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Early Experiences, Maternal Care and Behavioural Test Design

Effects on the Temperament of Military Working Dogs

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Front and back cover: German Shepherd pup
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"A dog´s got personality and
personality goes a long way."

Jules Winnfield, from the movie *Pulp Fiction*

ABSTRACT

Domestication has resulted in animals with broad variations between as well as within breeds, which allows for the selection and breeding of animals for preferred traits. This selection has affected both the genotypes and phenotypes of animals. In dogs, it has allowed for breeding for different purposes, such as companionship or the performance of specific tasks, e.g., herding, hunting, searching and protecting. Each of these types of working dogs has specific traits that are, in part, controlled by genes; however, genes are not solely responsible for the variations in the traits of an individual. The environment also plays a role, which has been studied in rodents and primates in recent decades. For instance, it has been shown that the amount of maternal care that a rat receives as a pup affects its temperament later in life; the more maternal care, i.e., licking, grooming and arched-back nursing (LG-ABN) that a rat receives, the more stress resistant, less reactive and more explorative it will be as an adult. However, the question is whether this is also true for dogs, and the investigation of how temperament in dogs is affected by environmental factors early in life is the main objective of this thesis. Three of the studies presented in this thesis focused on investigating the general parameters, particularly maternal care, that influences offspring behaviour to contribute to the understanding of temperament development in military working dogs. One of these studies concentrated on the environmental factors that influence dogs early in life, and the results indicated that some factors, such as parity, litter size and birth season, affect temperament later in life. Another study investigated how females take care of their young, and the results demonstrated that females vary in their maternal style during the first three weeks postpartum and that this variation affects the temperament of the offspring. The third study focused on factors in the home environment, and the results showed that dogs approved through the evaluative temperament test were significantly associated with being hyperactive or restless and having difficulty settling down in the home environment. However, those dogs were also left home alone for more hours in a day than non-approved dogs. To be able to operate functionally, a military working dog needs to possess certain traits, or a certain temperament, and a vital characteristic is the way it responds to and copes with stress. This was investigated during an evaluative temperament test used to select dogs suitable for further training. Surprisingly, the results in the fourth study showed that the dogs approved for further training had significantly higher levels of salivary cortisol both before and after the test compared with the non-approved dogs. These findings may be of profound importance for

understanding individual variations in behaviour and improving breeding schemes for working dogs.

POPULÄRVETENSKAPLIG SAMMANFATTNING

För över 15 000 år sedan började våra anfäder avla på vargar och lade då grunden för den uppsjö av olika hundraser vi ser idag. Exakt hur den här processen såg ut, när eller vart den startade vet vi faktiskt inte med säkerhet, men att vargen/hunden var det första djur att påbörja en sådan förändring, det vet vi.

Att aktivt välja ut och avla på önskvärda egenskaper påverkar och förändrar gradvis djuret. Den här förändringen styrs i hög grad av gener, vilket medför att ett djurs s.k. genotyp förändras. Den här förändringsprocessen, där ett djur gradvis anpassas till ett liv som tamdjur, kallas för domesticering och innebär inte bara att djuret förändras genetiskt, utan också att den ändrar utseende och beteende, dvs. djurets fenotyp ändras också. Det är därför vi bl. a. ser så många olika hundraser som vi gör idag, allt från en liten hårlös Chihuahua till en stor raggig St. Bernard. Alla är de hundar, men de ser väldigt olika ut och har delvis olika egenskaper eller temperament. Det medför att de passar till att göra olika saker och därför också kan vara till stor nytta i samhället i allt från sällskapshunden som kan lära sig leta kantareller, till olika typer av tjänstehundar. Bra ledarhundar åt synskadade, polishundar som söker försvunna människor och narkotika, och försvarsmaktens tjänstehundar som kan förhindra angrepp eller terrorverksamhet genom att leta efter t ex. bomber och vapen - alla kan i förlängningen innebära ökad livskvalité och räddade människoliv. Men för det krävs att hunden passar för jobbet.

