measurement of the defecation rate in an open field; ii) exploration/boldness: e.g., interactions with a novel object; iii) sociability: e.g., frequency of social encounters; iv) aggression: e.g., latency to attack another individual; v) activity: e.g., amount of enclosures (e.g., open field or arena test) covered; vi) dominance/assertiveness: e.g., the individual's rank in the dominance hierarchy. Of course, these variables can be used to analyse other personality factors as well, and the mentioned personality factors can be measured by other variables or even a mixture thereof.

The most important aspect is to find the most appropriate test with the most appropriate variables to record the behaviours that are desired to analyse the intended personality factors for each species. Different species have different environmental requirements because they have different habitats and different life-histories. Koski (22) indicated that most studies about personality focus on boldness, aggressiveness, activity, exploration and sociability as the most prominent personality factors. However, she writes that the focus on these personality factors derived from human personality research may ignore the possibility of other factors that are more important for the investigated species and that such a focus limits our understanding of the full repertoire of personality factors [also reviewed by Gosling and John (20)]. Therefore, it is possible that species not only differ in the type of relevant factors, but also in the number of

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such factors (22): A study done on 1223 horses of eight different breeds with a Horse Personality Questionnaire also identified approximately six personality factors (88). Carter et al. (89) found boldness to be one of the most commonly measured personality factors in animal personality research, and it has been interpreted as the propensity to take risks, especially in novel situations, and as an individual's response to a risky situation faced alone. Boldness is often tested by quantifying behavioural responses to novel objects, responses to a novel environment, and/or responses to predation risk. However, these three types of tests are not necessarily comparable and demonstrate a lack of standardization for quantifying this behaviour. For example, measuring boldness in cavies is slightly different than measuring boldness in pigs and cattle. For the three species, one can use the novel object test. While in cavies, the novel object test is conducted in the home enclosure (18, 38, 39), with pigs and cattle, the test is normally conducted in an arena outside the home pen after a habituation period or after an open field test [reviewed by Forkman et al. (90)]. Tests like the novel human test or the open-door test are conducted with farm animal species and measure the reactivity of an individual towards unknown persons or places (91-93). This type of test is only feasible with domesticated species that are used to human manipulation such as farm animals. In most cases, the measured trait is suggested to mirror fearfulness when describing an animal having a higher latency in approaching an unknown person [reviewed by Murphy et al. (84)]. In rodents, tests like the elevated plus maze [e.g., in mice and rats (94, 95)] or leaving a plastic shelter in an open field [e.g., in cavies (38)] are used to measure fearfulness or its opposite, fearlessness. Exploration is measured in most mammal studies and in most farm animal species

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with an open field test [reviewed by Forkman et al. (90), but see recent critiques by Peralas et al. (96)].

To measure different coping strategies in pigs, Hessing et al. (97) suggested conducting the backtest at an early age to measure defensive reactions like struggling while the piglet is turned over on its back. Zebunke et al. (98) used more than 3,000 individuals and repeated the test four times with each individual. The results showed a moderate consistency of behavioural reactions across repeated testing, which cannot be attributed to a randomly occurring pattern. The authors concluded that the backtest does not provide phenotypic evidence for definitive coping styles that are clearly separable. Instead, they found pronounced individual dispositions along a continuum from proactive to reactive coping behaviours. The results of an equivalent to the backtest conducted with juvenile cavies before weaning (the struggle test) show a similar pattern: the time spent struggling was not significantly repeatable but showed a trend (99). Therefore, the backtest may indicate a certain coping style in pigs, which is discussed to be a personality factor by itself (64, 85). The backtest should not be used as a reference on its own but rather should be used as an addition to other tests measuring behaviour and a certain personality type. Moreover, these examples confirm that one test can simultaneously be influenced by and therefore measure two or more personality factors (17).

Besides the fear of anthropomorphism in using the term personality, to know what is measured is one of the biggest lacking points in the field of farm animal personality research (see Tab. 2). Inspired by the definitions in Table 1, Figure 3 shows how researchers could proceed to know which personality related term they

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should use for their interpretation. Temperament and coping style overlap with personality, because they are sub-aspects of the whole personality concept. With all the behavioural tests used in farm animal personality research (e.g., open field test, novel object test, open door test, backtest etc.) applied ethologist can measure different aspects of personality: It depends of the approach they use. For instance, i) using a behavioural test to measure a response to an aversive or stressful stimulus or situation (e.g., approach or avoidance) means that primarily a specific coping style is assessed, ii) conducting various behavioural tests in a combination and/or conducted at least twice during lifetime, measures cross-context correlations and/or consistency and therefor assesses personality, iii) conducting behavioural tests during the juvenile stage and only once during lifetime, would assess temperament.

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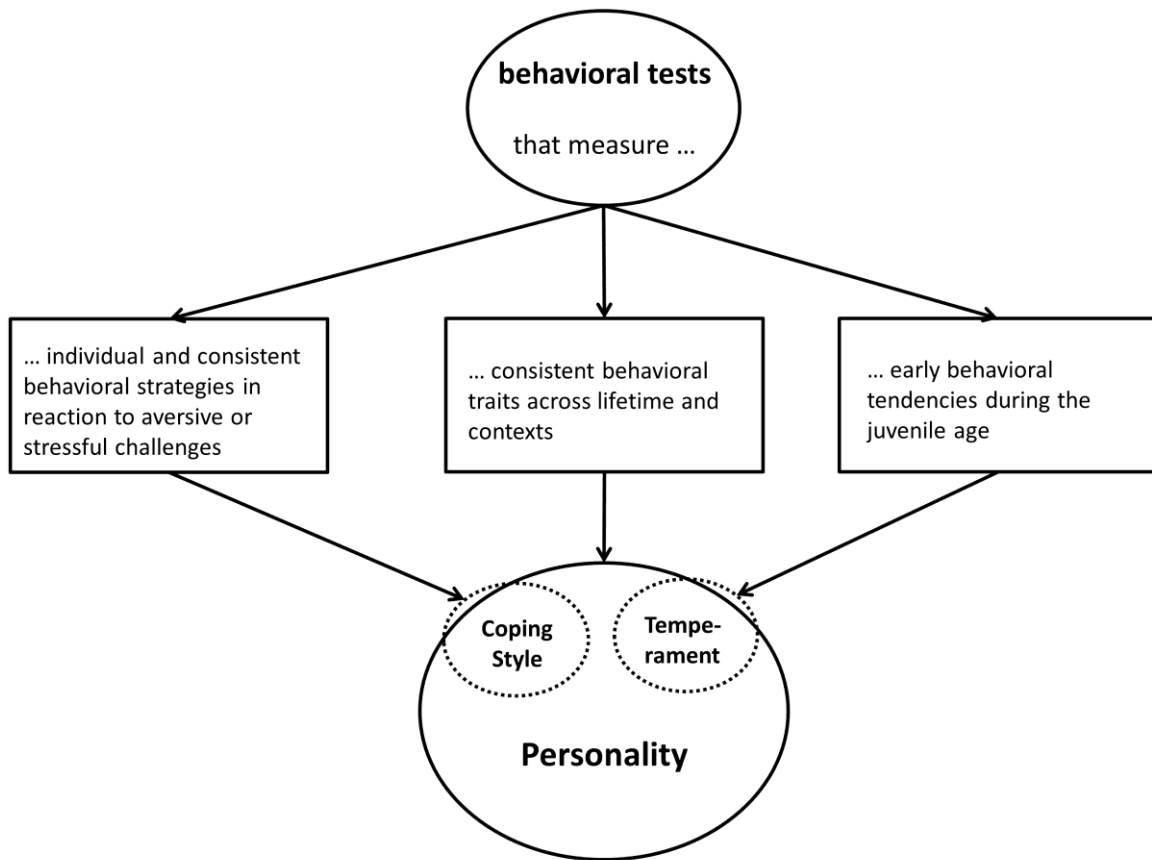


Figure 3: Various behavioural tests that can be used to assess different aspects of personality. It becomes evident that coping style and temperament are sub-aspects of the concept of personality.

2.5 Personality and Welfare in Farm Animals

In human psychology, studies show that subjective well-being is associated with health (100) and is linked to personality [reviewed by Weiss et al. (101)]. Well-being correlates with the five-factor model of personality, especially with neuroticism, extraversion and conscientiousness (102). In zoo animals, studies

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indicate that zoo keepers are able to reliably rate animal personality traits and that those ratings are implemented into zoo management practices to improve the welfare of captive animals (103). Personality research in farm animals has become important as well because welfare not only comprises the actual health status of an animal but also is affected by individual differences in behaviour and physiology (104). Dawkins (105) already stated that individual behaviour has a big advantage in welfare studies because it might become an “early warning system” of trouble yet to come. Changes in behaviour (e.g., aggressiveness towards the caretaker) can be a hint of pain or other problems (106). Therefore, investigating and understanding individual differences in behaviour, respective to personality, in farm animals is a possible means of measuring states of welfare and can also help to increase welfare. Individuals that are less well adapted to their environment may have reduced welfare, which in turn can lead to reduced productivity (107, 108). Figure 4 represents the influence of personality on individual welfare. Personality directly influences behaviour and physiology and therefore influences individual welfare, while as in a feedback-loop, welfare can directly influence behaviour and physiology. Behaviours can influence physiology and *vice versa* in a sort of positive feedback system as well. Especially in farm animals, domestication has an impact on behaviour and physiology and directly influences breeding.

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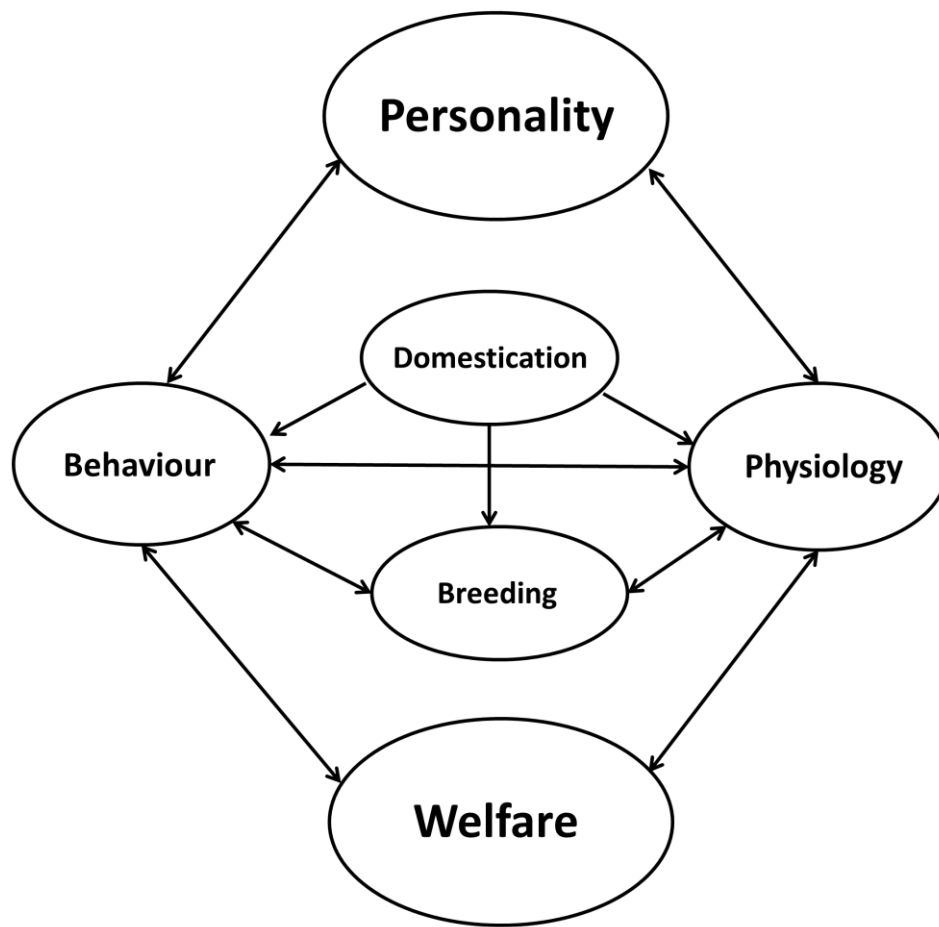


Figure 4: Relationship between personality and welfare. Personality directly influences behaviour and physiology and therefore influences individual welfare, while as in a feedback-loop, welfare can directly influence behaviour and physiology. Behaviour can influence physiology and *vice versa* in a sort of positive feedback system. Especially in farm animals, domestication has an impact on behaviour and physiology and directly influences breeding.

During domestication of most farm animal species, behaviour changed to lower levels of aggression and activity (109). Artificial selection for the improvement of production traits may have resulted in the selection of animals that would count as reactive copers (109). Genetic studies of captive animals often rely on the

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selection of specific production traits (110-112), because specific production traits are emphasized in the individual pedigree of an animal used for breeding [(113, 114); reviewed by Laine and van Oers (115)]. Recently, personality traits have been considered to a greater extent in the calculation of breeding indices because some of these traits show moderate to high heritability (112, 116-118). Aggression is highly heritable in pigs [ranging from $h^2=0.32$ to $h^2=0.48$ (119-121)]. In pigs as well as in cattle, aggressive behaviour towards stockpersons and group-members is related to increased maternal behaviour, which can be problematic [reviewed by Haskell et al. (117), (120)]. In beef and dairy cattle, handling shows moderate to high heritability scores: e.g., chute score ($h^2=0.24$), flight speed ($h^2=0.36$), and docility ($h^2=0.26$) [reviewed by Haskell et al. (117); (122, 123)]. Especially in dairy cattle, milking temperament shows a moderate heritability (e.g., on average $h^2=0.19$), but is also related to production traits such as milk yield [reviewed by Haskell et al. (117), (122)]. In France the docility test has been used to select for improved temperament in Limousin cattle since 1992, and dairy temperament (generally defined as the animal's response to milking) and milking speed have been included in the breeding objectives of some countries [e.g., United Kingdom and Norway (reviewed by Gibbons (60))]. Horses, especially stallions considered for breeding purposes, are judged for performance (e.g., the gaits under the rider, jumping ability, rideability, fitness, health, stamina) and personality (e.g., behaviour during handling (labelled as character), attention and reactivity (labelled as temperament) and braveness, willingness and ability to learn (labelled as willingness to work) (124)).

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Another approach to explain the relationship between personality and welfare has been reviewed by Koolhaas and van Reenen (85), and it describes a three-dimensional model with coping style, emotionality and sociability as independent factors. These factors are defined as being stable over time and across contexts within the individual. Emotionality seems to be one important aspect to increasing welfare because it makes the distinction between fearful animals that are highly emotionally aroused by a challenging situation and non-fearful animals that do not perceive the same situation as stressful or alarming (85). A highly emotionally aroused animal would therefore exhibit activation of neuroendocrine systems while a non-fearful animal do not show any enhanced biological responses (85). Some studies have shown evidence that emotionality, and therefore personality, seem to have an impact on production traits, such as meat quality and milk production. Studies on steers show that individual differences in stress responses (e.g., increase of cortisol in a stressful situation) or in blood lactate levels have an impact on meat tenderness (125, 126). In dairy cows, personality has an impact on behavioural and physiological responses to milking and on the stress associated with being milked in a novel environment (44, 127). A study on horses shows that personality has an influence on pain expression. Horses that were highly affected by vertebral problems showed more aggressive behaviour towards humans than horses with no vertebral problems (106). Lameness was more expressed by highly extraverted horses even if the severity level of the injury threshold was lower when compared to more neurotic individuals (41). A study on female sheep (*Ovis aries*) showed that animals typed as “nervous” (measurement of the behavioural reactivity to the psychosocial stress of social isolation and selected for “calm” or

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“nervous” temperament for 17 generations (128)) seem to show a decrease in agitation score, the frequency of vocalizations and the plasma concentrations of cortisol when treated with lavender oil as an alternative treatment to alleviate anxiety compared to the response of “calm” sheep (128). Moreover, these “nervous” sheep produced a lower volume of higher viscosity colostrum than “calm” sheep, and this disparity could be corrected by nutritional supplementation (with barley), which only had an effect on “nervous” sheep (129). These examples indicate that personality seems to be an important factor in the efficacy of certain substances and nutritional supplementations. Personalized medicine in animals and humans already indicates that personality is a strong indicator for pathology development, medical treatment and substance efficacy (130). Understanding the individual personalities of farm animals is not only important for their welfare but also has an impact on economic factors for farmers [reviewed by Clark et al. (131)]. Therefore, it is important to think about considering to draw an individual personality profile like in Figure 1 [adapted from Costa and McCrae (21)] to picture farm animal personality and in concordance to improve management, handling, breeding, medical treatment and the design of housing systems that allow the animal to perform effective coping behaviour [reviewed by Wechsler (11)].

2.6 Conclusion

This review gives an impression of how diverse farm animal personality research is and which aspects have to be considered in investigating personality in different farm animal species. Terminology in farm animal personality research is

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somewhat confusing and in some cases difficult to compare because the terms used seem somehow to be species-related. While studies in different mammals, birds, and other taxa widely use the term personality to describe between-individual consistency in behavioural variation, in farm animal research the terms temperament and coping style are predominantly used, probably because personality might be associated with anthropomorphism. The broad field of personality research generally needs more consistency in using theoretical concepts, terms and measures and we recommend that the terms should neither be regarded as synonyms nor as independent terms for consistent behavioural responses in animals, but as different aspects of the whole personality concept. Research on personality of farm animals is currently far from covering all possible aspects, but focuses in particular on the phenotyping of personality traits and potential relationships with cognition, emotion and welfare. We conclude that the assessment of personality in farm animals is of growing scientific, practical and economic interest, because it has an obvious verifiable impact on the individual behavioural reaction to different housing systems, management practices and veterinary interventions and is therefore important for the improvement of animal welfare.

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2.8 References

1. John OP, Srivastava S. The Big Five trait taxonomy: history, measurement and theoretical perspectives. In: Handbook of personality: theory and research. New York: Guilford, (1999) pp. 102-138
2. Goldberg LR. The structure of phenotypic personality traits. Am. Psychol. (1993) 48: 26-34
3. Gosling SD. From mice to men: What we can learn about personality from animal research? Psychol. Bull. (2001) 127: 45-86
4. Buss AH. Personality: Temperament, social behavior and the self. Needham Heights, MA: Allyn & Bacon (1995)
5. Goldsmith H, Buss A, Plomin R, Rothbart M, Thomas A, Chess S, Hinde R, McCall R. Roundtable: What is temperament? Four approaches. Child Dev. (1987) 58: 505-529
6. McCrae RR, Costa JR, Paul T, Ostendorf F, Angleitner A, Hřebíčková M, Avia MD, Sanz J, Sánchez-Bernardos ML, Kusdil ME, Woodfield R, Saunders PR, Smith PB. Nature over nurture: Temperament, personality and life span development. J. Pers. Soc. Psychol. (2000) 78: 173-186
7. Rothbart MK, Ahadi SA, Evans DE. Temperament and personality: Origins and outcomes. J. Pers. Soc. Psychol. (2000) 78: 122-135

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

8. Buss AH. Personality: primate heritage and human distinctiveness. In: Aronoff, J., Rabin, A. (Eds.), *Emergence of Personality*. Springer Publishing Co., New York, NY, (1987) pp. 57–101.
9. Affleck G, Tennen H. Construing benefits from adversity: Adaptional significance and dispositional underpinnings. *J. Pers.* (1996) 64: 899-922
10. Lazarus RS. Coping theory and research: past, present, and future. *Psychosom. Med.* (1993) 55: 234–247
11. Wechsler B. Coping and coping strategies: a behavioural view. *Appl. Anim. Behav. Sci.* (1995) 43: 123-134
12. Henry JP, Stephens PM. *Stress, Health, and the Social environment*. Springer, New York (1977)
13. Moos RH. *Coping Response Inventory Youth Form: Professional Manual*. Odessa, FL: Psychological Assessment Resources, Inc. (1993)
14. Sih A, Bell A, Chadwick Johnson J. Behavioural syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* (2004) 19: 372-378
15. Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MAW, Blokhuis HJ. Coping styles in animals: current status in behaviour and stress-physiology. *Neurosci. Biobehav. Rev.* (1999) 23: 925-935

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

16. Korte SM, Koolhaas JM, Wingfield JC, McEwen BS. The Darwinian concept of stress: benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neurosci. Biobehav. Rev.* (2005) 29: 3-38
17. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.* (2007) 82: 291-318
18. Guenther A, Finkemeier MA, Trillmich F. The ontogeny of personality in the wild guinea pig. *Anim. Behav.* (2014) 90: 131-139
19. Verbeek MEM, Boon A, Drent PJ. Exploration, aggressive behavior and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* (1996) 113:945-63
20. Gosling SD, John OP. Personality dimensions in nonhuman animals: A cross-species review. *Curr. Dir. Psychol. Sci.* (1999) 8: 69-75
21. Costa PT, McCrae RR. Revised NEO personality inventory (NEO PI-R) and NEO five-factor inventory (NEO-FFI): Professional manual. Psychological Assessment Resources, Incorporated. (1992)
22. Koski SE. Broader horizons for animal personality research. *Front. Ecol. Evol.* (2014) 2: 1-6
23. Altschul DM, King JE, Inoue-Murayama M, Ross SR, Weiss A. Longevity and personality in captive chimpanzees (*Pan troglodytes*). *Peer J. Preprints* (2016) e1916w2

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

24. Eckardt W, Steklis HD, Steklis NG, Fletcher AW, Stoinski TA, Weiss A. Personality dimensions and their behavioral correlates in wild virunga mountain gorillas (*Gorilla beringei beringei*). *J. Comp. Psychol.* (2015) 129: 26-41
25. David M, Dall SRX. Unravelling the Philosophies Underlying ‘Animal Personality’ Studies: A Brief Re-Appraisal of the Field. *Ethol.* (2016) 122: 1-9
26. Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio PO. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos. Trans. R. Soc. B.* (2010) 365: 4051-4063
27. Dall SRX, Houston AI, McNamara JM. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* (2004) 7: 734-739
28. Dingemanse NJ, Both C, Van Noordwijk AJ, Rutten AL, Drent PJ. Natal dispersal and personalities in great tits (*Parus major*). *Proc. R. Soc. Lond. Biol.* (2003) 270: 741-747
29. Dingemanse NJ, Réale D. Natural selection and animal personality. *Behaviour* (2005) 142: 1159-1184
30. Biro PA, Stamps JA. Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* (2008) 23: 361-368
31. Bouwhuis S, Quinn JL, Sheldon BC, Verhulst S. Personality and basal metabolic rate in a wild bird population. *Oikos* (2013) 123: 56-62

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

32. Constantini D, Ferrari C, Pasquaretta C, Cavallone E, Carere C, Von Hardenberg A, Réale D. Interplay between plasma oxidative status, cortisol and coping styles in wild alpine marmots, *Marmota marmota*. *J. Exp. Biol.* (2012) 215: 374-383
33. Réale D, Dingemanse NJ. *Animal Personality*. eLS (2012)
34. West-Eberhard MJ. Phenotypic accommodation: Adaptive innovation due to developmental plasticity. *J. Exp. Zool.* (2005) 304B: 610-618
35. Piersma T, Drent J. Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol.* (2003) 18: 228-233.
36. Groothuis TGG, Maestripieri D. Parental influences on offspring personality. In: *Animal Personalities* (Carere, C. & Maestripieri, D. eds). Univ. of Chicago Press, Chicago, IL, (2013) pp. 317-352.
37. Biro PA, Beckmann C, Stamps JA. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proc. R. Soc. Lond. Biol.* (2009) 277: 71-77
38. Finkemeier MA, Trillmich F, Guenther A. Match-mismatch experiments using photoperiod expose developmental plasticity of personality traits. *Ethol.* (2016) 122: 80-93
39. Guenther A, Trillmich F. Photoperiod influences the behavioral and physiological phenotype during ontogeny. *Behav. Ecol.* (2013) 24: 402-411

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

40. Haage M, Bergvall UA, Maran T, Kiik K, Angerbjörn A. Situation and context impacts the expression of personality: the influence of breeding season and test context. *Behav. Process.* (2013) 100: 103—109
41. Ijichi C, Collins LM, Elwood RM. Pain expression is linked to personality in horses. *Appl. Anim. Behav. Sci.* (2014) 152: 38-42
42. Melotti L, Oostindjer M, Bolhuis JE, Held S, Mendl M. Coping personality type and environmental enrichment affect aggression at weaning in pigs. *Appl. Anim. Behav. Sci.* (2011) 133: 144-153
43. Randle HD. Facial hair whorl position and temperament in cattle. *Appl. Anim. Behav. Sci.* (1998) 56: 139-147
44. Sutherland MA, Rogers AR, Verkerk GA. The effect of temperament and responsiveness towards humans on the behavior, physiology and milk production of multi-parous dairy cows in a familiar and novel milking environment. *Physiol. Behav.* (2012) 107: 329-337
45. Górecka-Bruzda A, Jastrzębska E, Sosnowska Z, Jaworski Z, Jezierski T, Chruszczewski MH. Reactivity to humans and fearfulness tests: Field validation in Polish Cold Blood Horses. *Appl. Anim. Behav. Sci.* (2011) 133: 207-215
46. Sibbald AM, Erhard HW, McLeod JE, Hooper RJ. Individual personality and the spatial distribution of groups of grazing animals: An example with sheep. *Behav. Process.* (2009) 82: 319-326

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

47. Beausoleil NJ, Blach D, Stafford KJ, Mellor DJ, Noble ADL. Exploring the basis of divergent selection for “temperament” in domestic sheep. *Appl. Anim. Behav. Sci.* (2008) 109: 261-274
48. Beausoleil NJ, Blache D, Stafford KJ, Mellor DJ, Noble ADL. Selection for temperament in sheep: Domain-general and context-specific traits. *Appl. Anim. Behav. Sci.* (2012) 139: 74-85
49. Jones AC, Gosling SD. Temperament and personality in dogs (*Canis familiaris*): A review and evaluation of past research. *Appl. Anim. Behav. Sci.* (2005) 95: 1-53
50. Benus RF, Bohus B, Koolhaas JM, van Oortmerssen GA. Behavioral strategies of aggressive and nonaggressive male-mice in active shock avoidance. *Behav. Processes* (1989) 20: 1-12
51. Boersma GJ, Scheurink AJ, Wielinga PY, Steimer TJ, Benthem L. The passive coping Roman Low Avoidance rat, a non-obese rat model for insulin resistance. *Physiol. Behav.* (2009) 97: 353-358.
52. Posner J, Russell JA, Peterson BS. The circumplex model of affect: an integrative approach to affective neuroscience, cognitive development, and psychopathology. *Dev. Psychopathol.* (2005) 17: 715-734
53. Meager JJ, Fernö A, Skjæraasen JE, Järvi T, Rodewald P. Multidimensionality of behavioural phenotypes in Atlantic cod, *Gadus morhua*. *Physiol. Behav.* (2012) 106: 462-470

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

54. Weinstein TAR, Capitanio JP. Individual differences in infant temperament predict social relationships of yearling rhesus monkeys, *Macaca mulatta*. *Anim. Behav.* (2008) 76: 455-465
55. Foyer P, Wilsson E, Jensen P. Levels of maternal care in dogs affect adult offspring temperament. *Sci. Rep.* (2016) 6:19253
56. Iki T, Ahrens F, Pasche KH, Bartels A, Erhard MH. Relationships between scores of the feline temperament profile and behavioural and adrenocortical responses to a mild stressor in cats. *Appl. Anim. Behav. Sci.* (2011) 132: 71-80
57. Sant’Anna AC, Paranhos da Costa MJR. Validity and feasibility of qualitative behavior assessment for the evaluation of Nellor cattle temperament. *Livest. Sci.* (2013) 157: 254-262
58. Le Neindre P, Trillat G, Sapa J, Ménissier F, Bonnet JN, Chupin JM. Individual differences in docility in limousin cattle. *J. Anim. Sci.* (1995) 73: 2249-2253
59. Webb LE, van Reenen CG, Jensen MB, Schmitt O, Bokkers EAM. Does temperament affect learning in calves? *Appl. Anim. Behav. Sci.* (2015) 165: 33-39
60. Gibbons J. The Effect of Selecting for “Robustness” on Temperament in Dairy Cows. PhD – Thesis, The University of Edinburgh (2009)
61. Burdick NC, Carroll JA, Hulbert LE, Dailey JW, Willard ST, Vann RC, Welsh TH, Randel RD. Relationships between temperament and transportation

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

with rectal temperature and serum concentrations of cortisol and epinephrine in bulls. *Livest. Sci.* (2010) 129: 166-172

62. Cannon WB. Bodily changes in pain, hunger, fear and rage. Appleton, New York (1929)

63. Coleman K, Wilson DS. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.* (1998) 56: 927-936

64. Zidar J, Balogh A, Favati A, Jensen P, Leimar O, Løvlie H. A comparison of animal personality and coping styles in the red junglefowl. *Anim. Behav.* (2017) 130: 209-220

65. Carere C, Drent PJ, Privitera L, Koolhaas JM, Groothuis TGG. Personalities in great tits, *Parus mayor*: stability and consistency. *Anim. Behav.* (2005) 70: 795-805

66. Carere C, Caramaschi D, Fawcett T. Covariation between personalities and individual differences in coping with stress: converging evidence and hypotheses. *Curr. Zool.* (2010) 56: 728-740

67. Coppens CM, De Boer SF, Koolhaas JM. Coping styles and behavioural flexibility: towards underlying mechanisms. *Philos. Trans. R. Soc. B.* (2010) 365: 4021-4028

68. Koolhaas JM, De Boer SF, Coppens CM, Buwalda B. Neuroendocrinology of coping styles: towards understanding the biology of individual variation. *Front. Neuroendocrinol.* (2010) 31: 307-321

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

69. Uher J. Individual behavioural phenotypes: An integrative meta-theoretical framework. Why “Behavioral Syndromes” are not analogs of “personality”. *Dev. Psychobiol.* (2011) 53: 521-548
70. Koolhaas JM. Coping style and immunity in animals: Making sense of individual variation. *Brain Behav. Immun.* (2008) 22: 662-667
71. Careau V, Thomas D, Humphries M, Réale D. Energy metabolism and animal personality. *Oikos* (2008) 117: 641-653
72. Trompf L, Brown C. Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. *Anim. Behav.* (2014) 88: 99-106
73. Brust V, Wuerz Y, Krüger O. Behavioural flexibility and personality in zebra finches. *Ethol.* (2013) 119: 559-569
74. Silva PIM, Martins CIM, Engrola S, Marino G, Øverli Ø, Conceição LEC. Individual differences in cortisol levels and behaviour of Senegalese sole (*Solea senegalensis*) juveniles: Evidence for coping styles. *Appl. Anim. Behav. Sci.* (2010) 124: 75-81
75. Colléter M, Brown C. Personality traits predict hierarchy rank in male rainbowfish social groups. *Anim. Behav.* (2011) 81: 1231-1237
76. Holbrook CT, Wright CM, Pruitt JN. Individual differences in personality and behavioural plasticity facilitate division of labour in social spider colonies. *Anim. Behav.* (2014) 97: 177-183

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

77. v. Erp – v. d. Kooij E, Kuijpers AH, Schrama JW, van Eerdenburg FJCM, Schouten WGP, Tielen MJM. Can we predict behaviour in pigs? Searching for consistency in behaviour over time and across situations. *Appl. Anim. Behav. Sci.* (2002) 75: 293-305
78. Ruis MAW, te Brake JHA, Engel B, Buist WG, Blokhuis HJ, Koolhaas JM. Adaptation to social isolation acute and long-term stress responses of growing gilts with different coping characteristics. *Physiol. Behav.* (2001) 73: 541-551
79. Frondelius L, Järvenranta K, Koponen T, Mononen J. The effects of body posture and temperament on heart rate variability in dairy cows. *Physiol. Behav.* (2015) 139: 437-441
80. Krause A, Puppe B, Langbein J. Coping style modifies general and affective autonomic reactions of domestic pigs in different behavioral contexts. *Front. Behav. Neurosci.* (2017) 11
81. Oster M, Scheel M, Muráni E, Ponsuksili S, Zebunke M, Puppe B, Wimmers K. The Fight-Or-Flight Response Is Associated with PBMC Expression Profiles Related to Immune Defence and Recovery in Swine. *Plos One* (2015) 10: e0120153
82. Bolhuis JE, Parmentier HK, Schouten WGP, Schrama JW, Wiegant VM. Effects of housing and individual coping characteristics on immune responses of pigs. *Physiol. Behav.* (2003) 79: 289-296
83. Ponsuksili S, Zebunke M, Murani E, Trakooljul N, Krieter J, Puppe B, Schwerin M, Wimmers K. Integrated genome-wide association and hypothalamus

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

eQTL studies indicate a link between the circadian rhythm-related gene PER1 and coping behaviour. *Sci. Rep.* (2015) 5

84. Murphy E, Nordquist RE, van der Staay FJ. A review of behavioural methods to study emotion and mood in pigs, *Sus scrofa*. *Appl. Anim. Behav. Sci.* (2014) 159: 9-28

85. Koolhaas JM, van Reenen CG. Animal Behavior and Well-Being Symposium: Interaction between coping style/personality, stress, and welfare: Relevance for domestic farm animals. *J. Anim. Sci.* (2016) 94: 2284-2296

86. Mendl M, Burman OHP, Paul, ES. An integrative and functional framework for the study of animal emotion and mood. *Proc. R. Soc. Lond. Biol.* (2010) 277: 2895-2904.