Det är både generna, arvet och olika miljöfaktorer i den tidiga uppväxten som avgör egenskaperna hos en individ. Det är något som har visat sig gälla till exempel för råttor och primater. Studier på råttor har exempelvis pekat på att mängden omvårdnad en råtta får som liten (t ex hur mycket mamman slickar sina barn) påverkar dess egenskaper som vuxen. Och att ju mer omvårdnad de fått, desto mer stresståliga, mindre nervösa och mer nyfikna blev de. Även i studier på människor pekar resultaten i samma riktning. Men gäller detta även för våra hundar? För att öka kunskapen om och förståelsen för hur tidiga erfarenheter påverkar temperament, stress och arbetsförmåga hos våra blivande tjänstehundar i försvarsmakten har därför en rad olika studier på området genomförts.

Den här avhandlingen fokuserar således på att undersöka vilka generella tidiga erfarenheter och faktorer i den tidiga uppväxtmiljön som tycks kunna vara med och påverka temperamentet hos våra tjänstehundar. Specifikt undersöker den

hur tikens omvårdnad påverkar vissa egenskaper. Avhandlingen undersöker vidare hur stresståliga våra hundar är och hur detta yttrar sig i samband med de lämplighets test som hundarna genomgår i syfte att bedöma vilka individer som bör gå vidare till fortsatt träning efter ett och ett halvt års ålder.

Resultaten i en studie visar att de hundar som bedömts som lämpliga vid lämplighetstestet något oväntat uppvisade ett högre påslag av stresshormonet kortisol, och i en annan studie att lämpliga hundar bedömts vara hyperaktiva/rastlösa och ha vissa svårigheter att ta det lugnt i hemmiljö. Detta samtidigt som de uppvisade en önskvärd temperamentsprofil vid uttagningsprovet, vilket kan antyda att dessa hundar är mer flexibla och motståndskraftiga mot stress, vilket skulle kunna vara resultatet av en lyckad avel.

Vidare visade resultaten att det finns generella faktorer i den tidiga uppväxtmiljön, såsom tikens tidigare erfarenhet av att vara mamma, kullstorlek och när på året kullen föds, som är med och påverkar olika egenskaper. Den visar också att tikarnas sätt att ta hand om sina valpar varierade men var konsekvent under den första omvårdnadstiden på tre veckor och att det finns en koppling mellan mammans omvårdnads-stil och hur deras valpar blir som vuxna.

Sammantaget visar avhandlingen att det finns faktorer i den tidiga uppväxtmiljön som påverkar temperamentet senare i livet på våra tjänstehundar.

LIST OF PUBLICATIONS

This thesis is based on the work contained in the following papers, which will be referred to in the text by their Roman numerals (I-IV).

I. **Early experiences modulate stress coping in a population of German shepherd dogs.**
Foyer, P., Wilsson, E., Wright, D., Jensen, P. (2013). Applied Animal Behaviour Science 146, 79–87.

II. **Levels of Maternal care in dogs affect adult offspring temperament**
Foyer, P., Erik Wilsson., Jensen, P. Submitted manuscript.

III. **Behaviour and experiences of dogs during the first year of life predict the outcome in a later temperament test**
Foyer, P., Bjällerhag, N., Wilsson, E., Jensen, P. (2014). Applied Animal Behaviour Science 155, 93-100.

IV. **Behaviour and Cortisol Responses of Dogs Evaluated in a Standardised Temperament Test for Military Working Dogs**
Foyer, P., Svedberg, A-M., Nilsson, E., Wilsson, E., Faresjö, Å., Jensen, P. Manuscript accepted for publication in Journal of Veterinary Behavior: Clinical Applications and Research Articles. DOI: 10.1016/j.jveb.2015.09.006.

CONTENTS

INTRODUCTION

The domestic dog is one of the most widespread species on Earth today, and the functions of individuals range from being private pets to working dogs dedicated to specific tasks such as herding, hunting or serving with the military. This thesis investigates the parameters that may influence behaviour and aid in understanding the complexity of the temperament of military working dogs (MWD). Because good health and temperament are key elements to producing a functional MWD, and the costs of breeding, raising and training are high, it makes sense to produce puppies with good prospects for long, healthy and productive lives. Links between early experiences and temperament later in life have been observed in other species, such as rodents, and this thesis aims to investigate which, if any, early experiences influence temperament in dogs. It also investigates whether dogs differ in the amount of maternal care they provide, which has also been observed in other species; and if they do, does this have any effect on the temperament of the offspring? A better understanding of these behavioural responses and how they develop may improve the process of selecting and managing MWD breeding programs; this is discussed in the section titled **Breeding of working dogs**. Given the current global political climate, there is a need for specialised working dogs, so it is important to learn more about the development of temperament and how it may be affected by early experiences and maternal care. Other factors, such as learning capacity and genetics, also affect temperament, but this thesis does not expand beyond early experiences in general and maternal care in particular.

The dog (*Canis familaris*) was the first species to be domesticated, and wolves/dogs have co-existed with humans for millennia; this process is described in the **Domestication** and **Breeding of working dogs** sections. Over time, humans have artificially selected for specific tasks, such as hunting or herding, or looks, thereby creating hundreds of breeds. This diversification has lead to breeds with different behavioural responses, or different personalities, that make dogs suitable for a range of functions from being pets to working. For example, dogs may be employed to aid visually impaired people, help the police search for drugs or missing people, or aid the military in the search for explosives. Although personalities can be qualitatively described, there are currently several methods also for quantifying dog behaviour, which are described in the **Behaviour** section. To study personality has been of great interest for many years, and the way in which it is affected by early experiences is an important area of

personality research within applied ethology. Factors, such as early experiences, may alter the phenotypic expression and mental development of an animal, and these differences can persist through adulthood and may have a profound impact on animal welfare. Several studies of early experiences and how they affect adult behaviour have been conducted in recent decades to understand the mechanisms behind these phenotypic, genomic and behavioural variations. Previous studies with laboratory animals have indicated that factors like maternal and litter effects, such as litter composition, litter size, previous maternal experiences and housing and management routines, as well as other environmental and genomic factors (Kikusui et al., 2008) could affect maternal behaviour and hence the development of the offspring in rodents (Francis et al., 1999; Caldji et al., 2000; Champagne and Meaney, 2006), chickens (Groothuis et al., 2005), rhesus monkeys (Schapiro et al., 1995) and other species. In fact, there have been a few earlier studies suggesting that maternal and litter effects also influence behaviour in dogs (Slabbert and Rasa, 1997; Wilsson and Sundgren, 1998); Scott and Fuller, 1965; Scott and Bielfelt, 1976). Additional information about early experience and how it may affect temperament can be found in the **Early experiences** and **Mother-offspring interactions** sections. Much of the information about early experiences comes from studies of how stress inflicted both before and after birth influences the behaviour and physiology of animals. Furthermore, stress is a factor with which dogs, especially MWDs, must cope with in our modern society, and this topic is addressed in the section titled **Stress**.

Following these introductory sections, the section **Summary of papers** briefly summarises the background, aim, main results and conclusions from each of the four papers in this thesis. Finally, a **General discussion** is presented in which I attempt to relate my work to the work of others and provide an overall conclusion from this project. I also present some thoughts about possible future research.

DOMESTICATION

Domestication is the process through which captive animals adapt to humans and their environment (Price, 1999). The dog was the first animal to become domesticated; although this thesis is not about domestication, it will begin with an overview of the process. Hopefully, this will clarify how breeds have been created and how behaviours and temperament can develop and differ, thereby leading to different phenotypes.

Through artificial selection, it is possible to modify a number of genetic, physiological and behavioural traits, and prolonged and controlled breeding has formed domestic animals that differ quite substantially from their wild ancestors. The abundance of morphological changes and phenotypic variation seen in domesticated animals inspired Darwin to formulate his theory of evolution in *On the Origin of Species* (1859), but his observations also raised a number of fundamental questions regarding domestication, such as when, why and how did it happen; where did it start; and what have been the consequences? Regardless, when our human ancestors domesticated wild animals, it was the beginning of a great revolution, and domesticated animals dramatically changed human life forever.