87. Russell J. A circumplex model of affect. *J. Pers. Soc. Psychol.* (1980) 39: 1161-1178.

88. Lloyd AS, Martin JE, Bornett-Gauci HLI, Wilkinson RG. Horse personality: Variation between breeds. *Appl. Anim. Behav. Sci.* (2008) 112: 369-383

89. Carter AJ, Feeney WE, Marshall HH, Cowlshaw G, Heinsohn R. Animal personality: what are behavioural ecologists measuring? *Biol. Rev. Camb. Philos. Soc.* (2013) 88: 465-475

90. Forkman B, Boissy A, Meunier-Salaün MC, Canali E, Jones RB. A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiol. Behav.* (2007) 92: 340-374

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

91. Brown JA, Dewey C, Delange CFM, Mandell IB, Purslow PP, Robinson JA, Squires EJ, Widowski TM. Reliability of temperament tests on finishing pigs in group-housing and comparison to social tests. *Appl. Anim. Behav. Sci.* (2009) 118: 28-35
92. Gibbons J, Lawrence A, Haskell M. (2009). Responsiveness of dairy cows to human approach and novel stimuli. *Appl. Anim. Behav. Sci.* (2009) 116: 163-173
93. Lansade L, Simon F. Horses' learning performances are under the influence of several temperamental dimensions. *Appl. Anim. Behav. Sci.* (2010) 125: 30-37
94. Handley SL, Mithani S. Effects of alpha-adrenoceptor agonists and antagonists in a maze-exploration model of 'fear'-motivated behaviour. *Naunyn Schmiedebergs Arch. Pharmacol.* (1984) 327: 1-5
95. Montgomery KC. The relation between fear induced by novel stimulation and exploratory drive. *J. Comp. Physiol. Psychol.* (1955) 48: 254-260
96. Peral D, Griffin AS, Bartomeus I, Sol D. Revisiting the open-field test: what does it really tell us about animal personality? *Anim. Behav.* (2017) 123: 69-79
97. Hessing MJC, Hagelso AM, Vanbeek JAM., Wiepkema PR, Schouten WGP, Krukow R. Individual behavioral characteristics in pigs. *Appl. Anim. Behav. Sci.* (1993) 37: 285–295
98. Zebunke M, Repsilber D, Nürnberg G, Wittenburg D, Puppe B. The backtest in pigs revisited – An analysis of intra-situational behaviour. *Appl. Anim. Behav. Sci.* (2015) 169: 17-25

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

99. Guenther A, Trillmich F. Within-litter differences in personality and physiology relate to size differences among siblings in cavies. *Physiol. Behav.* (2015) 145: 22-28
100. Diener E, Suh EM, Lucas RE, Smith HL. Subjective well-being: Three decades of progress. *Psychol. Bull.* (1999) 125: 276-302
101. Weiss A, Bates TC, Luciano M. Happiness is a personal(ity) thing: The genetics of personality and well-being in a representative sample. *Psychol. Sci.* (2008) 19: 205-210
102. DeNevre KM, Cooper H. Origins and functions of positive and negative affect: a control-process view. *Psychol. Rev.* (1998) 124: 197-229
103. Tetley CL, O'Hara SJ. Ratings of animal personality as a tool for improving the breeding management and welfare of zoo animals. *Animal Welf.* (2012) 21: 463-476
104. Dawkins MS. Evolution and animal welfare. *Q. Rev. Biol.* (1998) 73: 305-328
105. Dawkins MS. Using behaviour to assess animal welfare. *Anim. Welf.* (2004) 13: 3-7
106. Fureix C, Menguy H, Hausberger M. Partners with Bad Temper: Reject or Cure? A Study of Chronic Pain and Aggression in Horses. *Plos One* (2008) 5: e12434

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

107. Burrow HM, Dillon RD. Relationship between temperament and growth in a feedlot and commercial carcass traits in *Bos indicus* crossbreeds. *Aust. J. Exp. Agric.* (1997) 37: 407-11
108. Voisinet BD, Grandin T, Tatum JD, O'Connor SF, Struthers JJ. Feedlot cattle with calm temperaments have higher average daily gains than cattle with excitable temperaments. *J. Anim. Sci.* (1997) 75: 892-896
109. Rauw WM., Johnson AK, Gomez-Raya L, Dekkers JCM. A hypothesis and review of the relationship between selection for improved production efficiency, coping behavior and domestication. *Front. Genet.* (2017) 8:134
110. Drent PJ, van Oers K, Noordwijk AJ. Realized heritability of personalities in the great tit (*Parus major*). *Proc. Royal Soc. B.* (2003) 270: 45-51
111. van Oortmerssen GA, Bakker TC. Artificial selection for short and long attack latencies in wild *Mus musculus domesticus*. *Behav. Genet.* (1981) 11: 115-126
112. van Oers K, Drent PJ, Jong GD, Noordwijk AJ. Additive and nonadditive genetic variation in avian personality traits. *Heredity* (2004) 93: 496-503
113. Henderson CR. Applications of linear models in animal breeding. Guelph, Ont.: University of Guelph (1984)
114. Kruuk LE. Estimating genetic parameters in natural populations using the 'animal model'. *Proc. Royal Soc. B.* (2004) 359: 873-890

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

115. Laine VN, van Oers K. The Quantitative and Molecular Genetics of Individual Differences in Animal Personality. In: Vonk J., Weiss A., Kuczaj S. (eds) *Personality in Nonhuman Animals*. Springer, Cham (2017)
116. Careau V, Thomas D, Pelletier F, Turki L, Landry F, Garant D, Réale D. Genetic correlation between resting metabolic rate and exploratory behaviour in deer mice (*Peromyscus maniculatus*). *J. Evol. Biol.* (2011) 24: 2153-2163
117. Haskell MJ, Simm G, Turner SP. Genetic selection for temperament traits in dairy and beef cattle. *Front Genet.* (2014) 5: 368
118. Stirling DG, Réale D, Roff DA. Selection, structure and the heritability of behaviour. *J. Evol. Biol.* (2002) 15: 277-289.
119. D'Eath RB, Rohe R, Turner SP, Ison SH, Farish M, Jack MC, Lawrence AB. Genetics of animal temperament: aggressive behaviour at mixing is genetically associated with the response to handling in pigs. *Animal* (2009) 3: 1544-1554
120. Hellbrügge B, Tölle KH, Bennewitz J, Henze C, Presuhn U, Krieter J. Genetic aspects regarding piglet losses and the maternal behaviour of sows. Part 2. Genetic relationship between maternal behaviour on sows and piglet mortality. *Animal* (2008) 2: 1281-1288
121. Stukenborg A, Traulsen I, Stamer E, Puppe B, Presuhn U, Krieter J. Heritabilities of agonistic behavioural traits in pigs and their relationships within and between different age groups. *Livest. Sci.* (2012) 149: 25-32

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

122. Graunke KL, Nürnberg G, Repsilber D, Puppe B, Langbein J. Describing Temperament in an Ungulate: A Multidimensional Approach. *Plos One* (2013) 8: 1-12
123. Hoppe S, Brandt HR, König S, Erhardt G, Gauly M. Temperament traits of beef calves measured under field conditions and their relationships to performance. *J. Anim. Sci.* (2010) 88: 1982–1989
124. von Borstel UK, Pasing S, Gauly M. Towards a more objective assessment of equine personality using behavioural and physiological observations from performance test training. *Appl. Anim. Behav. Sci.* (2011) 135: 277-285
125. Boles JA, Kohlbeck KS, Meyers MC, Perz KA, Davis KC, Thomson JM. The use of blood lactate concentration as an indicator of temperament and its impact on growth rate and tenderness of steaks from Simmental × Angus steers. *Meat Sci.* (2015) 103: 68-74
126. Cafe LM, Robinson DL, Ferguson DM, Geesink GH, Greenwood PL. Temperament and hypothalamic-pituitary-adrenal axis function are related and combine to affect growth, efficiency, carcass, and meat quality traits in Brahman steers. *Domest. Anim. Endocrinol.* (2011) 40: 230-240
127. Hedlund L, Løvlie H. Personality and production: Nervous cows produce less milk. *J. Dairy Sci.* (2015) 98: 5819-5828
128. Hawken PAR, Fiol C, Blache D. Genetic differences in temperament determine whether lavender oil alleviates or exacerbates anxiety in sheep. *Physiol. Behav.* (2012a) 105: 1117-1123

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

129. Hawken PAR, Williman M, Milton J, Kelly R, Nowak R, Blache D. Nutritional supplementation during the last week of gestation increased the volume and reduced the viscosity of colostrum produced by twin bearing ewes selected for nervous temperament. *Small Rumin. Res.* (2012b) 105: 308-314
130. Boersma GJ, Benthem L, van Beek AP, van Dijk G, Scheurink AJW. Personality, a key factor in personalized medicine? *Eur. J. Pharmacol.* (2011) 667: 23-25
131. Clark B, Stewart GB, Panzone LA, Kyriazakis I, Frewer LJ. Citizens, consumers and farm animal welfare: A meta-analysis of willingness-to-pay studies. *Food Policy* (2017) 68: 112-127
132. Grignard L, Boissy A, Boivin X, Garel JP, Le Neindre P. The social environment influences the behavioural responses of beef cattle to handling. *Appl. Anim. Behav. Sci.* (2000) 68: 1-11
133. Boissy A, Bouix J, Orgeur P, Poindron P, Bibe B, Le Neindre P. Genetic analysis of emotional reactivity in sheep: effects of the genotypes of the lambs and of their dams. *Genet. Select. Evol.* (2005) 37: 381-401
134. Miranda-de la Lama GC, Sepúlveda WS, Montaldo HH, María GA, Galindo F. Social strategies associated with identity profiles in dairy goats. *Appl. Anim. Behav. Sci.* (2011) 134: 48-55
135. Kilgour RJ, Melville GJ, Greenwood PL. Individual differences in the reaction of beef cattle to situations involving social isolation, close proximity of humans, restraint and novelty. *Appl. Anim. Behav. Sci.* (2006) 99: 21-40

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

136. Boissy A, Bouissou MF. Assessment of individual differences in behavioural reactions of heifers exposed to various fear-eliciting situations. *Appl. Anim. Behav. Sci.* (1995) 46: 17-31
137. Reimert I, Rodenburg TB, Ursinus WW, Kemp B, Bolhuis JE. Responses to novel situations of female and castrated male pigs with divergent social breeding values and different backtest classifications in barren and straw-enriched housing. *Appl. Anim. Behav. Sci.* (2014b) 151: 24-35
138. Phocas F, Boivin X, Sapa J, Trillat G, Boissy A, Le Neindre P. Genetic correlations between temperament and breeding traits in Limousin heifers. *Anim. Sci.* (2006) 82: 805-811
139. Brand B, Hadlich F, Brandt B, Schauer N, Graunke KL, Langbein J, Repsilber D, Ponsuksili S, Schwerin M. (2015). Temperament type specific metabolite profiles of the prefrontal cortex and serum in cattle. *PloS One* (2015) 10: e0125044.
140. del Campo M, Brito G, Soares de Lima J, Hernández P, Montossi F. Finishing diet, temperament and lairage time effects on carcass and meat quality traits in steers. *Meat Sci.* (2010) 86: 908-914
141. Lyons DM, Price EO, Moberg GP. Individual differences in temperament of domestic dairy goats: constancy and change. *Anim. Behav.* (1988) 36: 1323-1333
142. Lyons DM. Individual Differences in Temperament of Dairy Goats and the Inhibition of Milk Ejection. *Appl. Anim. Behav. Sci.* (1989) 22: 269-282

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

143. Nawroth C, Prentice PM, McElligott AG. Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. *Behav. Process.* (2017) 134: 43-53
144. Hazard D, Moreno C, Foulquie D, Delval E, Francois D, Bouix J, Salle G, Boissy A. Identification of QTLs for behavioral reactivity to social separation and humans in sheep using the OvineSNP50 BeadChip. *BMC Genomics* (2014) 15: 778
145. McBride SD, Wolf B. Using multivariate statistical analysis to measure ovine temperament; stability of factor construction over time and between groups of animals. *Appl. Anim. Behav. Sci.* (2007) 103: 45-58
146. Seaman SC, Davidson HPB, Waran NK. How reliable is temperament assessment in the domestic horse (*Equus caballus*)? *Appl. Anim. Behav. Sci.* (2002) 78: 175-191
147. Lansade L, Bouissou MF, Erhard HW. Fearfulness in horses: A temperament trait stable across time and situations. *Appl. Anim. Behav. Sci.* (2008) 115: 182-200
148. Graf P, von Borstel UK, Gauly M. Practical considerations regarding the implementation of a temperament test into horse performance tests: Results of a large-scale test run. *J. Vet. Behav.* (2014) 9: 329-340
149. Hausberger M, Muller C, Lunel C. Does Work Affect Personality? A Study in Horses. *Plos One* (2011) 6: e14659

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

150. Visser EK, van Reenen CG, Hopster H, Schilder MBH, Knaap JH, Barneveld A, Blokhuis HJ. Quantifying aspects of young horses' temperament: consistency of behavioural variables. *Appl. Anim. Behav. Sci.* (2001) 74: 241-258
151. Visser EK, van Reenen CG, Engel B, Schilder MBH, Barneveld A, Blokhuis HJ. The association between performance in show-jumping and personality traits earlier in life. *Appl. Anim. Behav. Sci.* (2003) 82: 279-295
152. Olsen HF, Klemetsdal G. Temperament of the Norwegian horse breeds - a questionnaire based study. *Appl. Anim. Behav. Sci.* (2017) 193: 60-66
153. Lansade L, Bouissou MF. Reactivity to humans: A temperament trait of horses which is stable across time and situations. *Appl. Anim. Behav. Sci.* (2008) 114: 492-508
154. Lansade L, Bouissou MF, Boivin X. Temperament in preweanling horses: Development of reactions to humans and novelty, and startle responses. *Dev. Psychobiol.* (2007) 49: 501-513
155. Krüger K, Farmer K, Heinze J. The effects of age, rank and neophobia on social learning in horses. *Anim. Cogn.* (2014) 17: 645-655
156. Lansade L, Philippon P, Herve L, Vidament M. Development of personality tests to use in the field, stable over time and across situations, and linked to horses' show jumping performance. *Appl. Anim. Behav. Sci.* (2016) 176: 43-51
157. Duberstein KJ, Gilkeson JA. Determination of sex differences in personality and trainability of yearling horses utilizing a handler questionnaire. *Appl. Anim. Behav. Sci.* (2010) 128: 57-63

Chapter 2 – Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

158. Roberts K, Hemmings AJ, Moore-Colyer M, Parker MO, McBride SD. Neural modulators of temperament: A multivariate approach to personality trait identification in the horse. *Physiol. Behav.* (2016) 167: 125-131
159. Bolhuis JE, Schouten WGP, de Leeuw JA, Schrama JW, Wiegant VM. Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behav. Brain Res.* (2004) 152: 351-360
160. Reimert I, Bolhuis JE, Kemp B, Rodenburg TB. Social support in pigs with different coping styles. *Physiol. Behav.* (2014a) 129: 221-229
161. Spake JR, Gray KA, Cassady JP. Relationship between backtest and coping styles in pigs. *Appl. Anim. Behav. Sci.* (2012) 140: 146-153
162. Zebunke M, Nürnberg G, Melzer N, Puppe B. The backtest in pigs revisited – inter-situational behaviour and animal classification. *Appl. Anim. Behav. Sci.* (2017) 194: 7-13
163. Janczak AM, Pedersen LJ, Bakken M. Aggression, fearfulness and coping styles in female pigs. *Appl. Anim. Behav. Sci.* (2003) 81: 13-28
164. Ruis MAW, te Brake JHA, van de Burgwal JA, de Jong IC, Blokhuis HJ, Koolhaas JM. Personalities in female domesticated pigs: behavioural and physiological indications. *Appl. Anim. Behav. Sci.* (2000) 66: 31-47

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

Chapter THREE:

Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses



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This chapter is redrawn from *Applied Animal Behaviour Science*: "Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses".

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Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

3.1 Abstract

The assessment of personality in farm animals and its relation to other behavioural and physiological traits is of growing scientific and practical interest. Therefore, the aims of the present study were first to assess the personality of dwarf goats in the context of the proactive/reactive dichotomy and second to elucidate cross-context correlations to other individual patterns in behaviour and physiology. We measured the behaviour of 108 Nigerian dwarf goats in repeated (two test periods within two weeks) open-field and novel-object tests to classify the subjects into proactive, reactive and intermediate personality types. In addition, we investigated the possible inter-relationships of inter-individual differences in personality with behaviours in other test situations and physiological measures (heart rate variability). To identify individual personality types, we selected the 11 most appropriate behavioural measures, identical in both test periods, from a total of 82 observed behaviours. Using these behaviours, we ran two separate principal component analyses (PCA1 and PCA2) for the two test periods. We found two main principal components (PCs), which were interpreted as “boldness” (PC1) and “activity” (PC2) and were identical in both PCAs. Based on PCA1, 30 goats could be grouped as the proactive, 25 as the reactive and 53 as the intermediate personality type. In PCA 2, 66 individuals (61%) showed a consistent personality type compared to PCA1. Goats that scored highly on PC2 were also more active in a social separation test, while no correlations were found between PC1 or PC2 and the dominance status. Regarding heart rate variability, the standard deviation of R-R intervals (SDNN) was positively correlated with PC2, while a negative

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correlation was found between PC1 and SDNN. PC2 was also positively correlated with weight gain. The present study is the first to quantify temporarily consistent and cross-context correlations of individual behavioural and physiological differences in goats. The relatively small number of animals that showed the same extreme behavioural phenotype in both test periods is in good agreement with studies on personality types in cattle and pigs and shows that intermediate and flexible personality types make up the main part of a population. The results provide new opportunities to investigate the inter-relationships of inter-individual differences in personality traits with other physiological measures and cognitive abilities in goats.

Keywords

Personality, personality types, farm animals, ruminants, dwarf goats

3.2 Introduction

In farm animals, understanding individual differences in personality has gained increased attention for welfare purposes, because personality may have an impact on economic factors as farm animals such as pigs, cattle, chickens and horses must cope with numerous challenging situations, automatic systems and different husbandry practises during their lifetime (reviewed by Finkemeier et al., 2018). Personality in animals can be assessed by measuring behaviours that are assigned to the most common personality factors: exploration, activity, aggressiveness, sociability, and boldness (reviewed by Finkemeier et al., 2018; Réale et al., 2012). Each factor is defined as a correlated set of individual behavioural and

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physiological traits that are consistent over time and contexts (Ferrari et al., 2014; Koolhaas et al., 1999; Réale et al., 2007; Sih et al., 2004; Wilson et al., 1994).

Personality is also assumed to correlate with other behavioural and physiological traits and differences seem to appear more pronounced in socially living species compared to solitary living species, suggesting that it may be the social environment that provides a range of different adaptive niches in which different personality strategies can succeed (Penke et al., 2007). The results of different species provide examples of a positive relationship between activity, aggressiveness and boldness with food intake rates and provide an argument that individual differences in behaviour can include variation in the size of internal organs related to food, energy metabolism and endocrine systems (reviewed by Biro and Stamps, 2008). In farm animals, proactive pigs had a higher resting heart rate and lower heart rate variability than reactive pigs (Krause et al., 2017), and more social goats had a more stable heart rate, suggesting lower reactivity of the autonomic nervous system (Briefer et al., 2015). In dairy cows, personality seems to have an impact on the behavioural and physiological responses to milking and on the stress associated with being milked in a novel environment (Hedlund and Løvlie, 2015; Sutherland et al., 2012). Personality traits are now considered to a greater extent in the calculation of breeding indices because some traits show moderate to high heritability (Careau et al., 2011, Haskell et al., 2014; van Oers et al., 2004; Stirling et al., 2002), and personality traits measured early in life can predict performance later in life (e.g., jumping performance in horses (Visser et al., 2003)).

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However, finding the variables or behavioural measures that might best explain personality in farm animals are different for each species. While the backtest (where a piglet is turned on its back and the struggle intensity for one minute is measured) is predominantly used to describe personality and/or coping in pigs (reviewed by Finkemeier et al. 2018), tests such as the open field (OF), novel object (NO), or human approach test and various other behavioural tests are predominantly used for cattle and horses to assess individual behavioural differences (Lansade et al., 2008; reviewed by Murphy et al., 2014). Particularly in ruminants, personality has been described using repeated measurements of the open-field and novel-object tests (Graunke et al., 2013; Foris et al., 2018; Neave et al., 2018). The open-field and novel-object tests have also been used to assess behavioural differences in dwarf goats (Oesterwind et al., 2016), and specific personality traits, such as exploration and sociability, were related to cognitive performance, learning flexibility and learning style (Nawroth et al., 2017).

The aim of the present study was to identify potential variables or behaviours that assess personality in goats and to reveal consistency and cross-context correlations of individual differences in behaviour and physiology within this species. We measured the behaviour of 108 Nigerian dwarf goats in a repeatedly conducted open-field and novel-object test using the proactive/reactive dichotomy to classify the subjects into proactive, reactive and intermediate personality types. To investigate connections between personality and other behavioural and physiological traits, we measured resting heart rate and weight and conducted a social separation test (sociality). We also observed agonistic interactions in the

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home pen and when the goats were given limited access to a learning device (aggressiveness/dominance) to disentangle the potential correlations across different behavioural contexts. The results of this study will provide a basis for further possibilities to investigate the connections of personality with other physiological measures and cognitive abilities in goats.

3.3 Animals, Materials and Methods

3.3.1 Animals and Housing

The experiments were conducted with 108 juvenile female Nigerian dwarf goats (*Capra aegagrus hircus*) bred from a line at the Leibniz Institute for Farm Animal Biology (FBN, Dummerstorf, Germany). The experiments were conducted within two years with two runs per year. Runs one and three were conducted in spring and runs two and four were conducted in autumn. Because of the different numbers of kids available, runs one and two were conducted with 32 kids each, run three with 14 kids and run four with 30 kids. From birth to weaning (at an age of seven weeks (Figure 1)), kids were housed in mixed groups consisting of three to five adult females with their male and female kids. The pens (12 m²) contained straw as bedding material, a hayrack and a round feeder to deliver pellets (800 g to 1000 g twice per day per pen, Vollkraft, Mischfutterwerk GmbH, Güstrow, Germany). Hay and water were fed ad libitum. The kids were equipped with collars and ear tags for individual recognition. After weaning and during the phase of repeated testing of the open-field and novel-object tests, animals were housed in groups of up to 16 animals per group in pens, as described above with a

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climbing rack as an enrichment item (Figure 1). After repeated testing (at 12 weeks of age), kids were housed in groups of up to eight animals per group in pens (described above) but with free access to a learning device (for further information about the device, see Langbein et al., 2007) (Figure 1). From then on, we conducted the social separation test, performed the dominance observation and the limited access test and measured the resting heart rate.

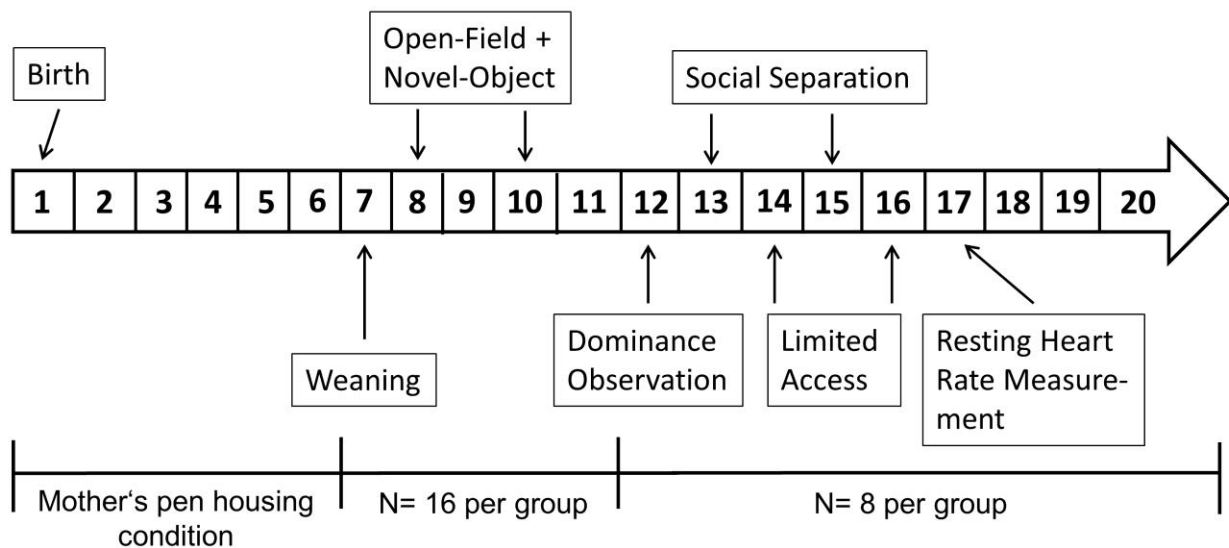


Figure 1: Experimental setup, test sequence, housing condition and age of each dwarf goat (given in weeks).

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3.3.2 Open-Field and Novel-Object Test

All kids were tested in an open-field test (OF-test) and novel-object test (NO-test) twice within two weeks (two test periods). They were eight weeks of age for the first test period and ten weeks of age for the second test period (Figure 1). For the OF-test and the NO-test we used an arena (3 m x 4.8 m) with opaque walls (2 m high) in a different part of the barn which was separated from the home pens by two doors. The arena was divided into 12 identical segments (1 x 1.2 m) which were indicated by white lines on the floor. A fully enclosed start box (1 x 1 x 1 m) was connected to the arena and was opened by a guillotine door. For the first NO-test, a traffic cone was used and for the second test, a medicine ball was used as the object. To ensure that the object could not be displaced by the focal animal, the object was fixed with a chain hanging from the ceiling. A camera (Panasonic WV-CP500) and an external microphone (TenluxDM-518) placed above the arena recorded the animal's movements and vocalizations. The OF- and NO-tests were conducted between 7 am and 12 am. Both tests were conducted for five minutes each. The OF-test was performed on all kids on the first day of the test period and the NO-test on the next day. The testing order of groups and the animal order within the group was randomised. For a test, the kid was taken from its home pen, placed in the start box and the door to the arena was opened after 20 seconds. If the kid did not enter the arena within 30 seconds voluntarily, it was gently pushed into the arena, and the guillotine door was closed immediately. At the end of the test, the kid was allowed to leave the arena by a side door and was taken back to its home pen. In cases of urination or defecation, the arena was cleaned after each

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test to avoid olfactory distraction of the following subjects. For both tests and both test periods we recorded 82 behaviours for each subject coded with Observer XT (Version 12, Noldus Information Technology, the Netherlands).

3.3.3 Social Separation Test

All kids were tested in a social separation test (SST) twice within two weeks. They were 13 weeks of age for the first test and 15 weeks of age for the second test (Figure 1). For the SST, we used an arena that was divided into two parts (1.5 m x 3 m each). Both parts were separated by two opposing wire-mesh fences with a distance of 20 cm (Figure 2). During the test, the test group (eight animals) was brought in one part of the arena, and one focal animal was taken out of the group and brought in the opposite part of the arena. This part was divided into three identical segments, defined by their distance to the fence (1-right by the fence, 2-middle segment, 3-furthest from the fence), and the animal started the test in segment 2. For five minutes, we recorded “general duration of activity”, “general duration of rearing up” and “general duration of time spent at the fence” via camera (Panasonic WV-CP500). This test was conducted between 7 am and 12 am. The testing order of groups as well as the focal animal order within the group was randomised. At the end of the test the focal animal was returned to its group members. In cases of urination or defecation, the arena was cleaned after each test to avoid olfactory distraction of the following subjects.

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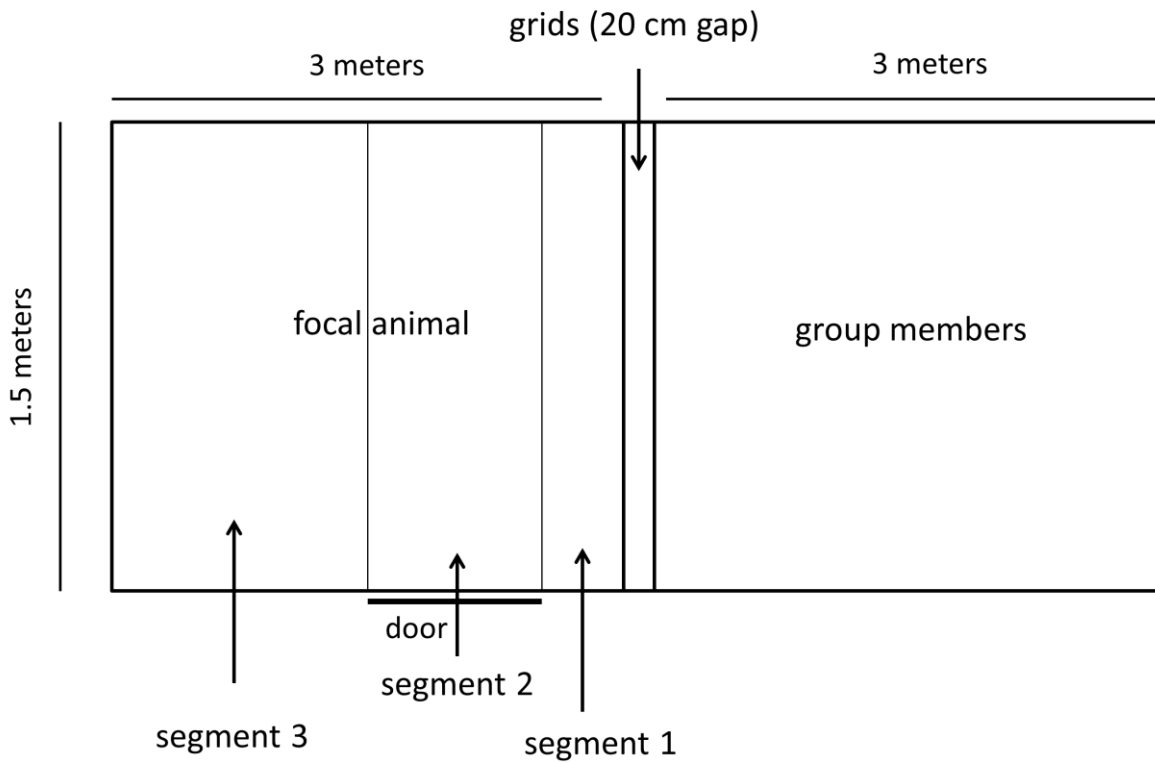


Figure 2: Setup of the social separation test. The focal animal is taken out of its group, which is in the right part of the arena, and brought to the left part of the arena. The left part of the arena is subdivided into three segments. The test starts in segment 2, when the door is closed. Both parts are separated by two grids.