The history of domestication

The origin of animal domestication is still a matter of debate, but combined research into morphology, behaviour, archaeology and molecular biology has established that the dog (*Canis familaris*) was the first species to be domesticated, and that its principal ancestor is the grey wolf, *Canis lupus* (Galibert et al., 2011). Several studies have tried to answer the questions about the origin of dog domestication, but depending on the techniques and data employed, the answers differ, and no consensus has been reached. However, it has been suggested that domestication took place in two evolutionary stages, so-called bottlenecks, when the dog population drastically declined for various reasons. The first was the ancient domestication process during the early agricultural revolution, when humans changed from a nomadic, hunter-gatherer lifestyle to a sedentary lifestyle (Clutton-Brock, 1995; Axelsson et al., 2013). The second is the more recent breed diversification bottleneck, which is restricted to the last 300 years and characterized by selective goals for physical characteristics such as size, shape, and coat texture, length and colour, as well as for behavioural traits that lead to specialised breeds for guarding, hunting, herding or companionship

(Coppinger and Schneider, 1995; Lindblad-Toh and al, 2005; Wang et al., 2014) (Figure 1).

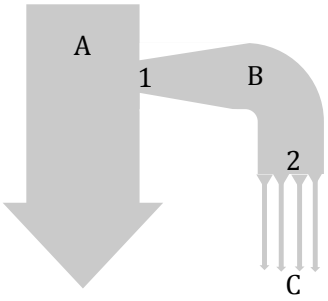

Figure 1. *The domestication of dogs includes at least two bottleneck episodes that have led to the diverse dog breeds seen today. A) Gene pool of wild ancestors, B) gene pool of domesticated stock, C) gene pools of modern breeds, 1) domestication bottleneck, and 2) breed-creating bottlenecks. Redrawn from Lindblad-Toh et al (2005).*

To answer the question of the origin of domestication, scientists have studied archaeological findings from Mesolithic human settlements in Europe, Asia and the Americas. The earliest findings dated back to at least 15,000 years BC (Clutton-Brock, 1995), but the earliest morphologically dog-like remains found in Siberia are 35,000 years old. Genome sequencing results by Skoglund et al (2015) indicate that the ancestors of dogs diverged from the ancestors of the modern wolf at least 27,000 years ago, meaning that dogs began to diverge from wolves long before they came in contact with human settlements. Using different molecular biology techniques, studies of genomic variation have concluded that domestication most likely began south of Yangtze River in China 16,300 years ago (Pang et al., 2009), whereas results from other approaches have indicated the Middle East as the place of origin (vonHoldt et al., 2010). One explanation for this apparent contradiction may be that domestication took place more than once and that the modern breeds are the only survivors. Therefore, although there is no consensus regarding the origin of dog domestication, and only speculation about how it occurred, there is a general agreement that a reduction in fear of humans and an increase in stress tolerance must have been critical to the domestication process (Price, 1999; Galibert et al., 2011; Jensen, 2014).

From wolf to dog

In the late 1950s, a research group led by Dmitry Belyaev at the Institute of Cytology and Genetics in Novosibirsk, Siberia, started a project on silver foxes (*Vulpes vulpes*), another member of the family *Canidae*. Belyaev believed that the key trait targeted for selection during domestication must have been tameness, so he designed a selective breeding program to test his hypothesis. Based on a score to measure the fear response to humans, less than 4 or 5% of the males and approximately 20% of the females of the least fearful foxes were allowed to contribute to the next generation, and the effect was remarkable. By the sixth generation, the foxes bred only for tameness displayed behaviours toward humans similar to dogs; they were very friendly and contact seeking and engaged in tail wagging, whining, whimpering and licking when in contact with the experimenter. The behavioural changes were not the only noticeable effects of the selection as the tame foxes also exhibited changes in morphology, such as altered coat colouration, as well as floppy ears and rolled tails. Soon thereafter, some individuals were born with altered skull proportions, including shorter snouts (brachycephaly), whereas others had shortened legs (chondrodystrofy) and tails (Trut, 1999). Moreover, the reduced fear response in the domesticated line was found to be correlated with decreased levels of plasma cortisol (Trut, 1999), a hormone involved in the stress response, but I will however return to the topic of stress response in the Stress section.

Belyaev and his co-workers have shown, without a doubt, that it is possible to mimic the domestication process through a selective breeding program involving successive adaptive changes, and create a line of domesticated animals that substantially differs in their behaviour, morphology and physiology compared with their ancestors. The majority of the changes observed in the fox experiment are also seen in other domesticated species such as sheep, goats, cattle, horses, pigs, cats and dogs (Trut, 1999), and it is rather amazing that different species domesticated at different times in history in different regions of the world share so many phenotypic traits. It indicates that the domesticated phenotype is a general adaption to selective breeding and captivity and most likely a result of side effects correlated with some major trait, e.g., being less fearful of humans, rather than independent selection on each trait (Jensen, 2006; Jensen, 2014). Furthermore, although the degree of fear shown on an individual level is largely a result of early environmental experiences during ontogeny, domesticated animals are more easily tamed than their wild ancestors (Jensen, 2014). An example of this is raising a wolf as a dog in a human family; a wolf is not automatically as tame and manageable as a dog at the same age (Miklósi, 2008).

During the second domestication process, which is thought to have started approximately 300 years ago (Lindblad-Toh and al, 2005; Wang et al., 2014), selective breeding has produced many varieties of domestic dog breeds. At this point, the Fédération Cynologique Internationale (FCI) currently recognizes approximately 350 different dog breeds. Domestic dogs are notable for their great variety of shapes, sizes and colours, ranging from the tiny, almost hairless Chihuahua to the massive, shaggy St. Bernard (Johnson and Aamodt, 1985). Selective breeding programs continue to shape dog phenotypes, of which behaviour is one example.

Selection and breeding for different purposes

In 1859, Charles Darwin introduced the concept of natural selection. He learned from farmers that individuals within a species differ in terms of their morphology, physiology and behaviour, i.e., there is *variation*, and that selecting and breeding animals with desirable traits, e.g., cows that yield more milk, leads to better livestock because some of those variations are *heritable*. In nature, he observed that different environments or niches promoted different varieties of organisms that seem to be *adapted* to its specific niches (e.g., the finches of the Galapagos). Furthermore, he could see that more offspring are produced than are needed to replace the individuals that die in a population, so not all young survive or get the opportunity to breed. Those individuals that can better *compete* for limited resources, e.g., food, mates and a place to live, within a niche stand a better chance to survive and breed. As a result of this competition, some variants leave more offspring than others and pass on their favourable characteristics to their progeny, so evolutionary change takes place by *natural selection*. Just as natural selection adapts a species to its environment, humans have selected animals for their needs, and as we saw in the Domestication section, dogs were the first species to be domesticated. Imagine that some 10,000 years ago, humans and dogs hunted for prey together and that by merely favouring the progeny of the best hunting dogs, humans caused breeds of hunting dogs to evolve (Beilharz, 2007). This initial form of domestication is the precursor of what we now call artificial selection or selective breeding.

Breeding affects behaviour

When studying behaviour, it is vital to distinguish between the expression of a trait and the frequency at which it is presented. The frequency is related to something called the threshold, which is best described as how easily a behaviour is elicited. Having a low threshold for a particular trait means that it is more easily provoked. One example is barking in dogs. Although the sound of a bark may be context-specific, i.e., all barks in a given circumstance sound more or less the same (if the dogs are of comparable size), different dog breeds or individuals within a breed may have different thresholds for barking. Some may bark often and very easily, whereas others may bark less. In terms of breeding, it is generally difficult to affect the expression (how a dog barks in a given context), whereas the

frequency (how often a dog barks) is more easily influenced (Fält, 2003). Put simply, if you want a dog that does not bark, you must choose and breed individuals that rarely bark, and with time, you will change the phenotype, as occurred in the tame fox experiment. This also applies to other behaviours or traits. Genes control behaviour; therefore, to change a phenotype, there must be genetic variation because selective breeding actually involves changing genotypes. However, breeding for behaviour is tricky as selecting for a specific trait sometimes changes other characteristics as well. Therefore, if not carefully monitored during breeding, unwanted behaviours or altered thresholds for certain unwanted behaviours might result.