3.3.4 Dominance

The observations of dyadic agonistic interactions were conducted in the home pen twice a day for 30 min after feeding (8 am and 1 pm) for five days after regrouping into groups of eight animals (Figure 1). As agonistic interactions, we considered behaviours such as threatening, chasing, pushing, displacing and

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fighting. We recorded the time of interaction as well as the initiator and recipient, and in the case of a fight, we recorded who won and generated a winner-looser matrix. We calculated a dominance index as suggested by Langbein and Puppe (2004) to obtain a value between -1 (low in the groups' hierarchy) and 1 (high in the groups' hierarchy) for each animal. Due to technical problems, we started the observations in the second run. Therefore, we only have values for 76 kids.

3.3.5 Limited Access

The limited access test (LA) was conducted twice within two weeks, when kids were 14 weeks of age for the first test and 16 weeks of age for the second test (Figure 1). During this test, the learning device in the home pen was closed at 4 pm and reopened after 16 hours at 10 am the following day. We recorded the order of the animals entering the learning device to obtain water until each animal of the group (eight in total) was able to enter the learning device.

3.3.6 Resting Heart Rate Variability (RHRV)

The resting heart rate (RHR) was measured, when kids were 17 weeks of age (Figure 1). RHR measurements were performed for four hours (7:30 am to 11:30 am) using the Polar heart rate monitor (RS800CX; Polar Pro Trainer 5, Polar Electro Oy, Finland). The electrode belt was strapped around the chest with the electrodes fixed on the left part of the body (for further details see Langbein et al., 2004). All kids were habituated to the equipment used for measurement for four hours one day before. During the RHR measurement, each kid was also equipped with an MSR data logger (MSR145W, Modular Signal Recorder Electronics

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GmbH, Switzerland) affixed to the right hind leg to reliably detect lying periods. RHR data were analysed using Polar software (Polar Pro Trainer 5, Polar Electro Oy, Finland). Heart rate intervals (R-R) were corrected for anomalies in five-minute intervals using standard settings in Polar. We analysed heart rate (heart beats per minute), the root mean square of the successive differences of neighbouring R-R intervals (RMSSD in ms) and the standard deviation of the R-R intervals (SDNN in ms) across one to four consecutive five-minute intervals of undisturbed lying for each kid.

3.3.7 Weight and Weight Gain

To obtain weight measurements, kids were weighed directly after birth, on the day of weaning and at the end of the testing period (Figure 1). We calculated the variance between weight at birth and weight at weaning (weight gain B-W), between weight at weaning and weight at the end of the testing period (weight gain W-E) and between weight at birth and weight at the end of the testing period to obtain measures about weight gain (weight gain B-E).

3.3.8 Data Analysis and Statistics

Statistical analysis was performed with SAS 9.4 (SAS Institute Inc., USA). In a preliminary analysis, we checked for the influence of weight at weaning and birth season on all 82 measured behaviours in the OF- and NO-tests using a univariate mixed model with the random effects of “individual ID” nested within “mother ID” and the fixed effects of “season” (spring vs. autumn) or “weight” because seasonal differences and weight differences between individuals are known to

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have an impact on behaviour (Finkemeier et al., 2016; Haage et al., 2013; Pyter and Nelson, 2006). As a result, we chose 11 measures from both tests that were not influenced by the mentioned effects and/or that are common for use in animal personality studies (e.g. Finkemeier et al., 2016; Forkman et al., 2007) for further analysis (Table 1).

Table 1: Definition and type of recording of 11 measures of 7 behaviours during the open-field (OF) and novel-object (NO) tests used for both PCAs; D = duration (total time in s), F = frequency, L = latency (time in s until behaviour was first shown).

Behaviour	Type of recording	Definition
General activity (OF +NO)	D	Max. 3 legs touching the ground, forward movement
Rearing up (OF + NO)	D	Animal stands on both hindlegs on the ground and touches the walls of the arena with the forelegs
Time spent in corner segments	D	Time that the animal spends in the corner segments of the arena
Time spent in inner segments	D	Time that the animal spends in the inner segments of the arena
Vocalizations	F	Any kind of bleats the goat makes
Time spent in the segments near the object	D	With at least the forelegs in the segments (5 in total) which are near the object
Contacts with object	D, F, L	Snout contact with the novel object

We performed a principal component analysis (PCA) separately for each test period (PCA1 + PCA2), which describes the relationship between new principal components (PCs) and the 11 chosen behaviours measured in both the OF- and NO-tests of each test period (test period 1 and test period 2). We used PCAs

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instead of a factor analysis because our measured variables were non-normally distributed (Budaev, 2010; Costello and Osborne, 2005) and because no a-priori theory or model exists (Gorsuch, 1983). We used a correlation matrix (the CORR procedure) of all pairwise correlations of the 11 behaviours by applying the non-parametric Spearman's rank correlation test, as input data set. Both PCAs were calculated with the FACTOR procedure in SAS with the following parameter settings: method=PRIN, prior=ONE, rotation=VARIMAX. Kaiser's measure of sampling adequacy (overall MSA/KMO) indicates how credible the calculated PCA is (e.g., an overall MSA above 0.9 is described as "marvellous", 0.7 is described as "middling", below 0.5 is described as "unacceptable" by Kaiser and Rice, 1974). For the choice of the final number of PCs, we used Kaiser's number of eigenvalues > 1 (Kaiser, 1960) and Cattell's scree-test (Cattell, 1966), where we considered behaviours with loadings above 0.7 and below -0.7 (since these are rated as "excellent" by Comrey and Lee, 1992)). Additionally, we discarded PCs that consisted only of one behaviour or of two complementary behaviours (e.g., "active" vs. "inactive"). Finally, we calculated PC scores for each animal in each of the two test periods with the SCORE procedure, where each individual score was calculated from the standardised original data and the respective loadings of each PC separately for PCA1 and PCA2. The animals were assigned to specific score classes (SC) according to the level of their scores in the PCs gained from each PCA (suggested by Mendl et al., 2010). We calculated a Spearman's rank correlation between the PCs of the first and the second test period as a measure of consistency and to determine the personality type (proactive, intermediate, reactive).

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We calculated a Spearman's rank correlation test between the PCs and the variables measured in the SST, dominance index, LA, RHRV and weight gain to assess relationships between personality factors and other behavioural (single and group situations) and physiological traits.

3.3.9 Ethical Note

All animal care and experimental procedures were performed in accordance with the German welfare requirements for farm animals and the ASAB/ABS Guidelines for the Use of Animals in Research (Anonymous, 2019). All procedures involving animal handling and treatment were approved by the Committee for Animal Use and Care of the Ministry of Agriculture, Environment and Consumer Protection of the federal state of Mecklenburg-Vorpommern, Germany (Ref. 7221.3-2-005/14).

3.4 Results

3.4.1 Principal Component Analysis

From the preliminary analysis of the 82 behaviours (see supplementary material), we selected 11 behaviours (Table 1) identical for both test periods, which were not affected by season and weight and/or are commonly used in animal personality studies. Using these behaviours, we calculated one PCA for each test period (PCA1 + PCA2). We found five PCs in PCA1 (Overall MSA= 0.7). The first PC (PC 1a; eigenvalue = 3.5) consists of four behaviours with loadings above 0.7 and below -0.7 describing the interaction with the novel object (Table 2). The second PC (PC 1b; eigenvalue = 2) consists of two behaviours with loadings

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above 0.7 and below -0.7 describing active-like behaviour. We labelled PC1a “boldness” and PC1b “activity”. The two PCs explained 32% and 18.2% of the variation in the data, respectively. The third, fourth and fifth PCs were discarded because one consisted of two complementary behaviours, the next consisted only of one behaviour and the last had an eigenvalue < 1 .

In PCA2 (Overall MSA = 0.71) we found the same five principal components, with the first describing the interaction with the novel object (PC2a; eigenvalue = 3.7) and the second describing active-like behaviour (PC2b; eigenvalue = 1.3), explaining 34% and 12% of the variation in the data, respectively. As in PCA1, we discarded the remaining PCs because one consisted of two complementary behaviours, the next consisted only of one behaviour, and the last had an eigenvalue < 1 .

As a measure of consistency between both PCAs, we used Spearman’s rank correlation test. Boldness ($r_s = 0.43$; $p < 0.001$) and activity ($r_s = 0.66$; $p < 0.001$) were highly correlated over both test periods (PCA1 and PCA2).

3.4.2 Determination of the Personality Type

Based on the two PCs, goats were assigned to four different SCs separately for each PCA (Figure 3 and Figure 4). We labelled SCs Q1 to Q4. Q1 represents the “highly active but shy”, Q2 the “highly active and bold”, Q3 the “less active but bold” and Q4 the “less active and shy” personality type. According to the reactive-proactive approach, Q2 represents a proactive and Q4 represents a reactive personality type. Corresponding to the results of PCA 1, 30 goats were assigned to Q1, 30 goats to Q2, 23 goats to Q3 and 25 goats to Q4 (Figure 3).

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Table 2: The table shows the principal component loadings of the selected behaviours from the OF- and NO-tests on both PCs of the two PCAs in the first (PC1a + PC1b) and second (PC2a + PC2b) test period. Loadings above 0.7 and below -0.7 are shown in bold.

Behaviour	PC 1a	PC 1b	PC 2a	PC 2b
General activity in OF	-0.142	0.742	-0.090	0.916
Rearing up in OF	0.182	0.189	-0.065	0.148
Time spent in corner segments in OF	-0.003	0.055	-0.069	-0.047
Time spent in inner segments in OF	0.076	0.097	0.074	0.135
General activity in NO	0.075	0.837	0.147	0.818
Rearing up in NO	0.093	0.594	0.112	0.032
Vocalizations in NO	0.259	0.690	0.395	0.288
Time spent in the segments near the object in NO	0.709	-0.087	0.704	-0.012
Duration of contacts in NO	0.951	0.132	0.965	0.043
Number of contacts in NO	0.956	0.159	0.965	0.047
Latency to touch the object in NO	-0.893	-0.031	-0.945	0.018

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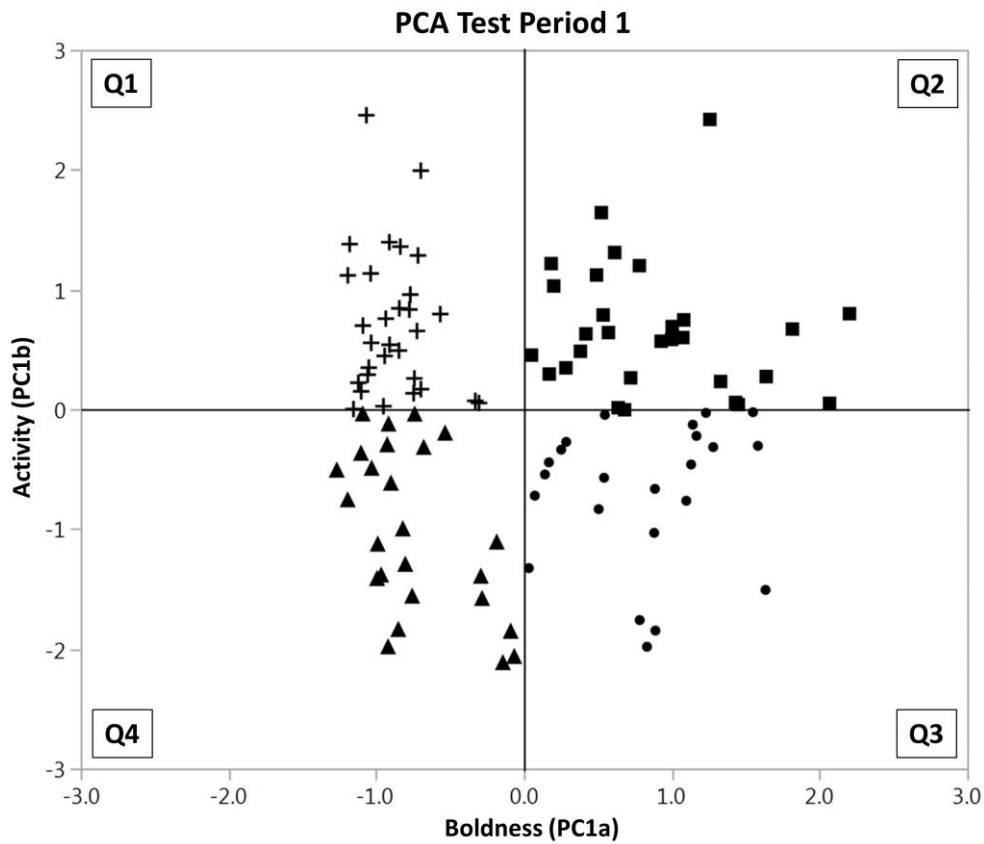


Figure 3: Individual scores of all goats (N = 108) in the first test period based on the loadings (given in bold in Table 2) of PC 1a (“boldness”) and PC 1b (“activity”). Q1 (crosses) = highly active but shy (intermediate personality type), Q2 (squares) = highly active and bold (proactive personality type), Q3 (dots) = less active but bold (intermediate personality type), Q4 (triangles) = less active and shy (reactive personality type).

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According to the score levels gained by PCA 2, 23 of 30 goats (76.6%) were assigned to Q1 (crosses in Figure 4), 15 of 30 goats (50%) to Q2 (squares in Figure 4), 11 of 23 goats (47.8%) to Q3 (dots in Figure 4) and 17 of 25 goats (68%) to Q4 (triangles in Figure 4). In total, 66 of the 108 goats (61%) showed consistent behaviour over both test periods, whereas 20.4% of the goats displayed consistent proactive or reactive behaviour. Of the remaining 42 animals, 34 moved to a neighbouring SC and 8 moved to the opposite SC.

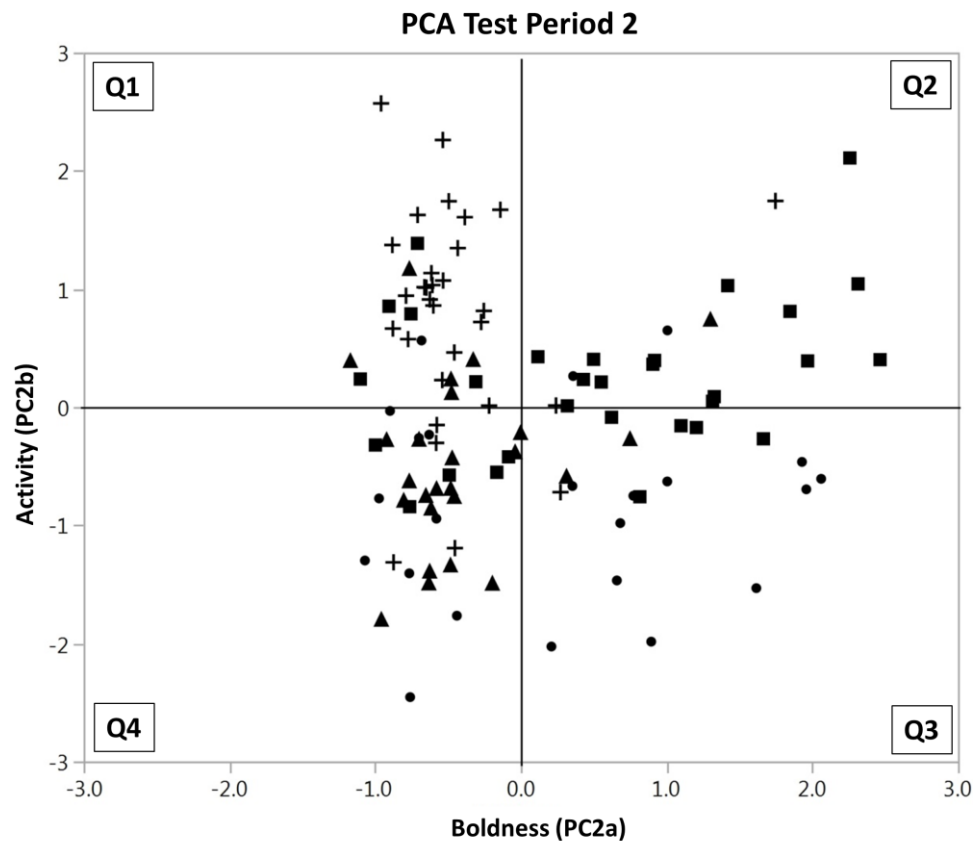


Figure 4: Individual scores of all goats (N = 108) in the second test period based on the loadings (given in bold in Table 2) of PC 2a (“boldness”) and PC 2b (“activity”). The **crosses in Q1** represent the goats that showed consistent highly active and shy behaviour in both test periods, the **squares in Q2** represent the goats that showed consistent

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proactive behaviour, the **dots in Q3** represent the goats that showed consistent less active but bold behaviour and the **triangles in Q4** represent the goats that showed consistent reactive behaviour in both test periods. The crosses, squares, dots and triangles located in other SCs show the individuals with a flexible behavioural phenotype.

3.4.3 Relationship to Behaviour and Physiology

To analyse correlations between personality types and other behavioural and physiological traits, we only considered those goats that showed consistent behaviour (N=66) over both test periods for further analysis.

Goats that scored high in the PC1b “activity” of PCA1 were also more active ($r_s = 0.31$; $p = 0.01$) and showed more rearing up behaviour ($r_s = 0.28$; $p = 0.03$) in the first SST. We also found correlations between the PC2b “activity” of PCA2 and activity ($r_s = 0.34$; $p = 0.006$) and rearing up ($r_s = 0.34$; $p = 0.006$) of the second SST. In comparison, goats that scored high in the PC1a “boldness” of PCA1 spent less time at the fence ($r_s = -0.33$; $p = 0.009$), while this effect was not found between PCA2 and the second SST. The measured behaviours during the SST did not correlate between the tests.

The dominance index did not correlate with any of the PCs, but we found a positive correlation between the PC1b “activity” of PCA1 and the order of the animals entering the learning device of the first test of LA ($r_s = 0.29$; $p = 0.03$), which we did not find between PCA2 and the second test of LA.

While heart rate and RMSSD did not correlate with any of the PCs, the SDNN correlated with both PCs of both PCAs. We found a negative correlation between

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PC1a of PCA1 and the SDNN ($r_s = -0.28$; $p = 0.04$), while PC1b and PC2b of PCA1 ($r_s = 0.3$; $p = 0.02$) and PCA2 ($r_s = 0.4$; $p = 0.0003$) correlated positively with the SDNN.

Weight only correlated with the PC2b “activity” of PCA2. Goats that scored high on the active factor weighed more at the end of the whole testing period ($r_s = 0.25$; $p = 0.04$). This effect could also be found for the weight gain parameters. However, “weight gain B-W” did not correlate with any of the PCs. PC2b of PCA2 correlated with “weight gain W-E” ($r_s = 0.36$; $p = 0.003$) and “weight gain B-E” ($r_s = 0.26$; $p = 0.036$), indicating that goats that scored high in “activity” had a higher increase of weight during the whole testing period.

3.5 Discussion

3.5.1 Consistency in Dwarf Goat Personality

Since the introduction of the evolutionary game theory by Maynard Smith (1982), it is well known that frequency-dependent fitness payoffs can lead to the stable coexistence of different behavioural types in populations (reviewed by Dall et al., 2004). This results in polymorphic populations that are composed of extreme types on both ends of the spectrum (Maynard Smith, 1982). If personality differences evolve together with morphological and other traits, they can facilitate speciation and the conservation of adaptive change, and the presence of different personality types in populations will determine the species’ ability to persist (Clune et al. 2013; Dall et al., 2004). This means that a population in the wild can only persist when there are fixed proportions of individuals who display

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consistent proactive, reactive and intermediate behaviours (Dall et al., 2004; Maynard Smith, 1982). Our results show that 66 of the 108 (approximately 61%) dwarf goats exhibited consistent behaviour over both test periods, and 20.4% of the subjects displayed consistent proactive or reactive behaviour. This matches previous studies with cattle (approximately 21%; Graunke et al., 2013) and pigs (approximately 34%; Zebunke et al., 2015) and corresponds to previous findings in wildlife populations, where proactive and reactive personality types are less represented in a population because they count as extreme personality types (Dall et al., 2004).

The results of our PCAs show similarities in the composition of the PCs compared to a study by Graunke et al. (2013) performed on another ruminant species: they used 361 calves and they determined two main PCs with behaviours measured in an NO-test, while our PCs were composed of behaviours measured in OF- and NO-tests. In both studies, the first PC is composed of behaviours explaining boldness (e.g., duration of contact with the novel object, number of contacts with the novel object, latency to touch the novel object), and the second PC is composed of behaviours explaining activity and/or exploration. These behaviours have similarly very strong loadings on the two components (e.g., from 0.7/-0.7 to 0.9/-0.9). Another study on 40 lactating Holstein cows conducted by Foris et al. (2018) also showed behaviours measured in an OF- and NO-test of the loadings on two different PCs describing personality factors activity and boldness and had similar high loadings. The measured behaviours in all three studies, seem to be of

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strong importance in describing boldness and activity in ruminants, and therefore, in goats.

On the other hand, 42 goats changed to the neighbouring score classes (SCs), indicating a flexible behavioural response. Only eight of them changed to the opposite SC. The majority reduced bold and active behaviour over the test repetitions. We can assume that some goats may have habituated to the test situations as this effect is also critically discussed by Forkman et al. (2007) and Perals et al. (2017). The other goats may show phenotype-specific developmental plasticity because some phenotypes seem to be able to change more than others (Sinn et al., 2008). Even if the concept of animal personality suggests consistency of behaviours, animal personality and behavioural plasticity coexist (Sih et al., 2004), and it has been suggested that more extreme personality phenotypes (e.g., reactive and proactive) might be less plastic than intermediate/flexible personality phenotypes (Sih, 2013).

One can criticise that we conducted only one repetition of the OF- and NO-tests (test period two), and this repetition was conducted two weeks after the first test period. “Boldness” and “activity” were highly correlated between both test periods and were consistent over the two test periods. As our test animals had to encounter learning tasks at a certain age, we chose to measure personality differences (e.g., analogous to the backtest procedure by Zebunke et al., 2015) before these tests started to obtain a better view about the relationship of personality and cognition in goats. When the interval between the observations of behaviour is short, it is likely that the animals are of a similar state (e.g., hunger,

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size, age, condition, dominance) during both observations and experience similar environments (Bell et al., 2009). Future directions could be to increase the delay between the two test periods or even adding a third test period.

3.5.2 Cross-context Correlations in Dwarf Goat Personality

3.5.2.1 Relationship between Personality and Behaviour during Social Separation

The social separation test (SST), similar to the OF- and the NO-tests, is a test that is performed with a focal animal and measures the behaviour of the individual when separated from conspecifics. We found that goats that scored high on the PC “activity” were also more active and showed more rearing up behaviour in the SST than goats that scored low on this PC. We found this effect between both PCAs and both SSTs, which may indicate a behavioural syndrome, as this type of correlation is discussed to be a behavioural syndrome in animal personality studies (Huang et al., 2018; Sih et al., 2004). In comparison, goats that scored high on the PC “boldness” spent less time on the fence, indicating that bold goats seem to be less social. However, we found this correlation only between PCA1 and the first SST, which can be explained with habituation to that situation. Nevertheless, the variable “time spent at the fence” did not correlate between both tests, therefore, we have no indication for a sociability factor in this study. In contrast, Nawroth et al. (2017) conducted two tests to measure sociability in goats: the attraction test in a familiar environment and an isolation test in an

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unfamiliar environment. Both tests were conducted twice, and behaviour was consistent over both test periods, indicating a sociability factor in goats.

3.5.2.2 Relationship between Personality and Dominance

The dominance index did not correlate with any of our measured personality factors. One reason could be that we only started to observe the group's hierarchy up to the second run. From our 66 individuals, which showed a consistent personality type, we have ten individuals with no value for the dominance index. The missing correlation between personality factors and dominance status could be due to these missing values. On the other hand, dominance is a complex domain in personality and is discussed as an independent personality factor in some species and seems to be important to consider when studying social species (reviewed by Finkemeier et al. 2018). However, we found a correlation between “activity” and behaviour in the limited access test. Goats that scored high on this factor were also the first to enter the learning device after 16 hours of water deprivation. Water is an important resource, so this result shows that the more active goats seem to have a higher rank in the group's hierarchy because they could get this resource earlier than the less active goats. Dominance seems to be defined by boldness and/or aggressiveness (Gosling and John, 1999), and aggressiveness serves to establish dominance relationships (Desire et al., 2015). In non-farm animals, a comparative study on domestic guinea pigs (*Cavia porcellus*) and wild cavies (*Cavia aperea*) showed that dominance proved to be stable over time, which is part of the definition of a personality factor (Zipser et al. 2013). In female domestic goats, the dominance rank seems to be influenced by

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aggressiveness, showing that more aggressive goats are the most dominant in the social hierarchy, which can be seen in the present study as well, as we defined dominance hierarchy by measuring agonistic interactions (Barroso et al., 2000). Moreover, age, body and horn size seem to have an influence on the dominance status, which also has an impact on reproductive success in goats: intermediate-ranked female goats have higher reproductive success than more dominant and subordinate goats (Barroso et al., 2000). The relationship between personality and dominance needs further investigation to prove whether dominance should be a fully accepted personality factor in goats or if it is only a social outcome (reviewed by Finkemeier et al., 2018).

3.5.2.3 Relationship between Personality and Physiology

“Boldness” was negatively correlated, and “activity” was positively correlated with the SDNN. These results indicate that shy and active goats seem to have a higher sympathetic activation at rest than bold and less active goats with a lower SDNN (Malik and Camm, 1995). The SDNN is a parameter that shows a combination of parasympathetic and sympathetic activation, whereas the RMSSD gives information about parasympathetic activation alone (Houle and Billman, 1999), which did not correlate with any of the personality factors in our study; thus we can only assume that those animals show a sympathetic shift in their sympathetic-parasympathetic balance. A sympathetic shift is known to promote an increased metabolic output to address environmental challenges (Porges, 1995). This would mean that goats, which are more active and/or shy, are more alert to environmental changes, even while resting. Regarding activity, this would support

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findings of the proactive/reactive dichotomy, as several studies in different species have already shown that proactive individuals have a stronger sympathetic activation in different contexts (Cannon, 1929; Korte et al., 1997; Krause et al., 2017). However, we measured heart rate at rest which makes it difficult to compare our results with the aforementioned studies. Interestingly, a study conducted on humans already found that the personality factor of neuroticism was significantly associated with HRV under baseline conditions (Čukić and Bates, 2014). As activity and boldness are the equivalent personality factors for neuroticism in animals (reviewed by Finkemeier et al., 2018), we can assume that both personality factors and their relationship to SDNN found in the present study are to some extent related to RHRV in goats.

Weight only correlated with the PC “activity”, indicating that goats that scored high on the activity factor were heavier at the end of the whole testing period. This effect could also be found for the weight gain parameters “weight gain W-E” and “weight gain B-E”, indicating that goats that scored high on the activity factor had a higher increase of weight during the whole testing period. Many studies indicate that boldness, activity and/or aggressiveness are positively related to food intake rates, productivity (e.g., weight and/or weight gain) and other life-history traits in a wide range of taxa (reviewed by Biro and Stamps, 2008). Individual differences in weight gain are likely to encourage consistent individual differences in personality factors that are related to the acquisition of food resources, such as boldness, exploration, aggression and activity (reviewed by Biro and Stamps, 2008). Therefore, the relationship between personality and weight gain in goats

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perfectly matches the results of other studies in other taxa, measuring the same effect (Arendt, 1997; Biro et al., 2006; Martins et al., 2005; Stamps, 2007).

3.6 Conclusion

The present study shows that individual differences in personality in goats are consistent over time and provides insight into cross-context correlations between the behaviour in different test situations (single vs. group) and physiological parameters (RHRV and weight gain). Conducting a repeated principal component analysis, the same behavioural parameters load on the same principal components. Based on these two personality factors, “boldness” and “activity”, we found a comparatively small number of extreme personality types in our dwarf goat population, which is consistent with the results of studies in other wild and domestic animal species. Personality should be considered to improve farm animal welfare by adjusting management and housing conditions.

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3.8 Appendix A: Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: <https://doi.org/10.1016/j.applanim.2019.05.004>.