Breeding of working dogs

The most important aspects of every professional breeding program for working dogs is to very precisely define the characteristics of the preferred phenotype, which, in turn, depends on the specific working task of the dog (Beilharz, 2007). The desirable traits need to be quantitatively measured and evaluated, and one way to evaluate breeding is to subject the dogs to a standardised and valid temperament test. However, the selection of breeding animals, rearing, housing, handling, recruitment and assessment processes, training techniques and skill of the handlers, and health and end-point management are all aspects of the production system that can affect the quality of the final product, the working dog (Cobb et al., 2015). All of these issues are important because, although limited, the available data suggest that success rates generally do not exceed 50% across the sectors of the working dog industry (Wilsson and Sundgren, 1997; Slabbert and Odendaal, 1999; Maejima et al., 2007; Sinn et al., 2010). Working dog units with their own breeding program may improve this percentage by clearly defining and continuously monitoring their specific phenotypes.

Breeding of MWDs in Sweden

After a decision by the Swedish parliament in 2003, the Swedish Armed Forces (SAF) launched their breeding program in 2005. The only breed in the program is the German Shepherd, and the goal is to improve the behavioural traits of importance for substance detection and personnel protection, which are the primary working tasks of MWDs (Wilsson and Sinn, 2012). The ambitions is to create a closed breeding colony of German Shepherds, with 70-80 females and 15 males, producing 300 pups yearly (Berg and Wilsson, 2014), with both replacement breeding animals and working dogs being recruited from within the program. The aim is to evaluate all dogs with a standardised temperament test, even the dogs dismissed for medical reasons (currently 18%), to strengthen the

evaluative value of the breeding animals (Berg and Wilsson, 2014). More about the temperament test used by the Swedish Armed Forces (the SAF T-test) to evaluate prospective MWDs is included in the following section on Behaviour.

The most common reasons for dismissal from the program are deficiencies in the temperament profile. 50% of the evaluated dogs are either dismissed directly after the SAF T-test or during the training that follows (Berg and Wilsson, 2014). Constantly improving temperament in accordance with the traits of importance in an MWD is a priority (Wilsson, 2013), so it is important to expand and deepen our knowledge of behavioural development. This thesis attempts to accomplish this.

The use of the SAF T-test

The results of the SAF T-test are mainly used for three purposes:

- to evaluate the individuals that will be put through training
- to choose replacement dogs for breeding
- to evaluate the breeding animals, i.e., progeny evaluation.
  When choosing animals for breeding, both the results of the breeding animal and those of its siblings are taken into consideration. Breeding animals are recruited from better than average litters, and the best individuals from those litters may become breeders (Wilsson, 2013).

All dogs are evaluated using subjective rating (SR) and behavioural rating (BR) protocols as described in the Behaviour section. In a study of MWDs, Wilsson and Sinn (2012) concluded that both rating methods are able to predict training success, BR at a slightly higher percentage (72.0-78.3%), compared with SR (70.3-71.7%), depending on the trait. In the same study, the authors concluded that the temperament of the dogs could be described with 3-5 traits: Confidence, Engagement (Physical and Social), Aggression and Environmental Sureness.