3.9 References

- Anonymous (2019). Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.*, 147: I-X
- Arendt, J.D. (1997). Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.*, 72: 149–177
- Barroso, F. G., Alados, C. L., Boza, J. (2000). Social hierarchy in the domestic goat: effect on food habits and production. *Appl. Anim. Behav. Sci.*, 69: 35-53
- Bell, A. M., Hankison, S. J., Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.*, 77: 771-783
- Biro, P.A., Abrahams, M. V., Post, J. R., Parkinson, E. A. (2006). Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *J. Anim. Ecol.*, 75: 1165–1171
- Biro, P. A., Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends Ecol. Evolut.*, 23: 361-368
- Briefer, E. F., Oxley, J. A., McElligott, A. G. (2015). Autonomic nervous system reactivity in a free-ranging mammal: effects of dominance rank and personality. *Anim. Behav.*, 110: 121-132

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

- Budaev, S. V. (2010). Using principal components and factor analysis in animal behaviour research: Caveates and Guidelines. *Ethol.*, 116: 472-480
- Cannon, W. B. (1929). Organization for physiological homeostasis. *Physiol. Rev.*, 9: 399–431
- Careau, V., Thomas, D., Pelletier, F., Turki, L., Landry, F., Garant, D., Réale, D. (2011). Genetic correlation between resting metabolic rate and exploratory behaviour in deer mice (*Peromyscus maniculatus*). *J. Evol. Biol.*, 24: 2153-2163
- Cattell, R. B. (1966). The scree test for the number of factors. *Multivar. Behav. Res.*, 1: 245-276
- Clune, J., Mouret, J.-B., Lipson, H. (2013). The evolutionary origins of modularity. *Proc. R. Soc. Lond. Biol.*, 280: 20122863
- Comrey, A. L., Lee, H. B. (1992). A first course in Factor Analysis. New York, USA. Psychology Press
- Costello, A. B., Osborne, J. W. (2005). Best practices in exploratory Factor Analysis: Four recommendations for getting the most from your analysis. *PARE*, 10: 1-9
- Čukić, I., Bates, T. C. (2014). Heart rate variability and adult personality: A nationally representative study. *Personal. Individ. Differ.*, 60: 31
- Dall, S. R. X., Houston, A. I., McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.*, 7: 734-739

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

Desire, S., Turner, S. P., D'Eath, R. B., Doeschl-Wilson, A. B., Lewis, C. R. G., Roehe, R. (2015). Analysis of the phenotypic link between behavioural traits at mixing and increased long-term social stability in group-housed pigs. *Appl. Anim. Behav. Sci.*, 166: 52-62

Ferrari, S., Benhaïm, D., Colchen, T., Chatain, B., Bégout, M.-L. (2014). First links between self-feeding behaviour and personality traits in European seabass, *Dicentrarchus labrax*. *Appl. Anim. Behav. Sci.*, 161: 131-141

Finkemeier, M.-A., Langbein, J., Puppe, B. (2018). Personality research in mammalian farm animals: Concepts, measures, and relationship to welfare. *Front. Vet. Sci.*, 5:131

Finkemeier, M.-A., Trillmich, F., Guenther, A. (2016). Match-mismatch experiments using photoperiod expose developmental plasticity of personality traits. *Ethol.*, 122: 80-93

Foris, B., Zebunke, M., Langbein, J., Melzer, N. (2018). Evaluating the temporal and situational consistency of personality traits in adult dairy cattle. *Plos One*, 13: 1-16

Forkman, B., Boissy, A., Meunier-Salaün, M.-C., Canali, E., Jones, R. B. (2007). A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiol. Behav.*, 92: 340-374

Gosling, S. D., John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Curr. Dir. Psychol. Sci.*, 8: 69-75

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

Gorsuch, R. L. (1983). Factor Analysis. Hillsdale, N. J.: Erlbaum

Graunke, K. L., Nürnberg, G., Repsilber, D., Puppe, B., Langbein, J. (2013). Describing Temperament in an Ungulate: A Multidimensional Approach. *Plos One*, 8: 1-12

Haage, M., Bergvall, U. A., Maran, T., Kiik, K. & Angerbjörn, A. (2013). Situation and context impacts the expression of personality: the influence of breeding season and test context. *Behav. Process.*, 100: 103-109

Haskell, M. J., Simm, G., Turner, S. P. (2014). Genetic selection for temperament traits in dairy and beef cattle. *Front Genet.*, 5: 368

Hedlund, L., Løvlie, H. (2015). Personality and production: Nervous cows produce less milk. *J. Dairy Sci.*, 98: 5819-5828

Houle, M. S., Billman, G. E. (1999). Low-frequency component of the heart rate spectrum: a poor marker of sympathetic activity. *Am. J. Physiol. Heart Circ. Physiol.*, 276: 215–223

Huang, P., Kimball, R. T., St Mary, C. M. (2018). Does the use of a multi-trait, multi-test approach to measure animal personality yield different behavioural syndrome results? *Behaviour*, 155: 115-150

Kaiser, H. F. (1960). The application of electronic computers to factor analysis. *Educ. Psychol. Meas.*, 20:141-151

Kaiser, H. F., Rice, J. (1974). Little Jiffy, Mark IV. *Educ. Psychol. Meas.*, 34: 111-117

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C., G., Hopster, H., De Jong, I. C., Ruis, M. A. W., Blokhuis, H. J. (1999). Coping styles in animals: current status in behaviour and stress-physiology. *Neurosci. Biobehav. Rev.*, 23: 925-935

Korte, S. M., Beuving, G., Ruesink, W., Blokhuis, H. J. (1997). Plasma catecholamine and corticosterone levels during manual restraint in chicks from a high and low feather pecking line of laying hens. *Physiol. Behav.*, 62: 437–441

Krause, A., Puppe, B., Langbein, J. (2017). Coping style modifies general and affective autonomic reactions of domestic pigs in different behavioral contexts. *Front. Behav. Neurosci.*, 11

Langbein, J., Nürnberg, G., Manteuffel, G. (2004). Visual discrimination learning in dwarf goats and associated changes in heart rate and heart rate variability. *Physiol. Behav.*, 82: 601-609

Langbein, J., Puppe, B. (2004). Analysing dominance relationships by sociometric methods—a plea for a more standardised and precise approach in farm animals. *Appl. Anim. Behav. Sci.*, 87: 293-215

Langbein, J., Siebert, K., Nürnberg, G., Manteuffel, G. (2007). Learning to learn during visual discrimination in group housed dwarf goats (*Capra hircus*). *J. Comp. Psychol.*, 121: 447-456

Lansade, L., Bouissou, M.-F., Erhard, H. W. (2008). Fearfulness in horses: A temperament trait stable across time and situations. *Appl. Anim. Behav. Sci.*, 115: 182-200

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

- Lansade, L., Philippon, P., Hervé, L., Vidament, M. (2016). Development of personality tests to use in the field, stable over time and across situations, and linked to horses' show jumping performance. *Appl. Anim. Behav. Sci.*, 176: 43-51
- Malik, M., Camm, A. J. (1995). Heart Rate Variability. Armonk, NY: Futura Publishing Company
- Martins, C. I. M., Schrama, J. W., Verreth, J. A. J. (2005) The consistency of individual differences in growth, feed efficiency and feeding behaviour in African catfish *Clarias gariepinus* (Burchell 1822) housed individually. *Aquacult. Res.*, 36: 1509–1516
- Maynard Smith, J. (1982). Evolution and the Theorie of Games. Cambridge, Cambridge University Press
- Mendl, M., Burman, O. H. P., Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Philos. Trans. R. Soc. London. Biol.*, 277: 2895-2904
- Murphy, E., Nordquist, R. E., van der Staay, F. J. (2014). A review of behavioural methods to study emotion and mood in pigs, *Sus scrofa*. *Appl. Anim. Behav. Sci.*, 159: 9-28
- Nawroth, C., Prentice, P. M., McElligott, A. G. (2017). Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. *Behav. Process.*, 134: 43-53

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

Neave, H. W., Costa, J. H. C., Weary, D. M., von Keyserlingk, M. A. G. (2018).

Personality is associated with feeding behavior and performance in dairy calves.

J. Dairy Sci., 101: 7437-7449

van Oers, K., Drent, P. J., Jong, G. D., Noordwijk, A. J. (2004). Additive and nonadditive genetic variation in avian personality traits. *Heredity*, 93: 496-503

Oesterwind, S., Nürnberg, G., Puppe, B., Langbein, J. (2016). Impact of structural and cognitive enrichment on the learning performance, behavior and physiology of dwarf goats (*Capra aegagrus hircus*). *Appl. Anim. Behav. Sci.*, 177: 34-41

Penke, L., Dennissen, J.J.A. & Miller, G.F. (2007). The evolutionary genetics of personality. *Eur. J. Pers.*, 21: 549–587

Perals, D., Griffin, A.S., Bartomeus, I., Sol, D. (2017). Revisiting the open-field test: what does it really tell us about animal personality? *Anim. Behav.*, 123: 69-79

Porges, S. W. (1995). Cardiac vagal tone: A physiological index of stress. *Neurosci. Biobehav. Rev.*, 19: 225-233

Pyter, L. M., Nelson, R. J. (2006). Enduring effects of photoperiod of affective behaviours in Siberian Hamsters (*Phodopus sungorus*). *Behav. Neurosci.*, 120: 125-134

Réale, D., Reader, S. M., Sol, D., McDougall, P.T., Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.*, 82: 291-318

Réale, D., Dingemanse, N. J. (2012). Animal Personality. eLS

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

Sih, A. (2013). Frontiers on the interface between behavioral syndromes and social behavioral ecology. In C. Claudio, & D. Maestriperi (Eds.), *Animal personalities: Behavior, physiology and evolution* (pp. 221e251). Chicago, IL: University of Chicago Press.

Sih, A., Bell, A., Chadwick Johnson, J. (2004). Behavioural syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.*, 19: 372-378

Sinn, D. L., Gosling, S. D., Moltschaniwskyj, N. A. (2008). Development of shy/bold behaviour in squid: context-specific phenotypes associated with developmental plasticity. *Anim. Behav.*, 75: 433-442

Stamps, J. A. (2007) Growth-mortality tradeoffs and ‘personality’ traits in animals. *Ecol. Lett.*, 10: 355–363

Stirling, D. G., Réale, D., Roff, D. A. (2002). Selection, structure and the heritability of behaviour. *J. Evol. Biol.*, 15: 277-289.

Sutherland, M. A., Rogers, A. R., Verkerk, G. A. (2012). The effect of temperament and responsiveness towards humans on the behavior, physiology and milk production of multi-parous dairy cows in a familiar and novel milking environment. *Physiol. Behav.*, 107: 329-337

Visser, E. K., van Reenen, C. G., Engel, B., Schilder, M. B. H., Barneveld, A., Blokhuis, H. J. (2003). The association between performance in show-jumping and personality traits earlier in life. *Appl. Anim. Behav. Sci.*, 82: 279-295

Chapter 3 – Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses

Wilson, D. S., Clark, A. B., Coleman, K., Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends Ecol. Evol.*, 9: 442-446

Zebunke, M., Repsilber, D., Nürnberg, G., Wittenburg, D., Puppe, B. (2015). The backtest in pigs revisited—An analysis of intra-situational behaviour. *Appl. Anim. Behav. Sci.*, 169: 17-25

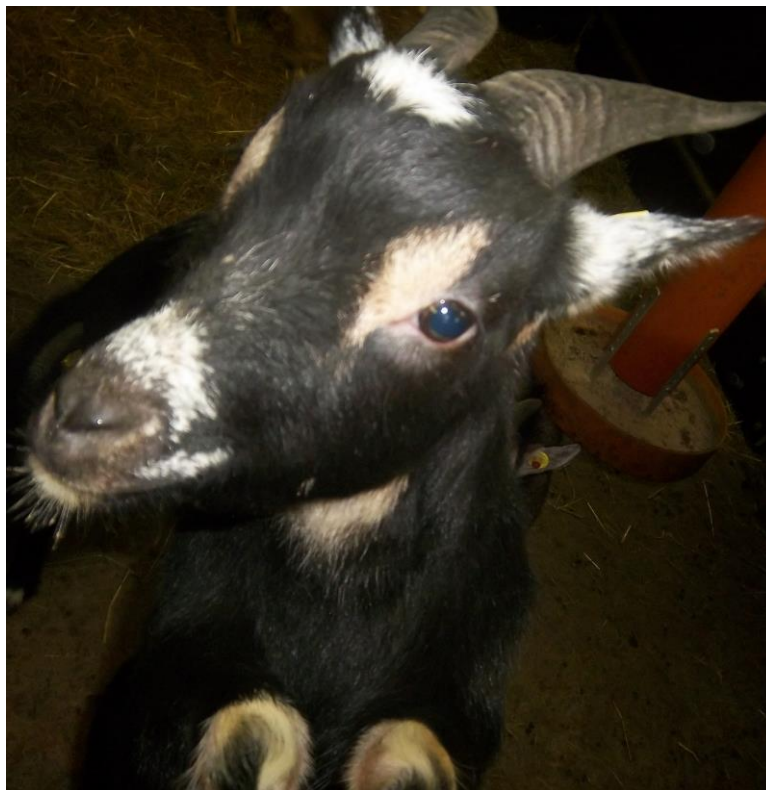
Zebunke, M., Nürnberg, G., Melzer, N., Puppe, B. (2017). The backtest in pigs revisited – inter-situational behaviour and animal classification. *Appl. Anim. Behav. Sci.*, 194: 7-13

Zipser, B., Kaiser, S., Sachser, N. (2013). Dimensions of personalities of guinea pigs. *Ethol.*, 119: 1-13

**Chapter 4 – Personality traits affect learning performance in
dwarf goats (*Capra hircus*)**

Chapter FOUR:

**Personality traits affect learning performance in
dwarf goats (*Capra hircus*)**



Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

This chapter is redrawn from *Frontiers in Veterinary Science*: "Personality traits affect learning performance in dwarf goats (*Capra hircus*)".

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Marie-Antoine Finkemeier and Annika Krause performed the experiments and analysed the data together with Armin Tuchscherer. Marie-Antoine Finkemeier and Annika Krause wrote the manuscript with the support of and in agreement with her supervisors Prof. Dr Birger Puppe and Dr. Jan Langbein.

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Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

4.1 Abstract

A wide range of species exhibit time- and context-consistent interindividual variation in a number of specific behaviours related to an individual's personality. Several studies have shown that individual differences in personality-associated behavioural traits have an impact on cognitive abilities. The aim of this study was to investigate the relationship between personality traits and learning abilities in dwarf goats. The behaviour of 95 goats during a repeated open field (OF) and novel object test (NO) was analysed, and two main components were identified using principal component analysis: boldness and activity. In parallel, the goats learned a 4-choice visual initial discrimination task (ID) and three subsequent reversal learning (RL) tasks. The number of animals that reached the learning criterion and the number of trials needed (TTC) in each task were calculated. Our results show that goats with the lowest learning performance in ID needed more TTC in RL1 and reached the learning criterion less frequently in RL2 and RL3 compared to animals with better learning performance in ID. This suggests a close relationship between initial learning and flexibility in learning behaviour. To study the link between personality and learning, we conducted two analyses, one using only data from the first OF- and NO-test (momentary personality traits), while the other included both tests integrating only animals that were stable for their specific trait (stable personality traits). No relationship between personality and learning was found using data from only the first OF- and NO-test. However, stability in the trait boldness was found to have an effect on learning. Unbold goats outperformed bold goats in RL1. This finding supports the general hypothesis that bold animals tend to develop routines and show less flexibility in

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the context of learning than unbold individuals. Understanding how individual personality traits can affect cognitive abilities will help us gain insight into mechanisms that can constrain cognitive processing and adaptive behavioural responses.

Keywords

Discrimination learning, personality, cognition, open-field test, novel-object test, serial reversal, goats.

4.2 Introduction

A wide range of species exhibit time- and context-consistent interindividual variation in behaviours, such as activity, exploration, boldness, aggressiveness and sociability, which are all traits related to an individual's personality (1-5). More than 100 years ago, Pavlov was the first to suggest that canine personality could also be a marker for differential performance in associative learning (6). Regardless, potential relationships between animal personality and interindividual differences in cognitive abilities have been relatively understudied in nonhuman animals (7, 8); however, in the last decade, they have attracted new interest across a wide range of taxa, while the causes and strengths of this variation are still under discussion (9).

Proximate factors (attention, selectivity, persistence, and experience) represent behavioural mechanisms that have a major impact on individual learning and cognitive performance (10). Current frameworks that determine behavioural phenotypes that are stable across time and context, such as animal personality (1,

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11), temperament (12), coping style theory (13) and behavioural flexibility (14), which are all interrelated (15) have been hypothesized to be functionally related to individual differences in learning and were used to explain consistent within-species interindividual variation in cognitive abilities such as learning and memory. In this way, personality may affect performance in cognitive tasks in that individual variation in attention and encounter rates of environmental stimuli act to either facilitate or inhibit learning (6). It is assumed that natural selection could have parallel effects on cognition and animal personality simultaneously, leading to a correlation between cognition and various personality traits, as both follow a continuum between fast and slow phenotypes (16). The link between variation in personality and cognition forms the basis of the cognitive style hypothesis and is centred on a speed-accuracy trade-off that assumes that individuals may apply different cognitive styles (fast or accurate) based on personality or coping style (7, 17). Proactive individuals, which tend to be bolder, more active, neophilic and fast explorers, learn at higher speeds but at the cost of accuracy. They are likely to become entrenched in a previously learned strategy and thus are less flexible when confronted with new challenges compared to reactive individuals, who are characterized as being rather shy, neophobic, and slow explorers (12, 13, 18). Furthermore, proactive animals are more rigid and fast in decision-making, while reactive animals are thought to be more attentive to environmental changes and stimuli. Attention to environmental cues and cognitive ability are positively related to behavioural flexibility and the ability of an individual to adjust to an ever-changing environment (6, 19). In contrast to much empirical work demonstrating a relationship between personality and learning abilities in different

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species (20-22), some recent authors cast doubt on a general parallelism between behavioural and cognitive dispositions, as some studies failed to show this link (8, 9, 23-25). For instance, while fast-exploring great tit males (*Parus mayor*) showed more flexible learning abilities than slow-exploring males, female slow explorers outperformed fast explorers, showing a sex dependency in the relationship between personality types and learning (26). Two different zebrafish (*Danio rerio*) strains classified as proactive and reactive were able to learn and recall the fearful association of an associative fear conditioning task. While both coping style strains showed no differences in memory, reactive zebrafish acquired fear memory at a significantly faster rate than proactive zebrafish (27). Another study on narrow-striped mongooses (*Mungotictis decemlineata*) tested the relationship between learning performance, social information and individual differences in boldness: learning performance of seven wild female groups (of two to six individuals each) was tested with an artificial feeding box using a demonstrator-observer paradigm. Bold individuals as well as individuals in groups with demonstrators were faster in learning the task, while individuals without a demonstrator learned the task more slowly, indicating an interaction between personality traits, use of social cues and learning performance (28). In male African striped mice (*Rhabdomys pumilio*), proactive individuals (measured by boldness, activity and exploration) performed better than reactive males in two learning tests: a string-pulling task to obtain food and a door-opening task to reach the nest (29). On the other hand, in guinea pigs and female guppies (*Poecilia reticulata*) exploration, sociability and boldness were not intercorrelated with

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learning performance (30, 31), again indicating that relationships between personality traits and learning are quite diverse in a number of different species.

In recent years, interest in individual differences in a variety of taxa has increased, including in livestock research (reviewed by 15). There is mounting evidence that these differences play an important role in various contexts in pigs (32-34), cows (35-37), horses (38-40), chickens (41, 42) and goats (43, 44). General knowledge about the cognitive capabilities of livestock (i.e., their ability to acquire, process, store and use information) is of great interest, as cognitive capacities have a major impact on how they are able to interact with their environment (45). Farm animals see themselves confronted with a multitude of challenges (i.e., automated feeding regimes, inflexible housing conditions, rigid management practices) during their lifetimes that have very specific and individual cognitive requirements. To date, numerous studies have focused on quantifying and understanding species-specific cognitive abilities and learning skills in farm animals. For instance, in a visual discrimination task, pigs were able to discriminate between two visual stimuli, and even 1/3 performed well in the reversal task (46). In an acoustic discrimination task, pigs were trained to visit the feeding site after discriminating an individual acoustic signal to obtain a food reward (47). In horses, observers were allowed to watch demonstrators opening a feeding apparatus: While young and lower ranking horses learned the task, older and higher ranking horses did not, showing an age and rank dependency in learning (48). Chickens were able to complete visual occlusion, have biological motion perception and were able to discriminate object and spatial representations, to name a few (reviewed by 42). Meyer and colleagues used an automated learning device that presents artificial

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symbols via a screen and found that goats have clear categorization capacities (49). They were also successful in object permanence tasks (50) and were seeking cognitive challenges by choosing to work for a reward even if they have the possibility of getting it for free, named ‘contrafreeloading’ (51, 52). In playback experiments, it has been shown that goats were able to recall offspring vocalizations for at least one year (53, 54). Training a series of visual discrimination tasks showed that goats were able to improve their performance in a learning-to-learn process and develop a learning set (55). In summary, a wide range of cognitive tests has been applied in farm animals to assess a range of cognitive traits. However, differences in cognitive ability between and within individuals of the same species across repeated measurements or across different experimental conditions have also been noted but the causes of these differences remain largely unexplained (7, 8, 45). To date, there is only limited knowledge about a phenotypic link between individual personality and learning capacities in farm animals.

In the current study, we investigated the potential relationship between specific personality traits and learning performance in female dwarf goats. A 4-choice visual discrimination task and three subsequent reversal learning tasks were applied to characterize the learning abilities of the goats. Reversal learning paradigms are commonly used to test behavioural flexibility, a type of phenotypic plasticity that can influence how animals cope with environmental changes. To investigate the relationship between the consistency of certain personality traits and learning, first only data from the first personality test and then the combined

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data from both personality tests were used separately to test the respective effect on learning performance.

First of all, we expected a relationship between learning and reversal learning in that good learners in the visual discrimination task would need more trials to reach the learning criterion in the reversal learning task and vice versa. This is based on the findings of other studies showing that fast learners exhibited lower behavioural flexibility and, therefore, performed worse in a reversal learning paradigm compared to slow learners (56).

Second, we expected no interrelation between the personality traits deriving only from the first personality test and discrimination learning or reversal learning. On the other hand, taking consistent personality traits into account (data from both personality tests), we expected the more active and bold individuals to disproportionately achieve the learning criterion in the discrimination task faster while inactive and unbold individuals would perform better in the reversal learning tasks, in line with studies regarding behavioural flexibility in the context of coping style (7, 57).

4.3 Animals, Materials and Methods

4.3.1 Animals and Housing

The experiments were conducted with 108 juvenile female Nigerian dwarf goats (*Capra aegagrus hircus*) bred from a line at the Leibniz Institute for Farm Animal Biology (FBN, Dummerstorf, Germany). Due to our breeding program, two experimental runs were conducted per year. From birth to weaning (Figure 1),

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goats were housed in mixed groups consisting of three to five adult females and their male and female kids. The pens (12 m²) were littered with wheat straw as bedding material and contained a hayrack and a round feeder to deliver concentrate (800 g to 1000 g twice per pen, Vollkraft, Mischfutterwerk GmbH, Güstrow, Germany). Hay and water were provided *ad libitum*. After weaning (seven weeks of age), female goat kids were kept in groups of up to 16 animals per group in pens as described above, with an additional climbing rack as an enrichment activity. All animals were ear tagged and wore a collar with a responder (Urban, Wuesting, Germany) for individual recognition at the free accessible automated learning device. The operating principle of the learning device has been described in detail elsewhere (49). In the following weeks, the kids were shaped to the learning device. During this time, we conducted repeated OF- and NO-tests (Figure 1). At 12 weeks of age, kids were kept in groups of up to eight animals per group in pens as described above. As the number of goat kids was different in every lambing season, runs one and two of the study were conducted with 32 kids each, run three with 14 kids and run four with 30 kids. From here on they will be referred to as goats.

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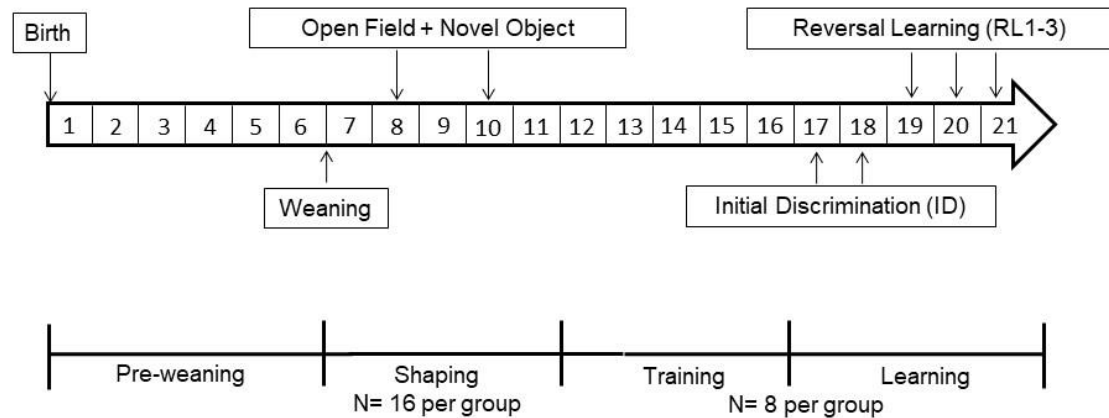


Figure 1: Timeline of the experimental procedure test sequence, housing condition and age of the dwarf goats (given in weeks).

4.3.2 Behavioral Testing

To obtain the respective personality traits, we conducted repeated OF- and NO-tests. Repetitions were performed after 14 days as Takola et al. (58), who conducted a meta-analysis including 115 studies, found that repeatability of responses to novel objects was significant and greater in short-term studies than in long-term studies. In both tests, each goat stayed alone in an arena for 5 minutes. For both tests, we used an arena (3 m×4.8 m) with opaque walls (2 m high) in a different part of the barn, which was separated from the home pens by two doors.

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The arena was divided into 12 identical segments (1×1.2 m), which were indicated by white lines on the floor. A fully enclosed start box (1 x 1 x 1 m) was connected to the arena and had a guillotine door. For the first NO-test, a traffic cone, and for the second test, a medicine ball was used as the object. To ensure that the object could not be displaced by the focal animal, the object was fixed with a chain hanging from the ceiling. All tests were video recorded (Panasonic WV-CP500). For both tests and both test repetitions, we recorded 82 behavioural measures for each subject coded with Observer XT (Version 12, Noldus Information Technology, The Netherlands). The OF- and NO-tests were conducted on two consecutive days, the same for the repetitions. Further details concerning the testing procedure and the recorded behavioural measures were described by Finkemeier et al. (44).

4.3.3 Visual Discrimination Learning

4.3.3.1 Shaping

Over six weeks, we shaped the goats stepwise to the learning device. The learning device was integrated into the home pen with free access for all goats 24/7. We used drinking water as a reward (30 ml for each correct choice), which was only accessible at the learning device. For detailed information regarding the shaping procedure, see Langbein et al. (59). In short, we started with a float switch hanging in a water bowl with a button directly above the switch. By pressing the button, the goats could add 30 ml of water to the bowl. After one week, the float switch was removed, and we installed first one, later two buttons 20 cm above the bowl, one of which had to be pressed to fill water in the bowl. The reward button

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was changed weekly and at the end of the shaping phase, daily. At the end of the shaping phase, all goats were able to push the buttons and ensure their water demand independently. According to the veterinary and food control government, the daily water demand of dairy goats ranges between 1.5 to 4 litres and based on our experience from previous learning experiments in dwarf goats, we can expect between 23.7 and 28.5 number of drinking actions (30 ml per action), which equals daily water consumption between 0.83 and 0.99 litres (51).

4.3.3.2 Training

After completing shaping, goats were regrouped to up to eight animals per group into identically equipped pens, including the learning device. The learning device consisted of a 15-inch LCD screen (resolution of 640 x 480 pixels) behind a transparent acrylic panel. The screen was divided into four virtual sectors. In each sector, we displayed a different symbol (size ~ 7 cm²). To allow the goats to choose one of the symbols, four press buttons were mounted on the acrylic panel, one button beside each sector. Figure 2 gives a schematic overview of the compartment with the learning device. For a detailed description of the training procedure, see Langbein et al. (59).

During the first week, the goats were presented with a white screen, and all four buttons were rewarded. Next, the goats were presented with the first two training sets (Figure 3 A + B). The symbol to learn was marked by a frame. The position of the symbols changed randomly after each trial. Each set was presented for 14 days. Similar to the shaping phase, goats were rewarded with 30 ml water for each correct choice. The device was accessible 24/7 for all goats. Even animals that did

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not learn the task were able to obtain enough water by increasing the number of trials at the device. At the end of training (60), all goats were able to use the device properly and reached the defined learning criterion (please see the Data analysis and statistics section for further details).

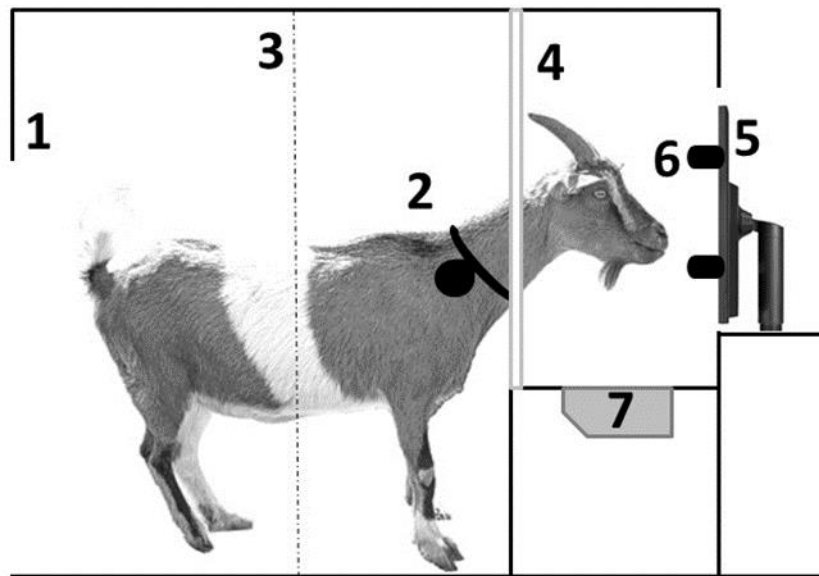


Figure 2: Lateral view of a goat inside the compartment with learning device: 1 = entrance (there is only space for one goat at a time at the device to avoid observational learning by the pen mates); 2 = collar with responder for individual recognition at the device; 3 = light beam indicating when a goat leaves the device; 4 = yoke to put only the head through; 5 = computer screen; 6 = buttons to choose a stimulus; 7 = water bowl for reward dispense.

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4.3.3.2 Initial Discrimination Learning and Reversal Learning

To investigate the impact of personality on the learning performance of the goats, a new 4-choice discrimination task was presented (Figure 3C). This initial discrimination task (ID) was trained for 14 days. To investigate the effect of personality on the flexibility of learning behaviour, three reversal-discrimination tasks were subsequently presented (RL1-3). The same set of symbols was used as in ID, but in each reversal task, a different one of the three previously unrewarded stimuli was now the stimulus to be discriminated (Figure 3D-F). All other conditions were identical to Training.

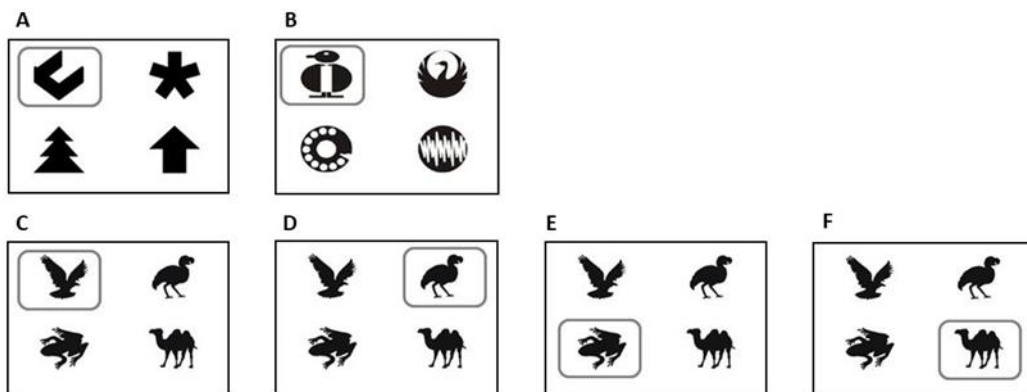


Figure 3: Symbol sets for training: training set 1 (A); training set 2 (B). Symbol sets during learning and reversal learning tasks: Initial discrimination learning task (ID, C) and the three reversal learning tasks: reversal learning 1 (RL1, D); reversal learning 2

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(RL2, E); reversal learning 3 (RL3, F). The rewarded symbols are marked with a square (for illustration purposes only). The position of the different stimuli changed after each individual choice.

4.4 Ethical Note

All animal care and experimental procedures were performed in accordance with the German welfare requirements for farm animals and the “Guidelines for the treatment of animals in behavioural research and teaching” (61). All procedures involving animal handling and treatment were approved by the Committee for Animal Use and Care of the Ministry of Agriculture, Environment and Consumer Protection of the federal state of Mecklenburg-Vorpommern, Germany (Ref. 7221.3-2-005/14).

4.5 Data Preparation

From 108 tested goats, we excluded those for whom technical issues concerning the learning device occurred (e.g. technical failure of the software and hardware of the learning device and/or loss of transponder for individual identification of the animal.). Finally, a total of 95 goats were included in all further analyses.

The learning performance of the goats was characterized by two steps: First, we analysed whether the animals reached the learning criterion in ID and in RL1-3, respectively and, if so, we analysed how many trials they needed to do so (trials to criterion, TTC). Given the four-symbol choice task where chance responding to a given symbol is 25%, the criterion for a statistically significant level ($p < 0.05$) of correct responding was determined according to the Binomial test when $n = 20$ and $p = 0.25$, to be 46% of correct choices in at least two consecutive blocks of 20 trials

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(learning criterion). This reflects the same learning success compared to the learning criterion of 75% in similar studies applying the common two-choice design (55).

Based on the TTC, we calculated the respective quartiles for the learning performance in ID (Table 1) to test its impact on learning performance in RL1-3. Consequently, Q1 indicated animals with the highest learning performance (lowest number of TTCs) in ID, and Q4 indicated the animals with the lowest learning performance (highest number of TTCs) in ID.

The personality traits *boldness* and *activity* were calculated by conducting a principal component analysis (PCA) for the initial OF- and NO-tests and their respective repetitions (please see 44 for further details). We selected 11 behavioural measures (see supplementary material) out of 82 identical for both test periods, which were not affected by season and body weight and/or are commonly used in animal personality studies (44, 62, 63). Using these measures, we calculated one PCA for each test repetition (PCA1+PCA2). We found two main PCs in PCA1 (overall MSA=0.7). The first PC (PC1a; eigenvalue=3.5) consists of four measures with loadings above 0.7 and below -0.7 describing the interaction with the novel object. The second PC (PC1b; eigenvalue=2) consists of two measures with loadings above 0.7 and below -0.7 describing active-like behaviour. We labelled PC1a “*boldness*” and PC1b “*activity*”. The two PCs explained 32% and 18.2% of the variation in the data, respectively. In PCA2 (overall MSA=0.71), we found two similar main principal components, with the first describing the interaction with the novel object (PC2a; eigenvalue=3.7) and the second describing active-like behaviour (PC2b; eigenvalue=1.3), explaining

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34% and 12% of the variation in the data, respectively. Finally, we calculated PC scores (from -3 to +3) for each personality trait for each animal in each of the two test periods, where each individual score was calculated from the standardized original data and the respective loadings of each PC separately for PCA1 and PCA2. These scores were used for any further statistical analysis.

We tested the impact of the personality traits on learning performance and characterized *momentary* and *stable* personality traits using either the first or both OF- and NO-tests as the basis for the calculations. Using the personality scores resulting from the PCA1 (*activity* and *boldness* scores from -3 to +3), the respective quartiles were calculated to test the impact of a *momentary* personality trait on cognitive performance (see Table 1 for *activity* and *boldness* quartiles). Conversely, to investigate whether consistency in these personality traits had an effect on learning performance, we selected animals that showed stable *activity* and *boldness* scores in the repeated OF- and NO-tests (= *stable* personality traits). Stability was met if the scores from the first and second OF- and NO-tests were similar (both either positive or negative) for each personality trait (including a protection zone of ± 0.5 from the zero line).

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Table 1: Calculation of the respective quartiles concerning A the learning performance (number of TTC) in the initial discrimination task (ID); B the *activity* scores based on the results of the principal component analyses of the first open field/novel object test (44); and C the *boldness* scores based on the results of the principal component analyses of the first open field/novel object test. Respective lower and higher limits as well as the category description and number of animals per quartile are indicated.

<i>A Quartile limits based on the number of TTCs</i>				
Quartile label	lower limit	higher limit	description	n (animals)
Q1	20	20	„high performer“	24
Q2	40	80	„good performer“	22
Q3	100	200	„poor performer“	24
Q4	220	1700	„low performer“	24
<i>B Quartile limits based on activity scores</i>				
Quartile label	lower limit	higher limit	description	n (animals)
A1	-3	-0.5248	„very inactive“	24
A2	-0.5249	0.0459	„inactive“	23
A3	0.046	0.6414	„active“	24
A4	0.6415	3	„very active“	24
<i>C Quartile limits based on boldness scores</i>				
Quartile label	lower limit	higher limit	description	n (animals)
B1	-3	-0.9164	„very unbold“	24
B2	-0.9165	-0.0655	„unbold“	24
B3	-0.0656	0.7794	„bold“	23
B4	0.7795	3	„very bold“	24

4.6 Statistical Analysis

All statistical analyses were conducted in SAS® 9.4 (SAS Institute Incorporated, Cary, North Carolina, USA). The data were evaluated by various analyses of variance (ANOVAs) using the GLIMMIX procedure in SAS (Version 9.4 for Windows, SAS Institute Inc., Cary, NC, USA).

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4.6.1 Relationship Between Learning Performance and Reversal Learning

To measure the impact of learning performance in ID, allocated among the four quartiles, on the overall achievement of the learning criterion during RL1-3, we used the variance function for the binomial distribution (binary data) and the logit link function in the statistical model. For more detailed analyses of learning, we ran a model with TTC in RL1-3 as our response variable and evaluated the effect of learning performance in ID (allocated to the respective quartiles, see above), task (RL1, RL2, RL3) and their interaction, which were fitted as fixed effects. Both models contained motherID, pens and season nested in replicates as random effects.

4.6.2 Impact of *Momentary* Personality Traits on Cognitive Performance

The impact of the quartiles of *activity* (A1-A4; from very inactive to very active) and *boldness* (B1-B4; from very unbold to very bold) in PCA1 as fixed factors was tested on the number of animals reaching the learning criterion and on the TTC in RL1-3. In each model, motherID, pen and season nested in replicates were included as random effects.

4.6.3 Impact of *Stable* Personality Traits on Learning Performance

To investigate whether consistency in specific personality traits had an effect on learning performance, we selected animals that showed stable *activity* and

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boldness scores in the repeated OF- and NO-tests. Out of 95 animals, 32 animals showed a stable value in *activity* (16 active, 16 inactive), and 42 animals showed a stable value in *boldness* (16 bold, 26 unbold) across the repeated OF- and NO-tests. The selected animals were then assigned to the groups *stable in activity* (inactive or active) or *stable in boldness* (unbold or bold), which were used as fixed effects on the TTC in ID and RL1-3 in the statistical model. In these models, motherID, replicates and season were included as random effects.

Least squared means (LSMs) and their standard errors (SEs) were computed for the fixed effects in all models, and pairwise differences in the LSM were tested using the Tukey–Kramer correction. All analyses included the animal as a repeated factor in the random statement, and mean differences with $p < 0.05$ were considered significantly different.

4.7 Results

4.7.1 Relationship Between Learning Performance and Reversal Learning

A significant effect of learning performance in ID (Q1–Q4) was found on the number of goats that reached the learning criterion in RL2 ($F_{3,41}=4.56$, $p < 0.01$) and RL3 ($F_{3,41}=5.05$, $p < 0.01$), while a tendency was found concerning RL1 ($F_{3,41}=2.48$, $p < 0.1$). In other words, 46% of the low performers in ID (Q4) were not able to learn the first reversal task ($n=11$). This effect was significant for the second (71%; $n=17$) and third reversal tasks (79%; $n=19$). Goats with the lowest learning performance in ID (Q4) reached the learning criterion in RL2 less frequently compared to goats with only poor learning performance in ID (Q3)

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($p < 0.01$) and also tend to reach the learning criterion less frequently compared to goats with good (Q2, $p < 0.1$) and very good (Q1, $p < 0.1$) learning performance in ID. Additionally, low performers in ID (Q4) reached the learning criterion in RL3 less frequently compared to all other groups of learning performance in ID (Q1-Q3), as shown in Figure 4A (Q1 and Q3: $p < 0.05$, Q2: 0.01). Regarding the animals that successfully reached the learning criterion in RL1, RL2 or RL3, we found an effect of learning performance in ID on TTC in the reversal tasks ($F_{3,145} = 5.21$, $p < 0.001$). Pairwise comparisons indicate that low performers (Q4) needed significantly more TTC than the other learning groups (Q1-Q3) in RL1 ($p < 0.01$, Figure 4B), while this difference is not apparent in RL2 and RL3 (all $p > 0.1$). Furthermore, we found a significant effect of task on TTC ($F_{2,145} = 20.3$, $p < 0.001$) in that the animals significantly reduced their TTC in RL3 compared to RL1 and RL2 ($p < 0.001$, respectively) that was mainly apparent in Q4 regarding the TTC in RL3 compared to RL1 ($p < 0.05$). However, the interaction between learning performance in the ID and RL tasks revealed no significant effect.

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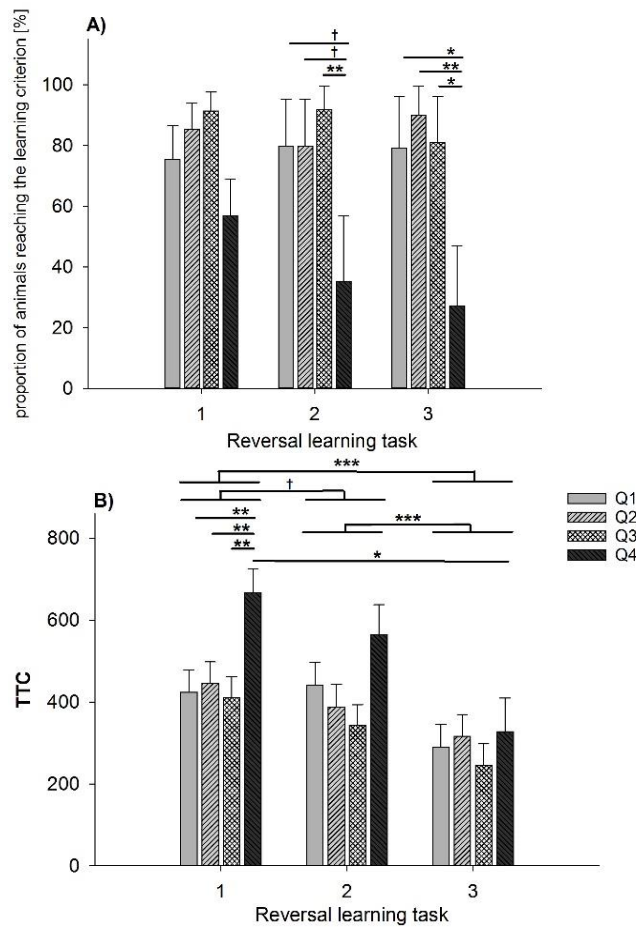


Figure 4: Performance of different groups of goats in the reversal learning task: A) proportion of goats that reached the learning criterion during reversal tasks RL1-RL3. B) Number of trials to reach the learning criterion (TTC) in reversal tasks RL1-RL3. The groups Q1-Q4 indicate the learning performance during the initial discrimination task (ID): Q1: TTC in ID=20, Q2: TTC in ID=40-80, Q3: TTC in ID=100-200, Q4: TTC in ID>220. Data are presented as least squared means and standard errors (LSM $\pm$ SE); * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4.7.2 Impact of *Momentary* Personality Traits on Learning Performance

The statistical analysis indicated no significant effects of *activity* (A1-A4) or *boldness* (B1-B4), based on only the first conducted OF- and NO-tests, on the

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number of goats that reached the learning criterion during RL1-3. Furthermore, *activity* and *boldness* did not show any significant effects on the TTC either during ID nor during RL1-3.

4.7.3 Impact of *Stable* Personality Traits on Learning Performance

We found no significant effects of *stability* in *activity* or *boldness* on the number of goats that reached the learning criterion in RL1-3. Regarding TTC, *stability in activity* (inactive vs. active) was not found to have a significant effect on TTC in ID or RL1-3 (Figure 4A). In contrast, *stability in boldness* (unbold vs. bold) significantly affected TTC in RL1 ($F_{1,7}=11.36$, $p<0.05$). As shown in Figure 5B, bold animals exhibited a lower learning performance (higher number of TTCs) in RL1 than unbold animals. This effect was not observed in RL2 and RL3.

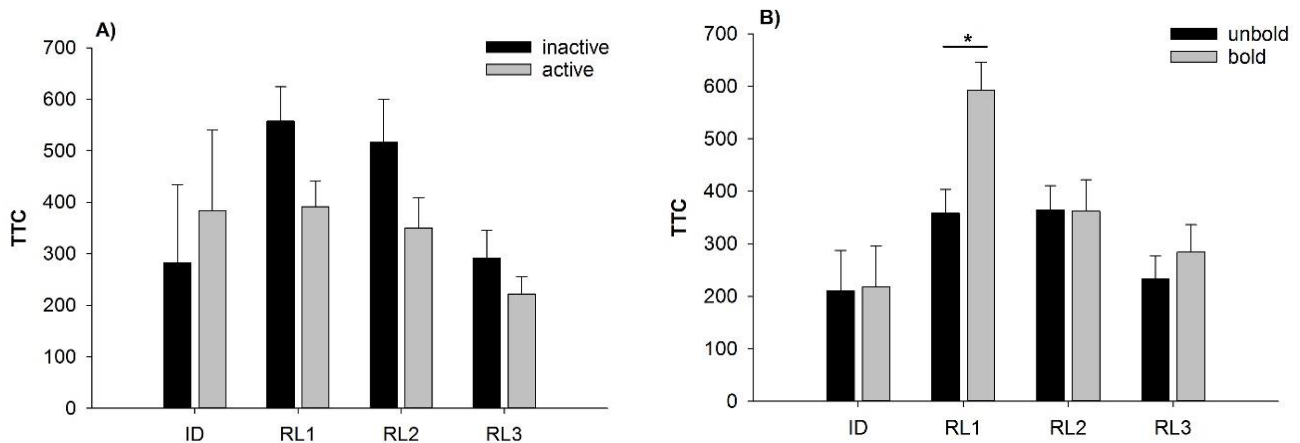


Figure 5: Performance of goats with *stable* personality scores in *activity* (Panel A) or *boldness* (Panel B) in the reversal learning tasks: A) number of trials to reach the learning criterion in the reversal tasks RL1-RL3 of goats assigned to the inactive (black bars) vs.

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active groups (grey bars). B) Number of trials to reach the learning criterion in the reversal tasks RL1-RL3 of goats assigned to the groups unbold (black bars) vs. bold (grey bars). Data are presented as least squared means and standard errors (LSM $\pm$ SE); * $p < 0.05$.

4.8 Discussion

Our study investigated the potential relationship between specific personality traits and individual learning performance by using a visual discrimination paradigm. Goats learned to associate a visual stimulus with a reward in the initial 4-choice visual discrimination task (ID) presented 24/7 using an automated learning device and were able to reverse their associations in a serial reversal task (RL1-3). Their performance in the three consecutive RL's depended on their learning success in the ID in that low performers in the ID also performed low in the RL's. Taking specific personality traits (measured once) into account, we did not find any evidence of a relationship between *activity* and/or *boldness* and learning performance, either in the discrimination task or in the reversal tasks. However, including only the animals that were *stable* for personality trait *activity* and/or *boldness* (measured twice), no evidence for any link between *activity* and learning performance was found, while *boldness* revealed a significant link to learning performance in the first reversal task in that unbold individuals outperformed bold individuals in RL1.

The learning performance of the goats in the three consecutive reversal tasks depended on their learning success in the initial learning task. A higher proportion of goats performing low in the initial discrimination task did not achieve the learning criteria in the reversal tasks compared to the goats that learned the initial

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discrimination task better. This effect is not as obvious in the first reversal task but reaches significance in the second and third reversal tasks. Additionally, the low-performing goats that were able to reverse the initially learned association needed more trials to solve the reversal task, which was significant at least in RL1. This indicates a relationship between visual discrimination learning and reversal learning in goats in the sense that the learning speed in the visual discrimination task would predict the learning performance in a reversal task regarding low-performing learners. Unexpectedly, goats who performed low in the initial discrimination task also performed low in the reversal task. This finding contrasts other learning studies showing that good learners (high learning speed) seem to be poor reversal learners (low learning speed), which has been demonstrated in guppies (64) and parrots (65). Discrimination learning underlies the ability to associate a stimulus with appetitive (or aversive) stimuli, whereas reversal learning involves the capability of extinguishing a previously learned association to form a new association. This is thought to be more cognitively challenging, as previously learned cues must be deleted before a new association can be formed. Reversal learning tasks are frequently used as a measure of behavioural flexibility, as they require the subjects to flexibly adjust their behaviour when the reward-related contingencies that they have previously learned are reversed (66). The clear difference between low performers and the other three learning groups in learning performance may indicate less flexibility and greater perseverance in low performers once they understood the initial discrimination task. One possible explanation comprises the role of the individual stress level during learning. A range of studies have demonstrated that elevated

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corticosterone levels affect learning performance across taxa, although the degree to which learning is affected and whether exposure results in benefits or decrements depends on the extent and timing of corticosterone exposure (67-69). The low-performing individuals in our study may be more stressed compared to the other three groups of learners due to the stress originating from the learning task itself or from external factors such as dominance or rank within the group. These factors have already been found to show a relationship to learning performance and might have impaired learning performance in the initial discrimination task. To shed light on this issue, and as we did not investigate the individual stress level in our study, future research should take into account the stress responses of animals in such learning tests. However, the learning performance of the other three learning groups in the discrimination task did not have an effect on reversal learning; thus, we did not find a negative correlation, as has been shown in red junglefowl (70). The learning groups might differ in several aspects associated with performance, such as motivation or physical strength. We also take into account differences in general learning ability, as some animals might be more cognitively impaired than others, which is likely to explain the differences observed in discrimination and reversal learning. Furthermore, goats seem to be able to improve their performance across three reversals by progressively reducing their TTC, indicating that they are getting better at switching to the alternative stimulus. Similar serial reversal learning experiments, in which the alternation of training to criterion and contingency reversal was repeated several times, have revealed that rats, pigeons, frogs and goats improve their performance over successive reversals in a learning-to-learn process (71-73).

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In our study, we found that low performers were able to improve their TTC across the reversal tasks, but we must note that goats that did not achieve the learning criterion at all in RL1-3 fell out of scope.

Taking specific personality traits into account, we did not find any evidence of a relationship between the two *momentary* personality traits *activity* and *boldness* (measured once) and learning performance either in the discrimination task or in the reversal tasks. We might have expected, based on previous studies concerning personality measures and learning/cognition, that bold and/or active individuals learn to associate a cue with a reward faster than unbold and/or inactive individuals (7, 74) but perform lower in reversal learning (56, 75, 76). A possible explanation for the lack of a link between personality traits and learning success in this analysis may be that only a single measurement of personality was integrated in the analysis. A recent review stated that personality measured just once cannot provide enough information about all aspects of personality differences (77). This is easily comprehensible, as animal personality refers per definition to the repeatable part of an individual's behaviour (12, 78), and a behaviour measured only once probably reflects mostly the within-individual rather than the among-individual component (77, 79). Among studies that have investigated the relationship between personality and cognition in nonhuman animals, some conducted a behavioural test only once to characterize specific personality traits and often failed to show interrelations between personality and learning, while it is recommended to measure personality traits across time and contexts by applying several repetitions of different tests to find a connection between personality and learning capabilities (28, 31, 80). For example,

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Christensen et al. (81) found that behaviour towards a novel object (labelled exploration) correlated with learning performance in a visual discrimination task in horses. More exploratory horses were more successful in a two-choice visual discrimination task (81). Similar to our study, the NO-test was conducted repeatedly, indicating that relationships between cognitive performance and personality can be found when personality traits are confirmed to be stable over time because they are measured at least twice.

In our study, the behaviour of the individuals was observed in two tests that were independent from each other, and two separate PCA were conducted. In a following step, we used the data from both personality tests, including only the animals that were stable for personality trait *activity* and/or *boldness*, to test whether stability in a specific personality trait would have an effect on learning performance. We found no evidence for any link between *activity* and learning, either in ID or in RL, whereas *boldness* revealed a significant link to learning performance in RL1. By exhibiting a higher level of activity and exploration, active personality types sample their environment more rapidly, albeit more superficially. As a consequence, these animals should learn novel tasks more quickly but at the cost of accuracy and responsiveness to changes in the meaning of cues (6, 13, 57). Caused by their superficial sampling and inaccuracy, they were thought not to perceive the change in cue meaning during reversal learning and thus would make a greater number of mistakes when associating the symbols with the reward. In contrast, inactive types were thought to have a reduced learning speed but reveal more learning flexibility through their greater attention towards cue relevancy, increasing their accuracy under variable environmental

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conditions. We therefore expected active individuals to successfully reach the learning criterion in the discrimination task more rapidly and that inactive individuals would outperform active individuals in the context of reversal learning tasks. In testing these predictions, we found that *activity* did not have any influence on learning success in the goats. Similar results were reported by Chung et al. (17), where active (“fast”) lizards did perceive a change in cue meaning (other than expected) and were not less accurate than their inactive (“slow”) conspecifics when tested in a two-phase associative task. In general, several terms in the context of animal personality research have referred to partially overlapping concepts (82), and traits such as exploration, boldness (and sociability) are most commonly used in the context of animal personality. Only a few studies find a direct relationship between activity and learning success, and if so, they reveal different results (17, 74, 83). This may be due to varying definitions and measurements of activity. While some studies measure activity as the number and rate of transitions between squares (17; lizard) or swim distance (83; guppies), others use locomotion behaviour that results in a change in body position in space as an indicator for activity (74; cavies). This impairs the general comparability across experimental studies, measurement methods and statistical analyses. There is some evidence that links between activity and learning abilities are highly task dependent. For example, fearful and active individuals perform better in an avoidance task, whereas the authors did not find such a relationship in a backwardss-forwards task in horses (84). It is therefore possible that activity might reveal a predisposition to react to specific stimuli involved in learning.

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However, we found a significant impact of the *stable* (repeatedly measured) personality trait *boldness* on learning performance in RL1 (unbold individuals outperform bold individuals) but not in ID. This partly reflects the general assumption that bold or proactive individuals are better at learning a discrimination task, but unbold or reactive individuals are better at adapting to changes in an already learned task reflecting a higher behavioural flexibility (57, 7, 76, 85-87). This association has been shown in studies with great tits (26) and red junglefowls (88), while others fail to show this relationship (31). Differences in the readiness to approach a novel stimulus have been described as risk-taking behaviour, novelty-seeking, proactivity or boldness in different studies across different species and have been shown to be a distinguishing factor between individuals differing in coping patterns or personality traits (13, 89-91). It is assumed that bold/proactive animals are more successful in forming routines during learning, which results in being less able to react flexibly in adapting their behaviour to changing environmental conditions (20, 92, 93). Interestingly, the difference in learning success only refers to the first reversal task and disappeared in RL2 and RL3, as bold individuals were able to improve their learning performance. We assume that they learned to form a new routine of the concept of reversal, strengthening the hypothesis that bold individuals are fast learners in the sense that they quickly form routines. This interpretation fits with Cockrem's (92) classification of personalities in that proactive individuals may perform better in environments that are constant or predictable compared to reactive individuals who perform better in unpredictable conditions. Reactive individuals may tend to generalize a formerly learned rule (i.e., "one of the symbols is rewarded") more

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quickly being able to shift the general rule to a new symbol. On the other hand, fast explorers may learn more about the absolute properties of the stimulus in the visual discrimination task and thus fail to classify new symbols immediately ‘correctly’. Once the reward reversal was no longer new (RL2 and RL3), proactive individuals learned that the general concept changes and were able to form a new routine. Even so, it is unclear why and how learning more or less flexibly is related to how individuals react to a novel object in the context of a standardized behavioural test. At least, novelty seems to play an important role in driving these processes, as differences between individuals refer to both the novel object and the novel (first) reversal learning task. In most studies, the trait boldness refers to behavioural reactions to novel stimuli and situations and is often measured in a NO- or novel human test (reviewed by 8). However, boldness has also been used in predator-dependent contexts showing a relationship to learning performance, whereas boldness measured in a NO-test did not, especially when measured only once (reviewed by 9). Furthermore, boldness concepts may refer to an individual's reactions to risky situations (12, 94), while exploration is often used in the context of an individual's reactions to new situations (12). The differences between a new and/or risky situation are not easily detectable and depend to a large amount on the type of experimental setup and recorded parameters (12, 18, 82).

To address our findings, the performance of the goats in the three reversal tasks depended on their learning success in the initial discrimination task in that low performers in the initial discrimination task also performed low in the reversal tasks. We found evidence in the current study that there is a relationship between

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learning and *boldness* in goats: bold individuals show reduced behavioural flexibility, as shown in the first reversal task; however, bold animals were able to adapt in the subsequent reversals once a new routine was formed.

4.9 Conclusion

To conclude, in the present study, one personality trait, *boldness*, proved to have substantial consequences on learning performance in a reversal task. Our findings show that we should take personality bias into account when conducting learning or cognitive experiments and underline the importance of the repeated measurement of individual personality traits. However, the explanation for the observed interrelations between personality traits and learning performance is currently unclear and requires further empirical and theoretical investigation. To understand whether intrinsic differences in learning exist across individuals, we need to investigate the extent to which learning and personality traits covary and identify the mechanisms that can constrain cognitive processing and adaptive behavioural responses.

4.10 Data Availability Statement

Raw data are available in a public repository:

https://osf.io/wudj7/?view_only=ed372f7bdded4ff2a46901a0bdc15081

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4.11 Author Contributions

JL conceptualised the study. MAF and AK collected and analysed the data and did the statistical analysis together with AT. MAF, AK, JL and BP contributed to the conception of the manuscript. MAF, AK and JL wrote the manuscript.

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4.14 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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4.16 Supplementary Material

The Supplementary Material for this article can be found online at:

<https://www.frontiersin.org/articles/10.3389/fvets.2022.916459/full#supplementary-material>

4.17 References

1. Groothuis, T. G. and Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.*, 29, 137-150. doi: 10.1016/j.neubiorev.2004.06.010
2. Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V. and Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil. Trans. Royal Soc. B*, 365, 4051-4063. doi: 10.1098/rstb.2010.0208
3. Tremmel, M. and Muller, C. (2013). Insect personality depends on environmental conditions. *Behav. Ecol.* 24, 386-392. doi: 10.1093/beheco/ars175
4. Kelleher, S. R., Silla, A. J. and Byrne, P. G. (2018). Animal personality and behavioral syndromes in amphibians: a review of the evidence, experimental approaches, and implications for conservation. *Behav. Ecol. Sociobiol.*, 72, 26. doi: 10.1007/s00265-018-2493-7

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

5. Roth, T. C., Rosier, M., Krochmal, A. R. and Clark, L. (2020). A multi-trait, field-based examination of personality in a semi-aquatic turtle. *Ethol.*, 126, 851-857. doi: 10.1111/eth.13030
6. Carere, C. and Locurto, C. (2011). Interaction between animal personality and animal cognition. *Curr. Zool.*, 57, 491-498. doi: 10.1093/czoolo/57.4.491
7. Sih, A. and Del Giudice, M. (2012). Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Phil. Trans. Royal Soc. B.*, 367, 2762-2772. doi: 10.1098/rstb.2012.0216
8. Griffin, A. S., Guillette, L. M. and Healy, S. D. (2015). Cognition and personality: an analysis of an emerging field. *Trends Ecol. Evol.*, 30, 207-214. doi: 10.1016/j.tree.2015.01.012
9. Dougherty, L. R. and Guillette, L. M. (2018). Linking personality and cognition: A meta-analysis. *Phil. Trans. Royal Soc. B.*, 373, 20170282. doi: 10.1098/rstb.2017.0282
10. Wat, K. K. Y., Banks, P. B. and McArthur, C. (2020). Linking animal personality to problem-solving performance in urban common brushtail possums. *Anim. Behav.*, 16, 35-45. doi: 10.1016/j.anbehav.2020.01.013
11. Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psych. Bul.*, 127, 45-86. doi: 10.1037/0033-2909.127.1.45
12. Réale, D., Reader, S. M., Sol, D., McDougall, P. T. and Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev. Cam. Philos. Soc.*, 82, 291–318. doi: 10.1111/j.1469-185X.2007.00010.x

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

13. Koolhaas, J. M., Korte, S. M., De Boer, S. F., van Der Vegt, B. J., van Reenen, C. G., Hopster, H., de Jong, I. C., Ruis, M. A. W. and Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.*, 23, 925-935. doi: 10.1016/S0149-7634(99)00026-3
14. Bond, A. B., Kamil, A. C. and Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral exibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *J. Comp. Psychol.*, 121, 372-379. doi: 10.1037/0735-7036.121.4.372
15. Finkemeier, M.-A., Langbein, J. and Puppe, B. (2018). Personality research in mammalian farm animals: concepts, measures, and relationship to welfare. *Front. Vet. Sci.*, 5, 131. doi: 10.3389/fvets.2018.00131
16. Jones, N. A. R., Webster, M., Newport, C., Templeton, C. N., Schuster, S. and Rendell, L. (2020). Cognitive styles: speed-accuracy trade-offs underlie individual differences in archerfish. *Anim. Behav.*, 160, 1-14. doi: 10.1016/j.anbehav.2019.11.019
17. Chung, M., Goulet, C. T., Michelangeli, M., Wong, B. B. M and Chapple, D. G. (2017). Does personality influence learning? A case study in an invasive lizard. *Oecologia*, 185, 641–651. doi: 10.1007/s00442-017-3975-4
18. Sih, A., Bell, A. and Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.*, 19, 372-378. doi: 10.1016/j.tree.2004.04.009

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

19. Wechsler, B. and Lea, S. E. G. (2007). Adaptation by learning: Its significance for farm animal husbandry. *Appl. Anim. Behav. Sci.*, 108, 197-214. doi: 10.1016/j.applanim.2007.03.012
20. Brust, V., Wuerz, Y. and Krüger, O. (2013). Behavioural flexibility and personality in zebra finches. *Ethol.*, 119, 559-569. doi: 10.1111/eth.12095
21. Mesquita, F. O., Borcato, F. L. and Huntingford, F. A. (2015). Cue-based and algorithmic learning in common carp: A possible link to stress coping style. *Behav. Proc.*, 115, 25-29. doi: 10.1016/j.beproc.2015.02.017
22. Udino, E., Perez, M., Carere, C. and d'Ettorre, P. (2017). Active explorers show low learning performance in a social insect. *Cur. Zool.*, 63, 555-560. doi: 10.1093/cz/zow101
23. Boogert, N. J., Reader, S. M., and Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Anim. Behav.*, 72, 1229-1239. doi: 10.1016/j.anbehav.2006.02.021
24. Lalot, M., Ung, D., Péron, F., d'Ettorre, P. and Bovet, D. (2017). You know what? I'm happy. Cognitive bias is not related to personality but is induced by pair-housing in canaries (*Serinus canaria*). *Behav. Proc.*, 134, 70-77. doi: 10.1016/j.beproc.2016.09.012
25. Harris, C., Liedtke, J., Drees, C. and Schuett, W. (2020). Exploratory behaviour is not related to associative learning ability in the carabid beetle *Nebria brevicollis*. *Behav. Proc.*, 180, 7. doi: 10.1016/j.beproc.2020.104224

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

26. Titulaer, M., van Oers, K. and Naguib, M. (2012). Personality affects learning performance in difficult tasks in a sex-dependent way. *Anim. Behav.*, 83, 723-730. doi: 10.1016/j.anbehav.2011.12.020
27. Baker, M. R. and Wong, R. Y. (2019). Contextual fear learning and memory differ between stress coping styles in zebrafish. *Sci. Rep.*, 9:9935. doi: 10.1038/s41598-019-46319-0
28. Rasolofoniaina, B. N., Kappeler, P. M. and Fichtel, C. (2021). Neophobia and social facilitation in narrow-striped mongooses. *Anim. Cog.*, 24, 165-175. doi: 10.1007/s10071-020-01429-5
29. Rochais, C., Pillay, N. and Schradin, C. (2021). Do alternative reproductive tactics predict problem-solving performance in African striped mice? *Anim. Cog.*, 24, 703-716. doi: 10.1007/s10071-020-01459-z
30. Brust, V. and Guenther, A. (2017). Stability of the guinea pig personality – cognition – linkage over time. *Behav. Proc.*, 134, 4-11. doi: 10.1016/j.beproc.2016.06.009
31. Kniel, N., Guenther, A. and Godin, J.-G. J. (2020). Individual personality does not predict learning performance in a foraging context in female guppies, *Poecilia reticulata*. *Anim. Behav.*, 167, 3-12. doi: 10.1016/j.anbehav.2020.07.007
32. Ruis, M. A. W., te Brake, J. H. A., van de Burgwal, J. A., de Jong, I. C., Blokhuis, H. J. and Koolhaas, J. M. (2000). Personalities in female domesticated pigs: behavioural and physiological indications. *Appl Anim Behav Sci.*, 66, 31–47. doi: 10.1016/S0168-1591(99)00070-2

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

33. Zebunke, M., Repsilber, D., Nürnberg, G., Wittenburg, D. and Puppe, B. (2015). The backtest in pigs revisited—an analysis of intra-situational behaviour. *Appl Anim Behav Sci.*, 169, 17–25. doi: 10.1016/j.applanim.2015.05.002
34. Krause, A., Puppe, B. and Langbein, J. (2017). Coping style modifies general and affective autonomic reactions of domestic pigs in different behavioral contexts. *Front. Behav. Neurosci.* 11, 103. doi: 10.3389/fnbeh.2017.00103
35. Graunke, K. L., Nürnberg, G., Repsilber, D., Puppe, B. and Langbein, J. (2013). Describing temperament in an ungulate: a multidimensional approach. *PLoS One*, 8, 1–12. doi: 10.1371/journal.pone.0074579
36. Foris, B., Zebunke, M., Langbein, J. and Melzer, N. (2018). Evaluating the temporal and situational consistency of personality traits in adult dairy cattle. *PLoS One*, 13, 1–16. doi: 10.1371/journal.pone.0204619
37. Neave, H. W., Costa, J. H. C., Weary, D. M. and von Keyserlingk, M. A. G. (2018). Personality is associated with feeding behavior and performance in dairy calves. *J. Dairy Sci.*, 101, 7437–7449. doi: 10.3168/jds.2017-14248
38. Lansade, L. and Bouissou, M. F. (2008). Reactivity to humans: a temperament trait of horses which is stable across time and situations. *Appl Anim Behav Sci.*, 114, 492–508. doi: 10.1016/j.applanim.2008.04.012
39. Ijichi, C., Collins, L.M . and Elwood, R. M. (2014). Pain expression is linked to personality in horses. *Appl Anim Behav Sci.*, 152, 38–42. doi: 10.1016/j.applanim.2013.12.007

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

40. Roberts, K., Hemmings, A. J, Moore-Colyer, M., Parker, M. O. and McBride, S. D. (2016). Neural modulators of temperament: a multivariate approach to personality trait identification in the horse. *Physiol Behav.*, 167, 125–31. doi: 10.1016/j.physbeh.2016.08.029
41. Agnvall, B., Ali, A., Olby, S., and Jensen, P. (2014). Red Junglefowl (*Gallus gallus*) selected for low fear of humans are larger, more dominant and produce larger offspring. *Animal*, 8, 1498-1505. doi : 10.1017/S1751731114001426
42. Marino, L. (2017). Thinking chickens: A literature review of cognition, emotion, and behavior in the domestic chicken. *Anim. Cog.*, 20, 127-141. doi: 10.1007/s10071-016-1064-4
43. Nawroth, C., Prentice, P. M. and McElligott, A. G. (2017). Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. *Behav. Proc.*, 134, 43-53. doi: 10.1016/j.beproc.2016.08.001
44. Finkemeier, M.-A., Oesterwind, S., Nürnberg, G., Puppe, B. and Langbein, J. (2019). Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses. *Appl. Anim. Behav. Sci.*, 217, 28-35. doi: 10.1016/j.applanim.2019.05.004
45. Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. Oxford university press, New York, NY, US.
46. Gieling, E. T., Musschenga, M. A., Nordquist, R. E. and van der Staay, F. J. (2012). Juvenile pigs use simple geometric 2D shapes but not portrait photographs

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

of conspecifics as visual discriminative stimuli. *Appl Anim Behav Sci.*, 142, 142–

53. doi: 10.1016/j.applanim.2012.10.018

47. Zebunke, M, Langbein, J, Manteuffel, G and Puppe, B. (2011). Autonomic reactions indicating positive affect during acoustic reward learning in domestic pigs. *Anim Behav.*, 81, 481–9. doi: 10.1016/j.anbehav.2010.11.023

48. Krüger, K, Farmer, K and Heinze, J. (2014). The effects of age, rank and neophobia on social learning in horses. *Anim Cogn.*, 17, 645–655. doi: 10.1007/s10071-013-0696-x

49. Meyer, S., Nürnberg, G., Puppe, B. and Langbein, J. (2012). The cognitive capabilities of farm animals: Categorisation learning in dwarf goats (*Capra hircus*). *Anim. Cog.*, 15, 567– 576. doi: 10.1007/s10071-012-0485-y

50 Nawroth, C., von Borell, E. and Langbein, J. (2015). Object permanence in the dwarf goat (*Capra aegagrus hircus*): Perseveration errors and the tracking of complex movements of hidden objects. *Appl. Anim. Behav. Sci.*, 167, 20–26. doi: 10.1016/j.applanim.2015.03.010

51. Langbein, J., Siebert, K. and Nürnberg, G. (2009). On the use of an automated learning device by group-housed dwarf goats: Do goats seek cognitive challenges? *Appl. Anim. Behav. Sci.*, 120, 150-158. doi: 10.1016/j.applanim.2009.07.006

52. Rosenberger, K., Simmler, M., Nawroth, C., Langbein, J. and Keil, N. (2020). Goats work for food in a contrafreeloading task. *Sci. Rep.*, 10, 22336. doi: 10.1038/s41598-020-78931-w

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

53. Briefer, E. F., de la Torre, M. P. and McElligott, A. G. (2012). Mother goats do not forget their kids' calls. *Phil. Trans. Royal Soc. B.*, 279, 3749–3755. doi: 10.1098/rspb.2012.0986
54. Briefer, E. F., Haque, S., Baciadonna, L. and McElligott, A. G. (2014). Goats excel at learning and remembering a highly novel cognitive task. *Front. Zool.*, 11, 20. doi: 10.1186/1742-9994-11-20
55. Langbein, J., Siebert, K., Nürnberg, G. and Manteuffel, G. (2007). Learning to learn during visual discrimination in group housed dwarf goats (*Capra hircus*). *J. Comp. Psychol.*, 121, 447-456. doi: 10.1037/0735-7036.121.4.447
56. Bebus, S. E, Small, T. W, Jones, B. C., Elderbrock, E. K. and Schoech, S. J. (2016). Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure. *Anim. Behav.*, 111, 251-260. doi: 10.1016/j.anbehav.2015.10.027
57. Bolhuis, J. E., Schouten, W. G. P., de Leeuw, J. A., Schrama, J. W. and Wiegant, V. M. (2004). Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behav. Brain Res.*, 152, 351-360. doi: 10.1016/j.bbr.2003.10.024
58. Takola, E., Krause, T. E., Müller, C. and Schielzeth, H. (2021). Novelty at second glance: a critical appraisal of the novel object paradigm based on meta-analysis. *Anim. Behav.*, 180, 123-142. doi: [10.1016/j.anbehav.2021.07.018](https://doi.org/10.1016/j.anbehav.2021.07.018)

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

59. Langbein, J., Nürnberg, G. and Manteuffel, G. (2004). Visual discrimination learning in dwarf goats and associated changes in heart rate and heart rate variability. *Physiol. Behav.*, 82, 601–609. doi: 10.1016/j.physbeh.2004.05.007
60. Langbein, J., Nürnberg, G., Puppe, B. and Manteuffel, G. (2006). Selfcontrolled visual discrimination learning of group-housed dwarf goats (*Capra hircus*): behavioral strategies and effects of relocation on learning and memory. *J. Comp. Psych.*, 120, 58–66. doi: 10.1037/0735-7036.120.1.58
61. Guidelines for the treatment of animals in behavioural research and teaching. (2020). *Anim. Behav.*, 159, I-XI. doi: 10.1016/j.anbehav.2019.11.002
62. Finkemeier, M.-A., Trillmich, F. and Guenther, A. (2016). Match-mismatch experiments using photoperiod expose developmental plasticity of personality traits. *Ethol.*, 122, 80-93. doi: 10.1111/eth.12448
63. Forkman, B., Boissy, A., Meunier-Salaun, M.-C., Canali, E. and Jones, R.B. (2007). A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiol. Behav.* 92, 340–374. doi: 10.1016/j.physbeh.2007.03.016
64. Lucon-Xiccato, T. and Bisazza, A. (2014). Discrimination reversal learning reveals greater female behavioural flexibility in guppies. *Biol. Let.*, 10, 20140206. doi: 10.1098/rsbl.2014.0206
65. van Horik, J. O. and Emery, N. J. (2018). Serial reversal learning and cognitive flexibility in two species of Neotropical parrots (*Diopsittaca nobilis* and *Pionites melanocephalia*). *Behav. Proc.*, 157, 664-672. doi: 10.1016/j.beproc.2018.04.002

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

66. Izquierdo, A., Brigman, J. L., Radke, A. K., Rudebeck, P. H. and Holmes, A. (2017). The neural basis of reversal learning: An updated perspective. *Neurosci.* 345, 12–26. doi: 10.1016/J.NEUROSCIENCE.2016.03.021
67. de Kloet, E. R., Oitzl, M. S. and Joels, M. (1999). Stress and cognition: are corticosteroids good or bad guys? *Trends Neurosci.*, 22, 422-426. doi: 10.1016/S0166-2236(99)01438-1
68. Pravosudov, V. V., Mendoza, S. P. and Clayton, N. S. (2003). The relationship between dominance, corticosterone, memory, and food caching in mountain chickadees (*Parus gambeli*). *Horm. Behav.*, 44, 93-102. doi: 10.1016/S0018-506X(03)00119-3
69. Kitaysky, A. S., Kitaishkaia, E. V., Piatt, J. F. and Wingfield, J. C. (2003). Benefits and costs of increased levels of corticosterone in seabird chicks. *Horm. Behav.*, 43, 140-149. doi: 10.1016/S0018-506X(02)00030-2
70. Sorato, E., Zidar, J., Garnham, L., Wilson, A. and Løvlie, H. (2018). Heritabilities and co-variation among cognitive traits in red junglefowl. *Phil. Trans. Royal Soc. B.*, 373, 20170285. doi: 10.1098/rstb.2017.0285
71. Pubols Jr., B. H. (1957). Successive discrimination reversal learning in the white rat: A comparison of two procedures. *J. Comp. Physiol. Psychol.* 50, 319-322. doi: 10.1037/h0048892
72. Bullock, D.H. and Bitterman, M.E. (1962). Habit reversal in the pigeon. *J. Comp. Physiol. Psychol.* 55, 958. doi: 10.1037/h0041070

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

73. Liu, Y., Day, L. B., Summers, K. and Burmeister, S. S. (2016). Learning to learn: advanced behavioural flexibility in a poison frog. *Anim. Behav.* 111, 167–172. doi: 10.1016/J.ANBEHAV.2015.10.018
74. Guenther, A., Brust, V., Dersen, M. and Trillmich, F. (2014). Learning and personality types are related in cavies (*Cavia aperea*). *J. Comp. Psychol.*, 128, 74–81. doi: 10.1037/a0033678
75. Guillette, L. M., Reddon, A. R., Hurd, P. L. and Sturdy, C. B. (2009). Exploration of a novel space is associated with individual differences in learning speed in black capped chickadees, *Poecile atricapillus*. *Behav. Proc.*, 82, 207–214. doi: 10.1016/j.beproc.2009.07.005
76. Guillette, L. M., Reddon, A. R., Hoeschele, M. and Sturdy, C. B. (2011). Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. *Phil. Trans. Royal Soc. B*, 278, 767–773. doi: 10.1098/rspb.2010.1669
77. Dingemanse, N. J. and Wright, J. (2020). Criteria for acceptable studies of animal personality and behavioural syndromes. *Ethol.*, 126, 865–869. doi: 10.1111/eth.13082
78. Dingemanse, N. J., Kazem, A. J., Réale, D. and Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.*, 25, 81–89. doi: 10.1016/j.tree.2009.07.013
79. Dingemanse, N. J., Dochtermann, N. A. and Nakagawa, S. (2012). Defining behavioural syndromes and the role of ‘syndrome deviation’ in understanding

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

their evolution. *Behav. Ecol. Sociobiol.* 66, 1543–1548. doi: 10.1007/s00265-012-1416-2

80. Dugatkin, L. A. and Alfieri, M. S. (2003). Boldness, behavioral inhibition and learning. *Ethol. Ecol. Evol.*, 15, 43-49. doi: 10.1080/08927014.2003.9522689

81. Christensen, J. W., Ahrendt, L. P., Malmkvist, J., Nicol, C. (2021). Exploratory behavior towards novel objects is associated with enhanced learning in young horses. *Sci. Rep.*, 11, 1428: doi: 10.1038/s41598-020-80833-w

82. Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlshaw, G. and Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biol. Rev.* 88, 465–475. doi: 10.1111/brv.12007

83. Burns, J. G. and Rodd, F. H. (2008). Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. *Anim. Behav.* 76, 911–922. doi: 10.1016/j.anbehav.2008.02.017

84. Lansade, L. and Simon, F. (2010). Horses' learning performances are under the influence of several temperamental dimensions. *Appl. Anim. Behav. Sci.*, 125, 30-37. doi: 10.1016/j.applanim.2010.02.010

85. Benus, R. F., Koolhaas, J. M., and van Oortmerssen, G. A. (1987). Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour*, 100, 105-122. doi: www.jstor.org/stable/4534578

86. Benus, R. F., Den Daas, S., Koolhaas, J. M. and van Oortmerssen, G. A. (1990). Routine formation and flexibility in social and non-social behaviour of

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

aggressive and non-aggressive male mice. *Behaviour*, 112,176–193. doi: 10.1163/156853990X00185

87. Range, F., Bugnyar, T., Schlägl, C. and Kotrschal, K. (2006). Individual and sex differences in learning abilities of ravens. *Behav. Proc.* 73, 100–106. doi: 10.1016/j.beproc.2006.04.002

88. Zidar, J., Balogh, A., Favati, A., Jensen, P., Leimar, O., Sorato, E. and Løvlie, H. (2018). The relationship between learning speed and personality is age- and task-dependent in red junglefowl. *Behav. Ecol. Sociobiol.*, 72, 168. doi: 10.1007/s00265-018-2579-2

89. Benus, R. F. (2001). Coping in female mice from lines bidirectionally selected for male aggression. *Behaviour*, 138, 997–1008. doi: 10.1163/156853901753286533

90. Campbell, T., Lin, S., DeVries, C. and Lambert, K. (2003). Coping strategies in male and female rats exposed to multiple stressors. *Physiol. Behav.* 78, 495–504. doi: 10.1016/S0031-9384(03)00033-7

91. de Boer, S. F., van der Vegt, B. J. and Koolhaas, J. M. (2003). Individual variation in aggression of feral rodent strains: A standard for the genetics of aggression and violence? *Behav. Genet.* 33, 485–501. doi: 10.1023/A:1025766415159

92. Cockrem, J. F. (2007). Stress, corticosterone responses and avian personalities. *J. Orni.*, 148, 169-178. doi: 10.1007/s10336-007-0175-8

Chapter 4 – Personality traits affect learning performance in dwarf goats (*Capra hircus*)

93. Coppens, C. M., de Boer, S. F. and Koolhaas, J. M. (2010). Coping styles and behavioural flexibility: towards underlying mechanisms. *Phil. Trans. Royal Soc. B.*, 365, 4021-4028. doi: 10.1098/rstb.2010.0217
94. Thomson, J. S., Watts, P. C., Pottinger, T. G. and Sneddon, L. U. (2012). Plasticity of boldness in rainbow trout: *oncorhynchus mykiss*: do hunger and predation influence risk-taking behaviour? *Horm Behav*, 61, 750–757. doi: 10.1016/j.yhbeh.2012.03.014

Chapter FIVE:
General Discussion



5.1 Discussion of the results

Personality is a concept which encompasses many aspects of an individual. One of the main goals of this thesis was to understand this concept and to investigate how personality is expressed, in which form it is related to physiology, dominance hierarchy and cognitive capacities (here learning and reversal learning) in farm animals on the example of dwarf goats.

In a first step, my colleagues and I reviewed (chapter two) about how personality is defined, which aspects are part of the concept, which terminology is used and how personality is measured especially in mammal farm animal species. In a second step, we conducted two studies, which are redrawn in detail in chapter three and chapter four. In the following chapter, I highlight and discuss the main results of each study and bring them into relationship to welfare implications. Further, I give a certain outlook how research in farm animals, especially in dwarf goats, can improve the understanding of farm animal personality.

5.1.1 Review: Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare

The aim of the review was to give a comprehensive overview about how concepts and personality related terms, which have their origin in human psychology, are currently used in animal and especially in farm animal personality research and to critically reveal how they are defined and what they measure. Since publication of our review, other reviews trying to give an overview of what personality is and

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how it can be measured properly, were published as well. The focus of these publications was different (e.g. a philosophical perspective (Martin, 2023), invertebrates (Kaiser & Müller, 2021), primates (Delval et al., 2024)), but what they all had in common with our review, is to give an overview about personality itself and to explain how the understanding of individuality in animals evolved over the last decades. Delval et al. (2024) gave a deeper overview about how the concept of personality evolved in human psychology. Interestingly, even in human psychology research the use of the term personality is not that clear as I thought. Delval et al. (2024) were able to explain that the use of the term personality or even temperament and what it means is highly dependent of the scientific framework adopted (e.g. psychoanalysis, behavioural science, developmental psychology to name a few). Temperament is broadly used by developmental psychologists as they are more interested in the beginning and the development of personality, while in psychiatry personality is seen as individual differences in adaptive systems which involved in the reception, processing, and storing of information about the environment (reviewed by Delval et al., 2024). In animal personality research as well, the use of the personality related terms is dependent of the scientific framework. Biologists and especially behavioural ecologists focus on specific personality traits (Kaiser & Müller, 2021) and their ecological consequences (proximate versus ultimate) within one species, the results are then highly dependent of the research question and experimental method used (reviewed by Delval et al., 2024). In human psychology, personality is measured as a whole framework, focussing on the big five model (openness, extraversion, agreeableness, conscientiousness, neuroticism), but a sixth factor is highly discussed: Honesty, which is defined by morality, sincerity or integrity and

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seems to be related to agreeableness (reviewed by Delval et al., 2024). The equivalent discussion can be found in animal personality research as here as well a sixth factor, besides of the accepted five (exploration, sociability, aggressiveness, boldness, activity), is found in primates: dominance which in parts seems to be related to aggressiveness (reviewed by Finkemeier et al., 2018 and Delval et al., 2024). In the definition of traits, there is still a lack of common definitions, which to a certain extend makes sense: The trait “boldness” is not the same in every species as each species has different requirements on its habitat; being bold is not the same for a predator than for a prey species (reviewed by Delval et al., 2024). Another aspect that my colleagues and I discussed in our review, was a potential fear to use the term personality in farm animal research because of anthropomorphism. To obtain an overview of published studies in selected mammalian farm animal species we carried out a systematic literature search using the Web of Science in December 2017 with keywords including the respective animal species (cattle, goat, sheep, horse, pig) and different synonyms applied in personality research (temperament, personality, coping). Then we exemplarily assessed the found studies within the context of terms and methodological approaches in general personality research. Finally, we discussed some findings on the possible impact of personality on the welfare of farm animals to especially highlight a future direction of personality research. One of our results was, that the use of the term personality was quite scarce. I repeated the search (February 2025) with the same mammalian farm animal species only including “personality” as keywords. I found over 1,500 publications (from 2018 to now, 2025) addressing the investigation of aspects of personality, but also using the term personality. Articles are addressing e.g. relationships to physiology

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(Papadaki et al., 2025), productive characteristics (Neave et al., 2022; Papadaki et al., 2025), feeding behaviour in calves (Setser et al., 2024), social rank and visit frequency in learning the usage of an automatic milking system (Johansen et al., 2025) and the usage of precision livestock technology to measure individual behaviour (Occhiuto et al., 2023; Setser et al., 2024) to name a few examples. In our review we concluded that more consistency is needed in using different theoretical concepts, terms and measures, especially in farm animal personality research. The terms coping style and temperament, which were used in different ways, should not be examined as independent concepts, but rather should be considered as different aspects of the whole personality concept. Farm animal personality should be increasingly considered for the improvement of animal housing, management, breeding and welfare. I see a remarkable development in farm animal personality research. We still lack in consistency in using the theoretical approaches, but the awareness of farm animals having a personality is on a very good way, leading up to ethical reflections and moral implications including farm animal welfare, husbandry and management practices (e.g. in “The moral implications of human and animal vulnerability” by Martin, 2023).

5.1.2 Study 1: Assessment of Personality Types in Nigerian Dwarf Goats (*Capra hircus*) and Cross-Context Correlations to Behavioural and Physiological Responses

Research about personality in goats is quite scarce. To date, only one study was able to categorize two of the five accepted personality traits in animal personality research – sociability and exploration (Nawroth et al., 2017). Another more recent study in male goat kids found repeatable behaviours classified as fearfulness by

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the authors (Vickery et al., 2024). Therefore, the third chapter of my thesis dealt with the investigation of personality traits in this species. Specifically, the investigation of other personality traits than sociability and exploration up to the formation of behavioural syndromes, to correlations with physiological traits and dominance hierarchy.

For this study, I expected:

1. that goats show different personality traits, based on measuring behaviours in repeatedly conducted open-field and novel-object tests and analysing these behaviours with a principal component analysis.
2. that the personality traits in goats are correlated with physiological traits and dominance hierarchy, based on heart rate variability measurement and weight, direct observations of dyadic agonistic interactions and a limited access test, and behaviour measured in a social separation test.

For this study, we measured the behaviour of 108 Nigerian dwarf goats in repeated (two test periods within two weeks) open-field and novel-object tests. In addition, we investigated the possible inter-relationships of inter-individual differences in personality with behaviours in other test situations (social separation test), dominance hierarchy (direct dyadic interactions) and physiological measures (heart rate variability and weight gain). To identify individual personality types and to be able to classify the goats into proactive, reactive and intermediate, we selected the 11 most appropriate behavioural measures, identical in both test periods, from a total of 82 observed behaviours. Using these behaviours, we ran two separate principal component analyses (PCA1 and PCA2) for the two test periods. We found two main principal components (PCs), which were interpreted as “boldness” (PC1) and “activity” (PC2) and were

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identical in both PCAs. Our results showed that based on PCA1, 30 goats could be grouped as the proactive, 25 as the reactive and 53 as the intermediate personality type. In PCA 2, 66 individuals (61%) showed a consistent personality type compared to PCA1. Goats that scored highly on “activity” were also more active in a social separation test, while no correlations were found between “boldness” or “activity” and the dominance status. Regarding heart rate variability, the standard deviation of R-R intervals (SDNN) was positively correlated with “activity”, while a negative correlation was found between “boldness” and SDNN. “Activity” was also positively correlated with weight gain.

The results show that 66 of the 108 (approximately 61%) dwarf goats exhibited consistent behaviour over both test periods, and 20.4% of the subjects displayed consistent proactive or reactive behaviour. My coauthors and I already discussed in chapter three, that our results perfectly match to results of previous studies with other farm animal species such as cattle (approximately 21%; Graunke et al., 2013) and pigs (approximately 34%; Zebunke et al., 2015). This corresponds also to previous findings in wildlife populations, where proactive and reactive personality types are less represented in a population because they count as extreme personality types (Dall et al., 2004).

The results of our PCAs show similarities in the composition of the PCs compared to two studies by Graunke et al. (2013) and Foris et al. (2018) performed on another ruminant species. Graunke et al. (2013) determined two main PCs with behaviours measured in a novel-object test, while the PCs in our study and of the study by Foris et al. (2018) were composed of behaviours measured in open-field and novel-object tests. In our study and the study conducted by Graunke et al. (2013), the first PC is composed of behaviours explaining boldness (e.g., duration

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of contact with the novel object, number of contacts with the novel object, latency to touch the novel object), and the second PC is composed of behaviours explaining activity and/or exploration. All three studies show similarly very strong loadings on the two components (e.g., from 0.7/-0.7 to 0.9/-0.9) describing personality factors activity and boldness. Another more recent study conducted on dairy cows also identified behaviours recorded in novel-object tests with high scoring PCs explaining exploration and boldness (Hasenpusch et al., 2024). The measured behaviours in all the mentioned studies, seem to be of strong importance in describing boldness, exploration and activity in ruminants, and therefore, also in goats.

In our study, 42 goats changed to the neighbouring score classes (SCs), indicating a flexible behavioural response. Only eight of them changed to the opposite SC. The majority reduced bold and active behaviour over the test repetitions. My co-authors and I assumed that some goats may have habituated to the test situations as this effect is also critically discussed by Forkman et al. (2007) and Peralas et al. (2017). The other goats may show phenotype-specific developmental plasticity because some phenotypes seem to be able to change more than others (Sinn et al., 2008). Even if the concept of animal personality suggests consistency of behaviours, animal personality and behavioural plasticity coexist (Sih et al., 2004), and it has been suggested that more extreme personality phenotypes (e.g., reactive and proactive) might be less plastic than intermediate/flexible personality phenotypes (Sih, 2013).

During the social separation test (SST) my co-authors and I measured the behaviour of the individual goat when separated from conspecifics by a fence. Goats that scored high on the PC “activity” were also more active and showed

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more rearing up behaviour in the SST than goats that scored low on this PC. This effect could be found between both PCAs and both SSTs and we assumed that this may indicate a behavioural syndrome, as this type of correlation is discussed to be a behavioural syndrome in animal personality studies (Huang et al., 2018; Sih et al., 2004). In comparison, goats that scored high on the PC “boldness” spent less time on the fence, indicating that bold goats seem to be less social. However, we found this correlation only between the first PCA and the first SST and not between the second PCA and second SST, which can be explained with habituation to that situation. Nevertheless, the variable “time spent at the fence” did not correlate between both SSTs, therefore, we have no indication for a sociability factor in this study. A recent study conducted on cavies (*Cavia aperea*) tested which effect cortisol has on behavioural traits related to stress coping, novelty seeking and social behaviour (Guenther et al., 2024). Already two hours after the treatment (each subject got a single dose of cortisol) nervous behaviours such as jumping, digging and rearing increased. Boldness was not affected, but aggressive interactions increased as well (Guenther et al., 2024). Jumping, digging and rearing are behaviours indicating stress in cavies equivalent to rearing up behaviour in goats. Goats that were more active showed more rearing up behaviour, those goats were maybe more stressed (in having maybe a higher cortisol level) because of the isolation of the conspecifics. The missing correlation between boldness and time spend at the fence in the second SST could confirm our idea of a habituation effect, as in the cavie study cortisol did not affect boldness as well. Thus, we did not measure cortisol levels before, during or after this test situation, but doing so in an improved SST test setting could maybe give

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more insights of goat's individual behaviour and its relationship to other traits during social separation.

In our study, the dominance index did not correlate with any of our measured personality factors. My co-authors and I assumed that the missing correlation between personality factors and dominance status could be due to these missing values as we only started to observe the group's hierarchy up to the second run. From our 66 individuals, which showed a consistent personality type, we have ten individuals with no value for the dominance index. On the other hand, dominance is a complex domain in personality research and is discussed as an independent personality factor in some species (reviewed by Finkemeier et al., 2018), but it seems to be important to consider when studying social species (reviewed by Finkemeier et al. 2018). In this study, we found a correlation between "activity" and behaviour in the limited access test. Goats that scored high on this factor were also the first to enter the learning device after 16 hours of water deprivation. Water is an important resource, so this result shows that the more active goats seem to have a higher rank in the group's hierarchy because they could get this resource earlier than the less active goats. Dominance is defined by boldness and/or aggressiveness (Gosling and John, 1999), and aggressiveness serves to establish dominance relationships (Desire et al., 2015). Barroso et al. (2000) showed that the dominance rank in female goats seems to be influenced by aggressiveness. Specifically, more aggressive goats are the most dominant in the social hierarchy, which can be seen in our study as well, as we defined dominance hierarchy by measuring agonistic interactions. A study conducted on cows measured agonistic interactions on the feeder and found a relationship of the use of a mechanical brush: Dominant cows used the brush more often than

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subordinate cows showing that even the use of resources that are not essential for survival can be affected by dominance hierarchy (Foris et al., 2021). A study on pigs highlighted another aspect of dominance, leadership (Khatiwada et al., 2024). Leadership was assessed in a repeated group-based Human Approach Test: 6 groups out of 26 had a consistent leader by females having 4.13 times odds than males to be a leader (Khatiwada et al., 2024). The relationship between personality and dominance needs further investigation to prove whether dominance should be a fully accepted personality factor in goats or if it is only a social outcome (reviewed by Finkemeier et al., 2018).

In our study, “boldness” was negatively correlated, and “activity” was positively correlated with the SDNN. These results indicate that shy and active goats seem to have a higher sympathetic activation at rest than bold and less active goats with a lower SDNN (Malik and Camm, 1995). As the SDNN is a parameter that shows a combination of parasympathetic and sympathetic activation, whereas the RMSSD gives information about parasympathetic activation alone (Houle and Billman, 1999), which did not correlate with any of the personality factors in our study, my co-authors and I can only assume that those animals show a sympathetic shift in their sympathetic-parasympathetic balance. A sympathetic shift is known to promote an increased metabolic output to address environmental challenges (Porges, 1995). Therefore, we can conclude that goats, which are more active and/or shy, are more alert to environmental changes, even while resting. We measured heart rate at rest, which make our results difficult to compare with previous studies regarding “activity” even if several studies in different species have already shown that proactive individuals have a stronger sympathetic activation in different contexts (Cannon, 1929; Korte et al., 1997; Krause et al.,

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2017). Interestingly, a study conducted on humans already found that the personality factor of neuroticism was significantly associated with HRV under baseline conditions (Čukić and Bates, 2014). As activity and boldness are the equivalent personality factors for neuroticism in animals (reviewed by Finkemeier et al., 2018), we can assume that both personality factors and their relationship to SDNN found in the present study are to some extent related to RHRV in goats.

Weight only correlated with the PC “activity”, indicating that goats that scored high on the activity factor were heavier at the end of the whole testing period. This effect could also be found for the variance value calculated between weaning and the end of the testing period (weight gain W-E) and the variance value calculated between birth and the end of the testing period (weight gain B-E), indicating that goats that scored high on the activity factor had a higher increase of weight during the whole testing period. A recent study in male goat kids found no relationship between weight gain and behaviour in a novel object test (Vickery et al., 2024). However, many other studies indicate that boldness, activity and/or aggressiveness are positively related to food intake rates, productivity (e.g., weight and/or weight gain) and other life-history traits in a wide range of taxa (reviewed by Biro and Stamps, 2008). Individual differences in weight gain are likely to encourage consistent individual differences in personality factors that are related to the acquisition of food resources, such as boldness, exploration, aggression, and activity (reviewed by Biro and Stamps, 2008). Therefore, the relationship between personality and weight gain in goats used in our study perfectly matches the results of other studies in other taxa, measuring the same effect (Arendt, 1997; Biro et al., 2006; Martins et al., 2005; Stamps, 2007).

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5.1.3 Study 2: Personality traits affect learning in dwarf goats (*Capra hircus*)

As goats have sophisticated cognitive capacities, already shown in numerous studies (reviewed by Zobel & Nawroth, 2020), the fourth chapter of this thesis deals with the relationship of cognitive capacities and personality trait in dwarf goats. In other taxa it is hypothesised that bold animals tend to develop routines and show less flexibility in the context of learning than shy individuals (Sih & Del Giudice, 2012; Chung et al., 2017). Even if much research with different species has already been done, the results were quite diverse and somehow species-related as some studies found relationships, while others did not.

For this study, I expected that goat's personality traits have a relationship to cognitive capacities, especially in learning and reversal learning in a visual discrimination task. I expected that bold goats learn a visual discrimination task faster, than shy goats, while shy goats perform better in reversal learning.

For this study, my co-authors and I, analyzed the behaviour of 95 goats during a repeated open-field (OF) and novel object-test (NO). Two main components were identified using principal component analysis: boldness and activity. In parallel, the goats learned to associate a visual stimulus with a reward in the initial 4-choice visual discrimination task (ID) presented 24/7 using an automated learning device and were able to reverse their associations in a serial reversal task (RL1-3). The number of animals that reached the learning criterion and the number of trials needed (TTC) in each task were calculated. Our results showed that the performance in the three consecutive RL's depended on their learning success in the ID in that low performers in the ID also performed low in the RL's. Taking specific personality traits (measured once) into account, we did not find any

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evidence of a relationship between *activity* and/or *boldness* and learning performance, either in the discrimination task or in the reversal tasks. However, including only the animals that were *stable* for the personality traits *activity* and/or *boldness* (measured twice), no evidence for any link between *activity* and learning performance was found, while *boldness* revealed a significant link to learning performance in the first reversal task in that unbold individuals outperformed bold individuals in RL1.

My co-authors and I found that learning performance of the goats in the three consecutive reversal tasks depended on their learning success in the initial learning task. A higher proportion of goats performing low in the initial discrimination task did not achieve the learning criteria in the reversal tasks compared to the goats that learned the initial discrimination task. This effect is not as obvious in the first reversal task but reaches significance in the second and third reversal tasks. Additionally, the low-performing goats that were able to reverse the initially learned association needed more trials to solve the reversal task, which was significant at least in RL1. This indicates a relationship between visual discrimination learning and reversal learning in goats in the sense that the learning speed in the visual discrimination task would predict the learning performance in a reversal task regarding low-performing learners. This contrasts other learning studies showing that good learners (high learning speed) seem to be poor reversal learners (low learning speed), which has been demonstrated in guppies (Lucon-Xiccato & Bisazza, 2014) and parrots (van Horik & Emery, 2018). Discrimination learning underlies the ability to associate a stimulus with appetitive (or aversive) stimuli, whereas reversal learning involves the capability of extinguishing a previously learned association to form a new association. This

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is thought to be more cognitively challenging, as previously learned cues must be deleted before a new association can be formed. Reversal learning tasks are frequently used as a measure of behavioural flexibility, as they require the individuals to flexibly adjust their behaviour when the reward-related contingencies that they have previously learned are reversed (Izquierdo et al., 2017). The clear difference between low performers and the other three learning groups - “high performer”, “good performer”, “poor performer” - in learning performance may indicate less flexibility and greater perseverance in low performers once they understood the initial discrimination task. One possible explanation comprises the role of the individual stress level during learning. A range of studies have demonstrated that elevated corticosterone levels affect learning performance across taxa, although the degree to which learning is affected and whether exposure results in benefits or decrements depends on the extent and timing of corticosterone exposure (de Kloet et al., 1999; Pravosudov et al., 2003; Kitaysky et al., 2003). A recent study on mice showed that individual stress levels clearly impair learning: as spatial learning and problem-solving tasks have been repeatable in mice studies before, the mentioned study could show that stressed mice individually differed strongly in performance, which resulted in missing repeatability between both cognitive tasks (Delacoux & Guenther, 2023). The low-performing individuals in our study may be more stressed compared to the other three groups of learners due to the stress originating from the learning task itself or from external factors such as dominance or rank within the group (discussed in Finkemeier et al., 2019). As we did not investigate the individual stress level in our study, future research should take into account the stress responses of animals in such learning tests. However, the learning performance of

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the other three learning groups in the discrimination task did not have an effect on reversal learning; thus, we did not find a negative correlation between learning and reversal learning, as in a study shown in red junglefowl (Sorato et al., 2018).

The goats of all groups in our study were able to improve their performance across three reversals by progressively reducing their TTC, indicating that they are getting better at switching to the alternative stimulus. Similar serial reversal learning experiments, in which the alternation of training to criterion and contingency reversal was repeated several times, have revealed that rats, pigeons, frogs and goats improve their performance over successive reversals in a learning-to-learn process (Pubols, 1957; Bullock & Bitterman, 1962; Liu et al., 2016). We found that low performers in our study were less frequently able to improve their TTC across the reversal tasks in comparison to the other three groups, but we must note that goats that did not achieve the learning criterion at all in RL1-3 fell out of scope.

Taking specific personality traits into account, we did not find any evidence of a relationship between the two *momentary* personality traits *activity* and *boldness* (the *momentary* personality traits were measured once) and learning performance either in the discrimination task or in the reversal tasks. We might have expected, based on previous studies concerning personality measures and learning/cognition, that bold and/or active individuals learn to associate a cue with a reward faster than unbold and/or inactive individuals (Sih & Del Giudice, 2012; Guenther et al., 2014a) but perform lower in reversal learning, because those individuals are forming routines and are less behaviourally flexible (Guillette et al., 2009; Guillette et al., 2011; Bebus et al., 2016). A possible explanation for the lack of a link between personality traits and learning success in this analysis may

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be that we integrated only a single measurement of personality in the analysis. A review stated that personality measured just once cannot provide enough information about all aspects of personality differences (Dingemanse & Wright, 2020). This is easily comprehensible, as animal personality refers per definition to the repeatable part of an individual's behaviour (Réale et al., 2007; Dingemanse et al., 2010), and a behaviour measured only once probably reflects mostly the within-individual rather than the among-individual component (Dingemanse et al., 2012; Dingemanse & Wright, 2020). Among studies that have investigated the relationship between personality and cognition in nonhuman animals, some conducted a behavioural test only once to characterize specific personality traits and often failed to show interrelations between personality and learning, while it is recommended to measure personality traits across time and contexts by applying several repetitions of different tests to find a connection between personality and learning capabilities (Dugatkin & Alfieri, 2003; Kniel et al., 2020; Rasolofoniaina et al., 2021). For example, Christensen et al. (2021) found that behaviour towards a novel object (labelled exploration) correlated with learning performance in a visual discrimination task in horses. More exploratory horses were more successful in a two-choice visual discrimination task (Christensen et al., 2021). Similar to our study, the novel-object test was conducted repeatedly (repetition during the foal stage), indicating that relationships between cognitive performance and personality can be found when personality traits are confirmed to be stable over time because they are measured at least twice. Goulet et al. (2018) went a step further by stating that cognition or a “cognitive style” should be integrated in the pace-of-life-syndrome (POLS) framework by Réale et al. (2010). In the mentioned study, fast learning lizards in a discrimination task,

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scored also high in activity, exploration and boldness, indicating strong relationships between cognitive and behavioural traits (Goulet et al., 2018).

In a following step, my co-authors and I used the data from both personality tests, including only the animals that were stable for personality trait *activity* and/or *boldness*, to test whether stability in a specific personality trait would have an effect on learning performance. We found no evidence for any link between *activity* and learning, either in ID or in RL, whereas *boldness* revealed a significant link to learning performance in RL1. By exhibiting a higher level of activity and exploration, active personality types sample their environment more rapidly, albeit more superficially. As a consequence, these animals should learn novel tasks more quickly but at the cost of accuracy and responsiveness to changes in the meaning of cues (Koolhaas et al., 1999; Bolhuis et al., 2004; Carere & Locurto, 2011). Caused by their superficial sampling and inaccuracy, they are thought not to perceive the change in cue meaning during reversal learning and thus would make a greater number of mistakes when associating the symbols with the reward. In contrast, inactive types are thought to have a reduced learning speed but reveal more learning flexibility through their greater attention towards cue relevancy, increasing their accuracy under variable environmental conditions. We therefore expected active individuals to successfully reach the learning criterion in the discrimination task more rapidly and that inactive individuals would outperform active individuals in the context of reversal learning tasks. In testing these predictions, we found that *activity* did not have any influence on learning success in the goats. Similar results were reported by Chung et al. (2017), where active (“fast”) lizards did perceive a change in cue meaning (other than expected) and were not less accurate than their inactive (“slow”)

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conspecifics when tested in a two-phase associative task. In mice, time spent exploring the test set-ups and boldness were able to predict solving success (mice were tested in a battery of eight different tasks), while activity did not (Mazza & Guenther, 2021). In general, several terms in the context of animal personality research have referred to partially overlapping concepts (Carter et al., 2013), and traits such as exploration, boldness (and sociability) are most commonly used in the context of animal personality. Only a few studies find a direct relationship between activity and learning success, and if so, they reveal different results (Burns & Rodd, 2008; Guenther et al., 2014a; Chung et al., 2017). This may be due to varying definitions and measurements of activity. While some studies measure activity as the number and rate of transitions between squares (Chung et al., 2017; lizard) or swim distance (Burns & Rodd, 2008; guppies), others use locomotion behaviour that results in a change in body position in space as an indicator for activity (Guenther et al., 2014a; cavies). This impairs the general comparability across experimental studies, measurement methods and statistical analyses. There is some evidence that links between activity and learning abilities are highly task or even species dependent. For example, fearful and active horses perform better in an avoidance task, whereas the authors did not find such a relationship in a backwards-forwards task (Lansade & Simon, 2010). It is therefore possible that activity might reveal a predisposition to react to specific stimuli involved in learning.

However, we found a significant impact of the *stable* (repeatedly measured) personality trait *boldness* on learning performance in RL1 (unbold individuals outperform bold individuals) but not in ID. This partly reflects the general assumption that bold or proactive individuals are better at learning a

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discrimination task, but unbold or reactive individuals are better at adapting to changes in an already learned task reflecting a higher behavioural flexibility (Benus et al., 1987; Benus et al., 1990; Bolhuis et al., 2004; Range et al., 2006; Guillette et al., 2011; Sih & Del Giudice, 2012). This association has been shown in studies with great tits (Titulaer et al., 2012), red junglefowls (Zidar et al., 2018) and marmosets (Slipogor et al., 2022), while others fail to show this relationship (Kniel et al., 2020). Differences in the readiness to approach a novel stimulus have been described as risk-taking behaviour, novelty-seeking, proactivity or boldness in different studies across different species and have been shown to be a distinguishing factor between individuals differing in coping patterns or personality traits (Koolhaas et al., 1999; Benus, 2001; de Boer et al., 2003; Campbell et al., 2003). It is assumed that bold/proactive animals are more successful in forming routines during learning, which results in being less able to react flexibly in adapting their behaviour to changing environmental conditions (Cockrem, 2007; Coppens et al., 2010; Brust et al., 2013). Interestingly, the difference in learning success only refers to the first reversal task and disappeared in RL2 and RL3, as bold individuals were able to improve their learning performance. We assume that they learned to form a new routine of the concept of reversal, strengthening the hypothesis that bold individuals are fast learners in the sense that they quickly form routines. This interpretation fits with Cockrem's (2007) classification of personalities in that proactive individuals may perform better in environments that are constant or predictable compared to reactive individuals who perform better in unpredictable conditions. Reactive individuals may tend to generalize a formerly learned rule (i.e., "one of the symbols is rewarded") more quickly being able to shift the general rule to a new symbol. On

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the other hand, fast explorers may learn more about the absolute properties of the stimulus in the visual discrimination task and thus fail to classify new symbols immediately ‘correctly’. Once the reward reversal was no longer new (RL2 and RL3), proactive individuals learned that the general concept changes and were able to form a new routine. Even so, it is unclear why and how learning more or less flexibly is related to how individuals react to a novel object in the context of a standardized behavioural test. At least, novelty seems to play an important role in driving these processes, as differences between individuals refer to both the novel object and the novel (first) reversal learning task. In most studies, the trait boldness refers to behavioural reactions to novel stimuli and situations and is often measured in a novel-object or novel human test (reviewed by Griffin et al., 2015). However, boldness has also been used in predator-dependent contexts showing a relationship to learning performance, whereas boldness measured in a novel-object test did not, especially when measured only once (reviewed by Dougherty & Guillette, 2018). Furthermore, boldness concepts may refer to an individual's reactions to risky situations (Réale et al., 2007; Thomson et al., 2012), while exploration is often used in the context of an individual's reactions to new situations (Réale et al., 2007). The differences between a new and/or risky situation are not easily detectable and depend to a large amount on the type of experimental setup and recorded parameters (Sih et al., 2004; Réale et al., 2007; Carter et al., 2013).

A new idea came into my mind by reading the review by Davidson et al. (2018). They outlined in their review that the “gut-brain axis” could be another direction to explore individual differences in cognition as the enteric microbial community plays a central role in brain function and development. As it is also linked with the

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hypothalamic-pituitary-adrenal axis (HPA) and encompasses neurological, immunological and hormonal pathways, it could have a direct influence on cognitive capacities (Davidson et al., 2018). Considering the idea of Goulet et al. (2018) to include a “cognitive style” to the POLS framework, which already comprises behavioural and physiological parameters, I would even state, that relationships between cognitive capacities and individual differences in behaviour should also consider physiological traits and such pathways such as the “gut-brain axis” as influencing factors; maybe also in ruminants, especially in dwarf goats.

5.2 Implications for Welfare and Outlook

As already mentioned in the introduction of this thesis, research about animal personality, especially farm animal personality and its implications for welfare, is growing of scientific and practical interest. Even the consumer of farm animal products and society itself show higher interest about the animal’s welfare during a farm animal’s lifetime and German politics as well as the German ethic council (Deutscher Ethikrat) discuss how animal welfare can be defined (5 degrees of freedom) and how it can be approved (Deutscher Ethikrat, 2020). German supermarkets use the societal interest for commercial purposes, e.g. the initiative of animal welfare (Initiative Tierwohl - Gesellschaft zur Förderung des Tierwohls in der Nutztierhaltung mbH, 2024) with four different categories focusing on housing conditions starting at the legal minimum (Stufe 1) going to a certain maximum of space and possibilities to enter an external area (Stufe 4) depending on the farm animal species’ thought requirement. One can criticize the motivation of this initiative, mainly because of the commercial purposes, but it is a start to go into a direction to approve farm animal housing conditions in a certain way. This

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initiative already exists for 10 years (status: 2024) and it would not, if the consumer would not accept it and buy the products which are higher priced, especially in the third and fourth category. The expansion of many different other animal welfare labels, such as Naturland, Bioland, Deutscher Tierschutzbund, to name a few, shows that the consumer is seeking to have a possibility to buy farm animal products with a certain certainty that the animals lived in “good conditions”. Even the German ethic council stated that research about behavioural, neurological and cognitive capacities of farm animals show remarkable results, which to a certain extend were seen as only human capacities before. These results are a prerequisite to understand farm animal needs to improve their welfare (Deutscher Ethikrat, 2020). A recent review by Döpjan & Dawkins (2022) go into the same direction focusing on stress. Chronic stress in humans is known to result in glucocorticoid receptor resistance that in turn leads to an inflammatory immune response and that reversely, hedonic wellbeing can reduce the risk of developing stress-related cardiovascular diseases (reviewed by Döpjan & Dawkins, 2022). They define the essence of stress as uncertainty, more precisely: „the feeling of uncertainty, when we anticipate that outcomes will turn out to be something other than expected – and that we are unable to avoid surprise“ (Döpjan & Dawkins, 2022). Considering housing and management conditions that farm animals have to encounter in their everyday life, the point „uncertainty“ or „not being able to control its environment“ can lead to a decrease of welfare. Studies done on pigs could show that a discrimination task with signal feeding stations (every sow had its own signal) could reduce agonistic interactions and therefore veterinary interventions on grouped-housed sows (Kirchner et al., 2012; Kirchner et al., 2014). The next step was to bring those controlled lab

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experimental results into practical conditions. The results of the next study showed that even sows living under limited livestock farming conditions were able to learn the discrimination task (Manteuffel et al., 2022). Studies on goats, showed that they seek for cognitive challenges, named as „contrafreeloading“ (Langbein et al., 2009; Rosenberger et al., 2020). The study conducted by Rosenberger et al. (2020) even showed that selection lines do not have an effect on seeking for cognitive challenges (here dairy goats versus dwarf goats), both selection lines were similar interested in contrafreeloading. A former study conducted on dwarf goats showed that environmental cognitive challenges also have a positive impact on physiological parameters such as heart rate (Langbein et al., 2004). In the mentioned study the dwarf goats were subjected to a visual discrimination task similar to the conducted study presented in the fourth chapter of this thesis. In the study conducted by Langbein et al. (2004) the dwarf goats' heart rate were recorded during rest. The results showed that heart rate decreased over trials indicating that the goats relaxed depending on how familiar they were with the task. Differences in physiological traits can also depend on individual differences on personality traits, as differences in personality can lead to differences how situations are perceived (reviewed by Finkemeier et al., 2018). Another aspect to consider, is the aspect of stability of personality traits. In the first study of this thesis, we conducted only one repetition of the open-field and novel-object tests. One can criticize that this repetition was conducted two weeks after the first test period. “Boldness” and “activity” were highly correlated between both test periods and were consistent over the two test periods. As our test animals had to encounter learning tasks at a certain age, we chose to measure personality differences before these tests started to obtain a better view about the

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relationship of personality and cognition in goats. When the interval between the observations of behaviour is short, it is likely that the animals are of a similar state (e.g., hunger, size, age, condition, dominance) during both observations and experience similar environments (Bell et al., 2009). A study in humans shows that different stages in human life can have an impact on personality traits: The examined people scored higher in the trait conscientiousness in their first year of working life (Asselmann & Specht, 2021). Extraversion and agreeableness got higher scores after the first year of working life and when the examined people got retired, the scores for conscientiousness decreased (Asselmann & Specht, 2021). Lifetime observations in male C57Bl/6 mice showed that a group of mice, which had to encounter learning tasks in an IntelliCage-system since young age, showed higher activity compared to a control group of mice without learning tasks under young age (Kahnau et al., 2021). A future direction in goat personality research could be to increase the delay between the two test periods or even adding a third test period. This could maybe show similar results in the expression of personality traits as in the study of Asselmann & Specht (2021) as the goats used in our studies were used for other experimental approaches and breeding afterwards. And lifetime observations in dwarf goats and other farm animal species, similar to the study of Kahnau et al. (2021) could also show interesting results in learning processes and their impact on individual behaviour of goats and other farm animal species. In pigs, Goursot et al. (2019) could show that the expression of personality traits is also influenced by brain lateralization: pigs, with a right-brain-hemispheric dominance were bolder and more explorative in context of novelty, and more sociable than pigs with a left-brain-hemispheric dominance. In general, farm animals have to encounter regroupment and other challenging

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situations, which can make the expression of certain personality traits more important than others. The aspect of brain-hemispheric dominance by Goursot et al. (2019) could also give interesting insights in cerebral processing of individual personality in goats. As already mentioned, the “gut-brain-axis” could be another future direction to consider in understanding expression of personality traits and cognitive capacities in dwarf goats. Especially in ruminants the whole gut system is of high scientific interest as they are thought to be the largest methane emission source (Pethani et al., 2024). Research in the last years on improving methane emission focussed on by selection of low-methane producing animals, dietary formulations, the addition of ruminal metabolic modifiers, or vaccinations (Pethani et al., 2024). Another study on dairy cows showed a relationship between personality and milk production (Schwanke et al., 2024): more active cows gave less milk and showed more agonistic behaviours during milking in an automated milking system than less active cows (Schwanke et al., 2024). Future directions could be to explore possible relationships between differences in the gut microbiome, the methane emission and individual differences in personality traits and cognitive capacities.

5.3 Conclusion

The second chapter of my thesis specifically dealt with the different definitions used in animal personality research and how these are used in farm animal personality research. My colleagues and I concluded that the terminology and definitions are often confusing and somehow species-related. We stated that the broad field of personality research generally needs more consistency in using theoretical concepts, terms and measures and we recommended that the terms

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should neither be regarded as synonyms nor as independent terms for consistent behavioural responses in animals, but as different aspects of the whole personality concept. Research on personality of farm animals focuses in particular on the phenotyping of personality traits and potential relationships with cognition, emotion and welfare.

The study presented in chapter three of this thesis showed that individual differences in personality in goats are consistent over time and provides insight into cross-context correlations between the behaviour in different test situations (single vs. group) and physiological parameters such as resting heart rate variability and weight gain. Based on two personality factors, “boldness” and “activity”, we found a comparatively small number of extreme personality types in our dwarf goat population, which is consistent with the results of studies in other wild and domestic animal species. The missing relationship to dominance hierarchy in this setup should be further investigated to prove if it is a personality trait in dwarf goats or if it is just a social outcome.

The study presented in the fourth chapter showed that the performance of the goats in the three reversal tasks depended on their learning success in the initial discrimination task in that low performers in the initial discrimination task also performed low in the reversal tasks. Only one personality trait, “boldness”, proved to have substantial consequences on learning performance in a reversal task: bold individuals show reduced behavioural flexibility, but they were able to adapt in the subsequent reversals once a new routine was formed. Our findings show that we should take personality bias into account when conducting learning or cognitive experiments and underline the importance of the repeated measurement of individual personality traits.

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Personality in farm animals is of growing scientific, practical and economic interest, because it has an obvious verifiable impact on the individual behavioural reaction to different housing systems, management practices and veterinary interventions and is therefore important for the improvement of animal welfare. But, there are some other aspects that in turn can have an impact on the expression of personality for instance age, environmental changes, gut microbiome or other. The mentioned aspects and examples such as brain-hemispheric dominance or the gut-brain-axis and how personality influences e.g. milk production presented in the „Implications for Welfare and Outlook“ section together with the described results in this thesis lead to my personal conclusion that if we want to improve farm animal welfare independently of the species, we as researchers, have to consider many aspects of farm animal behaviour, physiology, cognition and their interrelationships within an individual.

5.4 Summarising discussion and conclusion

Personality is a concept which encompasses many aspects of an individual. Figure 1 roughly explained in chapter one of this thesis the concept of personality:

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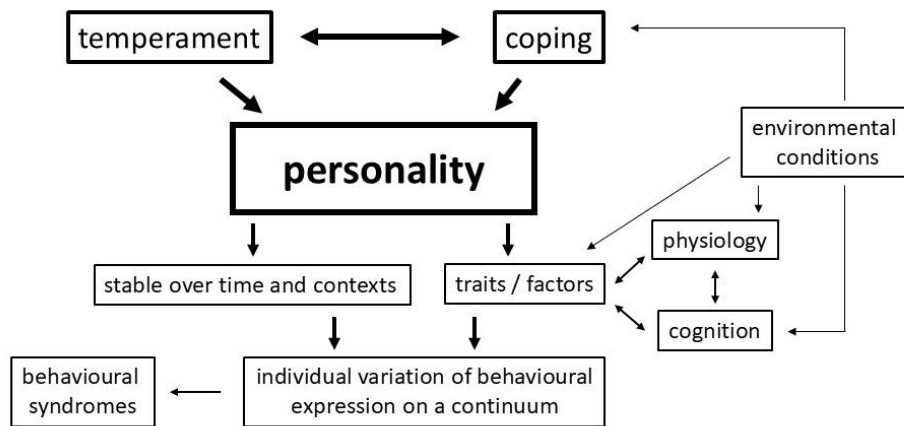


Figure 1: The concept of personality. The arrows describe relationships between components and parts of the personality concept.

The concept of personality is a broad field in (farm) animal research as well as in human psychology research. The whole concept for sure comprises many more components that need further investigation. Therefore, one of the main goals of this thesis was to understand this concept and to investigate how personality is expressed, in which form it is related to physiology, dominance hierarchy and cognitive capacities (here learning and reversal learning) in farm animals on the example of dwarf goats.

The aim of the review presented in chapter two was to give a comprehensive overview about how concepts and personality related terms are currently used in animal and especially farm animal personality research and to critically reveal how they are defined and what they measure. The results of my colleagues and me

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were, that the use of the term personality was quite scarce. We concluded that the terminology and definitions are often confusing and somehow species-related. While studies in different mammals, birds, and other taxa widely use the term personality to describe between-individual consistency in behavioural variation, in farm animal research the terms temperament and coping style are predominantly used, probably because personality might be associated with anthropomorphism. I repeated the literature search with the same mammalian farm animal species only including “personality” as keywords. I found over 1,500 publications addressing the investigation of aspects of personality, but also using the term personality. The use of the personality related terms seems to gain more and more clarity in our field. I conclude, that measuring aspects of personality in farm animals and naming it “personality” is not that scarce any more and I am eager to the results of future research.

In the third chapter my colleagues and I investigated personality traits in dwarf goats up to the formation of behavioural syndromes, to correlations with physiological traits and dominance hierarchy. The results of our conducted repeated principal component analysis showed that the same behavioural parameters load on the same principal components. Based on two personality factors, “boldness” and “activity”, we found a comparatively small number of extreme personality types in our dwarf goat population, which is consistent with the results of studies in other wild and domestic animal species. Moreover, the individual differences in personality in goats are consistent over time and provides insight into cross-context correlations between the behaviour in different test situations and physiological parameters. The missing relationship to dominance

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hierarchy in this setup should be further investigated to prove if it is a personality trait in dwarf goats or if it is just a social outcome.

In the fourth chapter my colleagues and I investigated the relationship of cognitive capacities, in form of a discrimination learning setup including one learning and three reversal learning tasks, and personality traits in dwarf goats. Many research with different species has already been done, but results were quite diverse and somehow species-related as some studies found relationships, while others did not. The results showed that the performance of the goats in the three reversal learning tasks depended on their learning success in the initial discrimination learning task in that low performers in the initial discrimination learning task also performed low in the reversal learning tasks. Only one personality trait, “boldness”, proved to have substantial consequences on learning performance in a reversal learning task: bold individuals showed reduced behavioural flexibility, but they were able to adapt in the subsequent reversals once a new routine was formed. These findings show that we should take personality bias into account when conducting learning or cognitive experiments and underline the importance of the repeated measurement of individual personality traits.

All in all, personality in farm animals is still of growing scientific, practical and economic interest, because it has an obvious verifiable impact on the individual behavioural reaction to different housing systems, management practices and veterinary interventions and is therefore important for the improvement of animal welfare.

Summary

Understanding individual differences in personality and its relation to cognitive abilities in farm animals, has gained increased attention for welfare purposes, because personality and its relationships to cognitive abilities may have an impact on economic factors as farm animals must cope with numerous challenging situations, automatic systems and different husbandry practises during their lifetime. Research about personality in goats is quite scarce, whereas cognitive capacities, especially discrimination learning is well studied in this species. In a former study, goats performing a cognitive task showed also a bolder response towards novel items indicating a relationship between learning and individual personality in this species. The aim of this thesis was to further investigate individual differences in personality and learning in this species. The behaviour of 108 Nigerian dwarf goats was measured in repeated open-field (OF) and novel-object (NO) tests to classify the subjects into proactive, reactive and intermediate personality types. Conducted principal component analysis helped to identify two main components: “boldness” and “activity”; 61% of the goats showed a consistent personality type. In parallel, the goats learned a 4-choice visual initial discrimination learning task and three subsequent reversal learning tasks. The results showed that goats with the lowest learning performance needed more trials in the first reversal and reached the learning criterion less frequently in the second and third reversal, suggesting a close relationship between initial learning and flexibility in learning behaviour. To study the link between personality and learning, the data from both OF- and NO-tests were integrated in the analysis. Stability in the trait “boldness” was found to have an effect on learning. Unbold

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goats outperformed bold goats in the first reversal. This finding supports the general hypothesis that bold animals tend to develop routines and show less flexibility in the context of learning than unbold individuals.

Zusammenfassung

Das Verständnis des Zusammenhangs zwischen individuellen Unterschieden in der Persönlichkeitsstruktur und kognitiven Fähigkeiten von Nutztieren hat aus Tierschutzgründen zunehmend an Bedeutung gewonnen, da der Zusammenhang zwischen Persönlichkeit und Kognition Auswirkungen auf wirtschaftliche Faktoren haben kann. Nutztiere sind im Laufe ihres Lebens zahlreichen Herausforderungen wie z. B. automatischen (Melk-)systemen und diversen Haltungsformen ausgesetzt. Persönlichkeitsstrukturen von Ziegen sind noch wenig erforscht, während die kognitiven Fähigkeiten, insbesondere im Diskriminierungslernen, gut untersucht sind. In einer früheren Studie zeigten Ziegen bei einer Lernaufgabe ein furchtloseres Verhalten gegenüber neuen Gegenständen. Dies deutet auf einen Zusammenhang zwischen Lernen und Persönlichkeitsstrukturen bei Ziegen hin. Ziel dieser Arbeit war es, individuelle Unterschiede in Persönlichkeit und Lernen bei Zwergziegen zu untersuchen. Das Verhalten von 108 nigerianischen Zwergziegen wurde in einem wiederholten Open-Field- (OF) und Novel-Object- (NO)-Test aufgenommen, um die Ziegen in proaktive, reaktive und intermediäre Persönlichkeitstypen zu klassifizieren. Durchgeführte Hauptkomponentenanalysen halfen bei der Identifizierung von zwei Hauptkomponenten: „Furchtlosigkeit“ und „Aktivität“; 61 % der Ziegen zeigten einen konsistenten Persönlichkeitstyp. Parallel dazu lernten die Zwergziegen vier Symbole in einer visuellen Diskriminierungsaufgabe und in drei Umkehrlernaufgaben zu unterscheiden. Die Ergebnisse zeigten, dass Zwergziegen mit der geringsten Lernleistung bei der ersten Umkehrlernaufgabe mehr Versuche benötigten um das Lernkriterium zu erreichen und dieses bei der zweiten und

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dritten Umkehrlernaufgabe seltener erreichten. Dies deutet auf eine enge Beziehung zwischen Lernen und Flexibilität im Lernverhalten hin. Um den Zusammenhang zwischen Persönlichkeit und Lernen zu untersuchen, wurden die Daten aus OF- und NO-Tests in die Analyse integriert. Es zeigte sich, dass das stabile Persönlichkeitsmerkmal „Furchtlosigkeit“ einen Einfluss auf das Lernen hat. Weniger furchtlose Zwergziegen schnitten bei der ersten Umkehrlernaufgabe besser ab als furchtlose Ziegen. Dieses Ergebnis unterstützt die allgemeine Hypothese, dass furchtlose Tiere dazu neigen, Routinen zu entwickeln und im Lernkontext weniger Flexibilität zeigen als weniger furchtlose Individuen.

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“Which is more important,” asked Big Panda, “the journey or the destination?”

“The company,” said Tiny Dragon

From “Big Panda and Tiny Dragon” by James Norbury, 2021

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Für Pope (1957-2019),

denn

“hinterm Horizont geht`s weiter

ein neuer Tag

Hinterm Horizont immer weiter

zusammen sind wir stark”

(Udo Lindenberg, 1986)

References

References

Affleck, G., Tennen, H. (1996). Construing benefits from adversity: Adaptional significance and dispositional underpinnings. *Journal of Personality*, 64: 899-922

Aldezabal, A., Garin, I. (2000). Browsing preference of feral goats (*Capra hircus* L.) in a Mediterranean mountain scrubland. *Journal of Arid Environments*, 44: 133–142

Arendt, J.D. (1997). Adaptive intrinsic growth rates: an integration across taxa. *The Quarterly Review of Biology*, 72: 149–177

Asselmann, E., Specht, J. (2021). Personality maturation and personality relaxation: Differences of the Big Five personality traits in the years around the beginning and ending of working life. *Journal of Personality*, 00: 1-17

Barroso, F.G., Alados, C.L., Boza, J. (2000). Social hierarchy in the domestic goat: effect on food habits and production. *Applied Animal Behavior Science*, 69: 35-53

Bebus, S.E, Small, T.W, Jones, B.C., Elderbrock, E.K., Schoech, S.J. (2016). Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure. *Animal Behavior*, 111: 251-260

Bell, A.M., Hankison, S.J., Laskowski, K.L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77: 771-783

Benus, R.F. (2001). Coping in female mice from lines bidirectionally selected for male aggression. *Behaviour*, 138: 997–1008

References

- Benus, R.F., Den Daas, S., Koolhaas, J.M., van Oortmerssen, G.A. (1990).** Routine formation and flexibility in social and non-social behaviour of aggressive and non-aggressive male mice. *Behaviour*, 112: 176–193
- Benus, R.F., Koolhaas, J.M., van Oortmerssen, G.A. (1987).** Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour*, 100: 105-122
- Biro, P.A., Abrahams, M.V., Post, J.R., Parkinson, E.A. (2006).** Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology*, 75: 1165–1171
- Biro, P.A., Stamps, J.A. (2008).** Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23: 361-368
- de Boer, S.F., van der Vegt, B.J., Koolhaas, J.M. (2003).** Individual variation in aggression of feral rodent strains: A standard for the genetics of aggression and violence? *Behavior Genetics*, 33: 485–501
- Bolhuis, J.E., Schouten, W.G.P., de Leeuw, J.A., Schrama, J.W., Wiegant, V.M. (2004).** Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behavioral Brain Research*, 152: 351-360
- Brajon, S., Laforest, J. P., Schmitt, O., Devillers, N. (2016).** A preliminary study of the effects of individual response to challenge tests and stress induced by humans on learning performance of weaned piglets (*Sus scrofa*). *Behavioural Processes*, 129: 27-36

References

- Briefer, E.F., de la Torre, M.P., McElligott, A.G. (2012).** Mother goats do not forget their kids' calls. *Proceedings of the Royal Society B Biological Science*, 279: 3749–3755
- Briefer, E.F., Haque, S., Baciadonna, L., McElligott, A.G. (2014).** Goats excel at learning and remembering a highly novel cognitive task. *Frontiers in Zoology*, 11, 20
- Briefer, E.F., McElligott, A.G. (2012).** Social effects on vocal ontogeny in an ungulate, the goat, *Capra hircus*. *Animal Behaviour*, 83: 991–1000
- Brust, V., Wuerz, Y., Krüger, O. (2013).** Behavioural flexibility and personality in zebra finches. *Ethology*, 119: 559-569
- Bullock, D.H., Bitterman, M.E. (1962).** Habit reversal in the pigeon. *Journal of Comparative and Physiological Psychology*, 55, 958-962
- Burns, J.G., Rodd, F.H. (2008).** Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. *Animal Behaviour*. 76: 911–922
- Buss, A.H. (1987).** Personality: primate heritage and human distinctiveness. In: Aronoff, J., Rabin, A. (Eds.), *Emergence of Personality*. Springer Publishing Co., New York, NY, pp. 57–101
- Buss, A.H. (1995).** *Personality: Temperament, social behavior and the self*. Needham Heights, MA: Allyn & Bacon

References

- Campbell, T., Lin, S., DeVries, C., Lambert, K. (2003).** Coping strategies in male and female rats exposed to multiple stressors. *Physiology & Behaviour*. 78: 495–504
- Cannon, W.B. (1929).** Bodily Changes in Pain, Hunger, Fear and Rage. New York, NY: Appleton
- Carere, C.; Locurto, C. (2011).** Interaction between animal personality and animal cognition. *Current Zoology*, 57: 491-498
- Carter, A.J., Feeney, W.E., Marshall, H.H., Cowlshaw, G., Heinsohn, R. (2013).** Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, 88: 465–475
- Carver, C.S., Connor-Smith, J. (2010).** Personality and coping. *Annual Review of Psychology*, 61: 679–704
- Christensen, J.W., Ahrendt, L.P., Malmkvist, J., Nicol, C. (2021).** Exploratory behavior towards novel objects is associated with enhanced learning in young horses. *Scientific Reports*, 11: 1428
- Chung, M., Goulet, C.T., Michelangeli, M., Wong, B.B.M, Chapple, D.G. (2017).** Does personality influence learning? A case study in an invasive lizard. *Oecologia*, 185: 641–651.
- Cockrem, J.F. (2007).** Stress, corticosterone responses and avian personalities. *Journal of Ornithology*, 148: 169-178

References

- Coppens, C.M., de Boer, S.F., Koolhaas, J.M. (2010).** Coping styles and behavioural flexibility: towards underlying mechanisms. *Philosophical Transactions of the Royal Society B*, 365: 4021-4028
- Čukić, I., Bates, T.C. (2014).** Heart rate variability and adult personality: A nationally representative study. *Personality and Individual Differences*, 60: 31
- Dall, S.R.X., Houston, A.I., McNamara, J.M. (2004).** The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7: 734-739
- Davidson, G.L., Cooke, A.C., Johnson, C.N., Quinn, J.L. (2018).** The gut microbiome as a driver of individual variation in cognition and functional behaviour. *Philosophical Transactions of the Royal Society B*, 373: 20170286
- Delacoux, M. Guenther, A. (2023).** Stressfulness of the design influences consistency of cognitive measures and their correlation with animal personality traits in wild mice (*Mus musculus*). *Animal Cognition*, 26: 997-1009
- Delval, I., Fernández-Bolaños, M., Izar, P. (2024).** Towards an Integrated Concept of Personality in Human and Nonhuman Animals. *Integrative Psychological and Behavioral Science*, 58: 271-302
- Desire, S., Turner, S.P., D'Eath, R.B., Doeschl-Wilson, A.B., Lewis, C.R.G., Roehe, R. (2015).** Analysis of the phenotypic link between behavioural traits at mixing and increased long-term social stability in group-housed pigs. *Applied Animal Behavior Science*, 166: 52-62

References

- Deutscher Ethikrat (2020).** Tierwohlachtung – Zum verantwortlichen Umgang mit Nutztieren – Stellungnahme. *Deutscher Ethikrat*: Berlin
- Dingemanse, N.J., Dochtermann, N.A., Nakagawa, S. (2012).** Defining behavioural syndromes and the role of ‘syndrome deviation’ in understanding their evolution. *Behavioral Ecology and Sociobiology*, 66: 1543–1548
- Dingemanse, N.J., Kazem, A.J., Réale, D., Wright, J. (2010).** Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25: 81—89.
- Dingemanse, N.J., Wright, J. (2020).** Criteria for acceptable studies of animal personality and behavioural syndromes. *Ethology*, 126: 865–869
- Dougherty, L.R.; Guillelte, L.M. (2018).** Linking personality and cognition: a meta-analysis. *Philosophical Transactions of the Royal Society B*, 373: 20170282
- Dugatkin, L.A., Alfieri, M.S. (2003).** Boldness, behavioral inhibition and learning. *Ethology. Ecology and Evolution*, 15: 43-49
- Dukas, R. (2004).** Evolutionary biology of animal cognition. *Annual Review of Ecology, Evolution and Systematics*, 35: 347-374
- Düpjan, S., Dawkins, M.S. (2022).** Animal Welfare and Resistance to Disease: Interaction of Affective States and the Immune System. *Frontiers in Veterinary Science*, 9: 929805.
- FAO (2018).** FAOSTAT - Livestock Primary [WWW Document]. URL <http://www.fao.org/faostat/en> (accessed 4.18.20).

References

- Finkemeier, M.-A., Langbein, J., Puppe, B. (2018).** Personality research in mammalian farm animals: Concepts, measures, and relationship to welfare. *Frontiers in Veterinary Science*, 5:131
- Finkemeier, M.-A., Oesterwind, S., Nürnberg, G., Puppe, B., Langbein, J. (2019).** Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses. *Applied Animal Behavior Science*, 217, 28-35
- Foris, B., Lecorps, B., Krahn, J., Weary, D.M., von Keyserlingk, M.A.G. (2021).** The effects of cow dominance on the use of a mechanical brush. *Scientific Reports*, 11, 22987
- Foris, B., Zebunke, M., Langbein, J., Melzer, N. (2018).** Evaluating the temporal and situational consistency of personality traits in adult dairy cattle. *Plos One*, 13: 1-16
- Forkman, B., Boissy, A., Meunier-Salaün, M.-C., Canali, E., Jones, R.B. (2007).** A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiology & Behaviour*, 92: 340-374
- Franks, B., (2019).** What do animals want? *Animal Welfare*, 28: 1–10
- Goldberg, L.R. (1993).** The structure of phenotypic personality traits. *American Psychologist*, 48: 26-34
- Goldsmith, H., Buss, A., Plomin, R., Rothbart, M., Thomas, A., Chess, S., Hinde, R., McCall, R. (1987).** Roundtable: What is temperament? Four approaches. *Child Development*, 8: 505-529

References

- Gosling, S.D. (2001).** From mice to men: What we can learn about personality from animal research? *Psychological Bulletin*, 127: 45-86
- Gosling, S.D., John, O.P. (1999).** Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, 8: 69-75
- Goulet, C.T., Michelangeli, M., Chung, M., Riley, J.L., Wong, B.B.M., Thompson, M.B., Chapple, D.G. (2018).** Evaluating cognition and thermal physiology as components of the Pace-of-Life syndrome. *Evolutionary Ecology*, 32: 469-488
- Goursot, C., Döpjan, S., Kanitz, E., Tuchscherer, A., Puppe, B., Leliveld, L. (2019).** Assessing animal individuality: links between personality and laterality in pigs. *Current Zoology*, 65: 541-551
- Graunke, K.L., Nürnberg, G., Repsilber, D., Puppe, B., Langbein, J. (2013).** Describing Temperament in an Ungulate: A Multidimensional Approach. *Plos One*, 8: 1-12
- Griffin, A.S, Guillelte, L.M., Healy, S.D. (2015).** Cognition and personality: an analysis of an emerging field. *Trends in Ecology & Evolution*, 30: 207-214
- Guenther, A., Brust, V., Dersen, M., Trillmich, F. (2014a).** Learning and personality types are related in Cavies (*Cavia aperea*). *Journal of Comparative Psychology*, 128: 74-81
- Guenther, A., Finkemeier, M.-A., Trillmich, F. (2014b).** The ontogeny of personality in the wild guinea pig. *Animal Behaviour*, 90: 131–139

References

- Guenther, A., Goerlich, V.C., Groneberg, E., Grothuis, A.G.G. (2024).** Short- and long-term effects of endogenous cortisol on personality traits and behavioural syndromes. *Animal Behaviour*, 211: 69-80
- Guillette, L.M., Reddon, A.R., Hoeschele, M., Sturdy, C.B. (2011).** Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. *Proceedings of the Royal Society B*, 278: 767–773
- Guillette, L.M., Reddon, A.R., Hurd, P.L., Sturdy, C.B. (2009).** Exploration of a novel space is associated with individual differences in learning speed in black capped chickadees, *Parus atricapillus*. *Behavioural Processes*, 82: 207-214.
- Hagen, K., Broom, D.M. (2004).** Emotional reactions to learning in cattle. *Applied Animal Behavior Science*, 85: 203–213
- Harcourt, J.L., Biau, S., Johnstone, R., Manica, A. (2010).** Boldness and Information Use in Three-Spined Sticklebacks. *Ethology*, 116: 440-447
- Hasenpusch, P., Wilder, T., Seidel, A., Thaller, G. (2024).** Dairy cow personality: Consistency in a familiar testing environment. *JDS Communications*, 5: 511-515
- Henry, J.P., Stephens, P.M. (1977).** Stress, Health, and the Social environment. Springer, New York
- van Horik, J.O., Emery, N.J. (2018).** Serial reversal learning and cognitive flexibility in two species of Neotropical parrots (*Diopsittaca nobilis* and *Pionites melanocephalia*). *Behavioural Processes*, 157: 664-672

References

- Houle, M.S., Billman, G.E. (1999).** Low-frequency component of the heart rate spectrum: a poor marker of sympathetic activity. *American Journal of Physiology-Heart and Circulatory Physiology*, 276: 215–223
- Huang, P., Kimball, R.T., St Mary, C.M. (2018).** Does the use of a multi-trait, multi-test approach to measure animal personality yield different behavioural syndrome results? *Behaviour*, 155: 115-150
- Initiative Tierwohl – Gesellschaft zur Förderung des Tierwohls in der Nutztierhaltung mbH (2024).** Pressemitteilung: Initiative Tierwohl startet in ihr 10. Jahr: so geht es ab Januar 2025 weiter. www.initiative-tierwohl.de (last download: 18.08.2024)
- Izquierdo, A., Brigman, J.L., Radke, A.K., Rudebeck, P.H., Holmes, A. (2017).** The neural basis of reversal learning: An updated perspective. *Neuroscience*, 345: 12–26.
- John, O.P., Srivastava, S. (1999).** The Big Five trait taxonomy: history, measurement and theoretical perspectives. In: *Handbook of personality: theory and research*. New York: Guilford, pp. 102-138
- Johansen, F.P., Buijs, S., Arnott, G. (2025).** Social rank and personality are associated with visit frequency in dairy cows learning to use an automatic milking system. *Animal*, 19: 101446
- Jones, A.C., Gosling, S.D. (2005).** Temperament and personality in dogs (*Canis familiaris*): a review and evaluation of past research. *Applied Animal Behaviour Science*, 95: 1–53

References

- Kahnau, P., Guenther, A., Boon, M.N., Terzenbach, J.D., Hanitzsch, E., Lewejohann, L., Brust, V. (2021).** Lifetime Observation of Cognition and Physiological Parameters in Male Mice. *Frontiers in Behavioral Neuroscience*, 15:709775
- Kaiser, M.I., Müller, C. (2021).** What is animal personality? *Biology and Philosophy*, 36:1
- Keil, N.M., Imfeld-Mueller, S., Aschwanden, J., Wechsler, B. (2012).** Are head cues necessary for goats (*Capra hircus*) in recognising group members? *Animal Cognition*, 15: 913–921
- Khatiwada, S., Turner, S.P., Farish, M., Camerlink, I. (2024).** Leadership amongst pigs when faced with a novel situation. *Behavioural Processes*, 222:105099
- Kirchner, J., Manteuffel, C., Manteuffel, G., Schrader, L. (2014).** Learning performance of gestating sows called to the feeder. *Applied Animal Behaviour Science*, 153: 18–25.
- Kirchner, J., Manteuffel, G., Schrader, L. (2012).** Individual calling to the feeding station can reduce agonistic interactions and lesions in group housed sows. *Journal of Animal Science*, 90: 5013–5020.
- Kitaysky, A.S., Kitaiskaia, E.V., Piatt, J.F., Wingfield, J.C. (2003).** Benefits and costs of increased levels of corticosterone in seabird chicks. *Hormones & Behavior*, 43: 140-149

References

- de Kloet, E.R., Oitzl, M.S., Joels, M. (1999).** Stress and cognition: are corticosteroids good or bad guys? *Trends in Neuroscience*, 22: 422-426
- Kniel, N., Guenther, A., Godin, J.-G.J. (2020).** Individual personality does not predict learning performance in a foraging context in female guppies, *Poecilia reticulata*. *Animal Behavior*, 167: 3-12
- Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A., Blokhuis, H.J. (1999).** Coping styles in animals: current status in behaviour and stress-physiology. *Neuroscience and Biobehavioral Reviews*, 23: 925–35.
- Korte, S.M., Beuving, G., Ruesink, W., Blokhuis, H.J. (1997).** Plasma catecholamine and corticosterone levels during manual restraint in chicks from a high and low feather pecking line of laying hens. *Physiology & Behavior*, 62: 437–441
- Korte, S.M., Koolhaas, J.M., Wingfield, J.C., McEwen, B.S. (2005).** The Darwinian concept of stress: benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neuroscience and Biobehavioral Reviews*, 29: 3–38
- Krause, A., Puppe, B., Langbein, J. (2017).** Coping style modifies general and affective autonomic reactions of domestic pigs in different behavioral contexts. *Frontiers in Behavioral Neuroscience*, 11

References

- Langbein, J. (2012).** Investigations on training, recall and reversal learning of a Y-maze by dwarf goats (*Capra hircus*): the impact of lateralisation. *Behavioral Processes*, 89: 304–10
- Langbein, J., Moreno-Zambrano, M., Siebert, K. (2023).** How do goats “read” 2D-images of familiar and unfamiliar conspecifics? *Frontiers in Psychology*, 14:1089566
- Langbein, J., Nürnberg, G., Manteuffel, G. (2004).** Visual discrimination learning in dwarf goats and associated changes in heart rate and heart rate variability. *Physiology & Behavior*, 82: 601-609
- Langbein, J., Siebert, K., Nürnberg, G. (2009).** On the use of an automated learning device by group-housed dwarf goats: Do goats seek cognitive challenges? *Applied Animal Behavior Science*, 120: 150–158
- Lansade, L., Simon, F. (2010).** Horses’ learning performances are under the influence of several temperamental dimensions. *Applied Animal Behavior Science*, 125: 30-37
- Lazarus, R.S. (1993).** Coping theory and research: past, present, and future. *Psychosomatic Medicine*, 55: 234–247
- Lazarus, R.S., Folkman, S. (1984).** Stress, Appraisal, and Coping. New York: Springer
- Liu, Y., Day, L.B., Summers, K., Burmeister, S.S. (2016).** Learning to learn: advanced behavioural flexibility in a poison frog. *Animal Behavior*, 111: 167–172.

References

- Lucon-Xiccato, T., Bisazza, A. (2014).** Discrimination reversal learning reveals greater female behavioural flexibility in guppies. *Biology Letters*, 10, 20140206.
- Malik, M., Camm, A.J. (1995).** Heart Rate Variability. Armonk, NY: Futura Publishing Company
- Manteuffel, C., Puppe, B., Hartwig, T., Wirthgen, E. (2022).** Learning, health and productivity of group-housed sows conditioned to signal-feeding under realistic husbandry conditions. *Livestock Science*, 266: 105111
- Martin, A.K. (2023).** The Moral Implications of Human and Animal Vulnerability. *Palgrave macmillan*. Springer Nature: Switzerland
- Martins, C.I.M., Schrama, J.W., Verreth, J.A.J. (2005)** The consistency of individual differences in growth, feed efficiency and feeding behaviour in African catfish *Clarias gariepinus* (Burchell 1822) housed individually. *Aquaculture Research*, 36: 1509–1516
- Mason, W.A. (1984).** Animal learning: experience, life modes and cognitive style. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 77: 45-56
- Mazza, V., Guenther, A. (2021).** City mice and country mice: innovative problem solving in rural and urban noncommensal rodents. *Animal Behaviour*, 172: 197-210
- McCrae, R.R., John, O.P. (1992).** An introduction to the Five-Factor Model and its applications. *Journal of Personality*, 60: 175-215

References

- McCrae, R.R., Costa, J.R., Paul, T., Ostendorf, F., Angleitner, A., Hřebíčková, M., Avia, M.D., Sanz, J., Sánchez-Bernardos, M.L., Kusdil, M.E., Woodfield, R., Saunders, P.R., Smith, P.B. (2000).** Nature over nurture: Temperament, personality and life span development. *Journal of Personality and Social Psychology*, 78: 173-186
- Mellor, D.J., Beausoleil, N.J., Littlewood, K.E., McLean, A.N., McGreevy, P.D., Jones, B., Wilkins, C. (2020).** The 2020 Five Domains Model: Including Human-Animal Interactions in Assessments of Animal Welfare. *Animals*, 10: 1870
- Meyer, S., Nürnberg, G., Puppe, B., Langbein, J. (2012).** The cognitive capabilities of farm animals: Categorisation learning in dwarf goats (*Capra hircus*). *Animal Cognition*, 15: 567– 576
- Moos, R.H. (1993).** Coping Response Inventory Youth Form: Professional Manual. Odessa, FL: Psychological Assessment Resources, Inc.
- Nawroth, C., Langbein, J., Coulon, M., Gabor, V., Oesterwind, S., Benz-Schwarzburg, J., von Borell, E. (2019).** Farm Animal Cognition—Linking Behavior, Welfare and Ethics. *Frontiers in Veterinary Science*, 6: 24
- Nawroth, C., Prentice, P.M., McElligott, A.G. (2017).** Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. *Behavioral Processes*, 134: 43–53
- Nawroth, C., von Borell, E., Langbein, J. (2015).** Object permanence in the dwarf goat (*Capra aegagrus hircus*): Perseveration errors and the tracking of

References

complex movements of hidden objects. *Applied Animal Behavior Science*, 167: 20–26

Neave, H.W., Zobel, G., Thoday, H., Saunders, K., Edwards, J.P., Webster, J. (2022). Toward on-farm measurement of personality traits and their relationships to behavior and productivity of grazing dairy cattle. *Journal of Dairy Science*, 105: 6055-6069

Occhiuto, F., Vázquez-Diosdado, J.A., King, A.J., Kaler, J. (2023). Using precision technology to investigate personality and plasticity of movement in farmed calves and their associations with weight gain. *Animal – Science Proceedings*, 14: 406

Oesterwind, S., Nürnberg, G., Puppe, B., Langbein, J. (2016). Impact of structural and cognitive enrichment on the learning performance, behavior and physiology of dwarf goats (*Capra aegagrus hircus*). *Applied Animal Behavior Science*, 177: 34–41

Osborne, S.R. (1977). The free food (contrafreeloading) phenomenon: A review and analysis. *Animal Learning and Behavior*, 5: 221–235

Papadaki, K., Samaras, A., Pavlidis, M., Pafilis, P., Bizelis, I., Koutsouli, P., Laliotis, G.P. (2025). Association of sheep (*Ovis aries*) personality profiles with physiological and productive characteristics under intensive production system. *Applied Animal Behaviour Science*, 283: 106497

References

- Perals, D., Griffin, A.S., Bartomeus, I., Sol, D. (2017).** Revisiting the open-field test: what does it really tell us about animal personality? *Animal Behaviour*, 123: 69-79
- Pethani, K.B., Geick, T., Kuhla, B. (2024).** A pilot study to capture methane from exhausted air of dairy cows using a cryogenic approach. *Journal of Environmental Management*, 356:120588
- Poindron, P., Gilling, G., Hernandez, H., Serafin, N., Terrazas, A. (2003).** Early recognition of newborn goat kids by their mother: I. Non olfactory discrimination. *Developmental Psychobiology*, 43: 82–89
- Porges, S.W. (1995).** Cardiac vagal tone: A physiological index of stress. *Neuroscience and Biobehavioral Reviews*, 19: 225-233
- Pravosudov, V.V., Mendoza, S.P., Clayton, N.S. (2003).** The relationship between dominance, corticosterone, memory, and food caching in mountain chickadees (*Parus gambeli*). *Hormones & Behavior*, 44: 93-102
- Provenza, F.D., Lynch, J.J., Burritt, E.A., Scott, C.B. (1994).** How goats learn to distinguish between novel foods that differ in postingestive consequences. *Journal of Chemical Ecology*, 20: 609– 624
- Pubols Jr., B.H. (1957).** Successive discrimination reversal learning in the white rat: A comparison of two procedures. *Journal of Comparative and Physiological Psychology*, 50: 319-322
- Range, F., Bugnyar, T., Schlägl, C., Kotrschal, K. (2006).** Individual and sex differences in learning abilities of ravens. *Behavioral Processes*, 73: 100–106

References

- Rasolofoniaina, B.N., Kappeler, P.M., Fichtel, C. (2021).** Neophobia and social facilitation in narrow-striped mongooses. *Animal Cognition*, 24: 165-175
- Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V., Montiglio, P.-O. (2010).** Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365: 4051-4063
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J. (2007).** Integrating animal temperament within ecology and evolution. *Biological Reviews of the Cambridge Philosophical Society*, 82: 291–318
- Rosenberger, K., Simmler, M., Nawroth, C., Langbein, J., Keil, N. (2020).** Goats work for food in a contrafreeloading task. *Scientific Reports*, 10: 22336
- Rothbart, M.K., Ahadi, S.A., Evans, D.E. (2000).** Temperament and personality: Origins and outcomes. *Journal of Personality and Social Psychology*, 78: 122-135
- Schmitt, D.P., Realo, A., Voracek, M., Allik, J. (2008).** Why can't a man be more like a woman? Sex differences in Big Five Personality Traits across 55 cultures. *Journal of Personality and Social Psychology*, 94: 168-182
- Schwanke, A.J., Dancy, K.M., Neave, H.W., Penner, G.B., Bergeron, R., DeVries, T.J. (2024).** Impact of dairy cows personality traits and concentrate allowance on their response to training and adaptation to an automated milking system. *Journal of Dairy Science*, 107: 11446-11462

References

- Setser, M.M.W., Neave, H.W., Costa, J.H.C. (2024).** Individuality of calves: Linking personality traits to feeding and activity daily patterns measured by precision livestock technology. *Journal of Dairy Science*, 107: 3235-3251
- Shettleworth, S.J. (2001).** Animal cognition and animal behaviour. *Animal Behaviour*, 61: 277-286
- Shettleworth, S.J. (2010).** Cognition, evolution and behaviour. 2nd edn. *Oxford University Press*, Oxford
- Sih, A. (2013).** Frontiers on the interface between behavioral syndromes and social behavioral ecology. In C. Claudio, & D. Maestripieri (Eds.), *Animal personalities: Behavior, physiology and evolution* (pp. 221e251). Chicago, IL: University of Chicago Press.
- Sih, A., Bell, A., Chadwick Johnson, J. (2004).** Behavioural syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19: 372-378
- Sih, A., Del Giudice, M. (2012).** Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B*, 367: 2762–2772
- Sinn, D.L., Gosling, S.D., Moltschaniwskyj, N.A. (2008).** Development of shy/bold behaviour in squid: context-specific phenotypes associated with developmental plasticity. *Animal Behavior*, 75: 433-442

References

- Slipogor, V., Graf, C., Massen, J.J.M., Bugnyar, T. (2022).** Personality and social environment predict cognitive performance in common marmosets (*Callithrix jacchus*). *Scientific Reports*, 12, 6702
- Sorato, E., Zidar, J., Garnham, L., Wilson, A., Løvlie, H. (2018).** Heritabilities and co-variation among cognitive traits in red junglefowl. *Philosophical Transactions of the Royal Society B*, 373, 20170285
- Stamps, J.A. (2007).** Growth-mortality tradeoffs and ‘personality’ traits in animals. *Ecology Letters*, 10: 355–363
- Tembrock, G. (1978).** Wörterbücher der Biologie: Verhaltensbiologie. *Gustav Fischer Verlag*, Stuttgart, New York
- Thomas, A., Chess, S. (1977).** Temperament and development. New York: Brunner/Mazel
- Thomson, J.S., Watts, P.C., Pottinger, T.G., Sneddon, L.U. (2012).** Plasticity of boldness in rainbow trout: *oncorhynchus mykiss*: do hunger and predation influence risk-taking behaviour? *Hormones & Behavior*, 61: 750–757
- Titulaer, M., van Oers, K., Naguib, M. (2012).** Personality affects learning performance in difficult tasks in a sex-dependent way. *Animal Behaviour*, 83: 723-730.
- Trompf, L., Brown, C. (2014).** Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. *Animal Behaviour*, 88: 99-106

References

- Valenchon, M., Lévy, F., Fortin, M., Leterrier, C., Lansade, L. (2013a).** Stress and temperament affect working memory performance for disappearing food in horses, *Equus caballus*. *Animal Behaviour*, 86: 1233-1240
- Verbeek, M.E.M, Boon, A., Drent, P.J. (1996).** Exploration, aggressive behavior and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, 113: 945–963
- Vickery, H.M., Johansen, F.P., Meagher, R.K. (2024).** Evaluating the consistency of dairy goat kids’ responses to two methods of assessing fearfulness. *Applied Animal Behaviour Science*, 272: 106209
- Wat, K.K.Y., Banks, P.B. and McArthur, C. (2020).** Linking animal personality to problem-solving performance in urban common brushtail possums. *Animal Behaviour*, 16, 35-45.
- Webb, L.E., van Reenen, C.G., Jensen, M.B., Schmitt, O., Bokkers, E.A.M. (2015).** Does temperament affect learning in calves? *Applied Animal Behaviour Science*, 165: 33-39
- Wechsler, B. (1995).** Coping and coping strategies: a behavioural view. *Applied Animal Behaviour Science*, 43: 123-134
- Weinandy, R. (2006).** Kognition. In: Gattermann R (Hrsg.): Wörterbuch zur Verhaltensbiologie der Tiere und des Menschen. *Spektrum Akademisches Verlag*, München, 165

References

- Zebunke, M., Repsilber, D., Nürnberg, G., Wittenburg, D., Puppe, B. (2015).** The backtest in pigs revisited—An analysis of intra-situational behaviour. *Applied Animal Behaviour Science*, 169: 17-25
- Zentner, M., Bates, J.E. (2008).** Child temperament: An integrative review of concepts, research programs, and measures. *European Journal of Developmental Psychology*, 2: 7-37
- Zidar, J., Balogh, A., Favati, A., Jensen, P., Leimar, O., Sorato, E., Løvlie, H. (2018).** The relationship between learning speed and personality is age- and task-dependent in red junglefowl. *Behavioral Ecology and Sociobiology*, 72: 168
- Zobel, G., Nawroth, C. (2020).** Current state of knowledge on the cognitive capacities of goats and its potential to inform species-specific enrichment. *Small Ruminant Research*
- Zobel, G., Neave, H.W., Webster, J. (2019).** Understanding natural behavior to improve dairy goat (*Capra hircus*) management systems. *Translational Animal Science*, 3: 212–224

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10.2010 – 10.2013: Master's program "Systems of Biology of Brain and Behaviour" at the University of Bielefeld

01.2010 – 09.2010: Bachelor Thesis at the University of Bielefeld, Faculty of Biology, Department for Cognitive Sciences. Supervisors: Dr. Kai Petra Stich; Prof. Dr. York Winter

10.2007 – 09.2010: Bachelor's program "Biologie" at the University of Bielefeld

Curriculum Vitae

12.2006 – 09.2007: Bachelor's program "Biologie" at RWTH Aachen University

2006: Higher education entrance qualification (Abitur) Herder Gymnasium
Minden

1993 – 1997: Primary School Grundschule Domschule Minden

Languages

English: High Level

French: Native Speaker

German: Native Speaker

Technical Skills

Statistical Analysis: „R“; „JMP“; „SAS“; „Matman“; „SPSS“; „Statistica“

Video Analysis: „Observer“ (Noldus Information Technology, The Netherlands)

Data Analysis: „Polar ProTrainer 5“ (Polar Electro Oy, Finland) + „Kubios
HRV“ (Biosignal Analysis and Medical Imaging Group, Finland)

Science popularization

08.2016 – 07.2018: Representative for Public Relations of the PhD-Students of
the Research Institute for Farm Animal Biology (FBN) in Dummerstorf

26.04.2018: "Long night of sciences", University of Rostock – "Why can
behaviour help improving animal welfare?" Animation in German of the FBN
stand, in cooperation with Dr. Charlotte Goursot and Dr. Norbert Borowy

Curriculum Vitae

12.01.2018: “Science caravan“, FBN Dummerstorf – planning, organization and execution together with Dr. Robert Uhde (SphinxAg) and other PhD-students of the FBN. Animation for German pupils (up to 120) and local TV station (NDR)

12.01.2017: “Science caravan“, FBN Dummerstorf – planning, organization and execution together with Dr. Robert Uhde (SphinxAg) and other PhD-students of the FBN. Animation for German pupils (up to 120)

29.04.2016: “Long night of sciences“, University of Rostock – Support in German of the FBN stand for Dr. Christian Manteuffel

List of Publications

Peer-reviewed journal articles

Finkemeier, M.-A., Krause, A., Tuchscherer, A., Puppe, B., Langbein, J. (2022). Personality traits affect learning performance in dwarf goats (*Capra hircus*). *Frontiers in Veterinary Science*, 9:916459.
<https://10.3389/fvets.2022.916459>

Finkemeier, M.-A., Oesterwind, S., Nürnberg, G., Puppe, B., Langbein, J. (2019). Assessment of personality types in Nigerian dwarf goats (*Capra hircus*) and cross-context correlations to behavioural and physiological responses. *Applied Animal Behaviour Science*, 217: 28-35
<https://doi.org/10.1016/j.applanim.2019.05.004>

Finkemeier, M.-A., Langbein, J., Puppe, B. (2018). Personality research in mammalian farm animals: Concepts, measures, and relationship to welfare. *Frontiers in Veterinary Science*, 5:131 <https://doi.org/10.3389/fvets.2018.00131>

Finkemeier, M.-A., Trillmich, F., Guenther, A. (2016). Match-mismatch experiments using photoperiod expose developmental plasticity of personality traits. *Ethology*, 122: 80-93 <https://doi.org/10.1111/eth.12448>

Guenther, A., Finkemeier, M.-A., Trillmich, F. (2014). The ontogeny of personality in the wild guinea pig. *Animal Behaviour*, 90: 131–139
<https://doi.org/10.1016/j.anbehav.2014.01.032>

List of Publications

Dissertation

Finkemeier, M.-A. (2025). Assessment of individual personality and the effect of personality traits on discrimination learning in Nigerian dwarf goats (*Capra aegagrus hircus*). *Cumulative dissertation for the Dr. agr. (PhD) degree. Submitted in June 2025. Defended on the 5th Decembre 2025*

Chapter

Finkemeier, M.-A., Nawroth, C., Langbein, J. (2018). Personality und ihr Einfluss auf kognitive Prozesse bei Ziegen. *IGN-Schrift „Nutztierhaltung im Fokus“ ISBN: 978-3-9524555-6-2*

Conference Proceedings

Finkemeier, M.-A., Tuchscherer, A., Puppe, B., Langbein, J. (2019). Eigenschaften von „personality“ beeinflussen die kognitiven Fähigkeiten von westafrikanischen Zwergziegen (*Capra aegagrus hircus*). *Aktuelle Arbeiten zur artgemäßen Tierhaltung 2019 (Konferenzband), KTBL-Schrift 515: 135-148*

Finkemeier, M.-A., Oesterwind, S., Puppe, B., Langbein, J. (2016). Beschreibung von personality-Typen bei westafrikanischen Zwergziegen (*Capra aegagrus hircus*). *Aktuelle Arbeiten zur artgemäßen Tierhaltung 2016 (Konferenzband), KTBL-Schrift 511: 221-235*

List of Publications

Finkemeier, M.-A., Trillmich, F., Guenther, A. (2014). Einfluss der Photoperiode auf Verhalten und Physiologie beim Wildmeerschweinchen (*Cavia aperea*) während der Ontogenese. *Aktuelle Arbeiten zur artgemäßen Tierhaltung 2014 (Konferenzband)*, KTBL-Schrift 505: 222-232