The SAF T-test can also be used to calculate something called the mental index value (IV), which can be used to monitor progress within the breeding program over consecutive years (Figure 2). Furthermore, the IV can be used for scientific purposes; IV scores are employed in Papers III and IV. The IV is calculated from the scores of each subtest and is used to compare the results of dogs that have become MWDs with those of dogs that did not pass the SAF T-test. The calculation template used for 2014 is based on the records of 750 tested dogs, and the IV is constructed so that the dogs that pass the test receive a positive number. Higher values indicate a greater chance of successfully completing the training and

becoming an MWD. The heredity of the IV has been estimated to be approximately 20%, i.e., 20% of the measured variation can be explained by genetic components, whereas 80% can be explained by environmental variables or an interaction between the different factors.

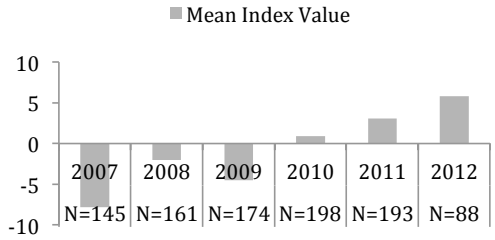

Figure 2. *Improvement in the mean mental index value, IV, in dogs born at the SAF K9 breeding kennel between 2007 and 2012. Redrawn from Berg and Wilsson (2014).*

Different temperamental traits in the SAF T-test

The Confidence trait is characterised foremost by the strength to act i.e., *courage*; the absence of fearful behaviour toward real or imagined danger, *nerve stability*; the appropriateness of a dog's reaction to a certain situation, which includes the dog's ability to adapt to various types of non-fearful situations, to concentrate when highly aroused or in a conflict situation, and to overcome a frightening situation, and *hardness*; which is a mental and/or physical resiliency to unpleasant experiences. Hard dogs are highly "recoverable" after disturbances (Wilsson and Sinn, 2012; Wilsson, 2013).

The Engagement trait summarises the dog's energy and willingness to work and can be divided into Physical and Social Engagement. Physical Engagement consists of *competitiveness*; a strong desire to have sole possession of objects, *hunting drive*; the dog's willingness, vigour, or enthusiasm to run after a moving object, *prey drive*; the dog's interest in and willingness to search for, bite and carry objects in the mouth, and *liveliness*; the dogs general degree of mental or physical arousal (Wilsson and Sinn, 2012; Wilsson, 2013). Social Engagement considers the dogs' willingness to interact with and play with humans.

The third trait is Aggression, which includes *sharpness*; an act of aggression or agonistic interaction, which can be appropriate or inappropriate and involve a threat, challenge or contest, and *defence drive*; the tendency for the dog to defend itself or its handler. In most cases, defence is combined with aggression, but a dog

may display defensive tendencies without being aggressive (Wilsson and Sinn, 2012; Wilsson, 2013).

By far the most important characteristics for all types of working dogs, and those that best predict their suitability as MWDs, are Engagement and Confidence, while Aggression is less important according to Wilsson and Sinn (2012). A dog with a high level of engagement is lively and energetic and loves to search for, run after, bite and carry various objects. Whereas high engagement is desirable in a working dog, lower engagement is usually preferred in companion dogs because highly engaged dogs are rather demanding as they need to be stimulated and able to work, and they sometimes have to learn how to be passive in some situations (Wilsson, 2013). Dogs with high confidence can be described as unafraid, brave, headstrong, independent and insensitive. High confidence is desired in all working dogs, but this may lead to them being perceived as demanding and difficult to train, so they must also be cooperative (Wilsson, 2013).

The characteristics or traits that are preferred in an MWD are known, so the questions raised in this thesis are whether there are any early experiences, such as litter size, previous maternal experience and the sex-ratio within the litter, that influence behaviour. What other factors early in life determine temperament in dogs? Does the mother dog's behaviour and treatment of her pups influence their temperament? What are the challenges for an MWD, and how can these challenges, e.g., stress, be investigated and quantified? Can these factors be studied and lead to a more informed system of animal breeding that promotes the development of dogs with the traits desired for an MWD?

To answer these questions, there are a number of things that must be considered. For instance, what are behaviour and temperament, and how can they be described and measured? What is stress, and if the dogs perceive the SAF T-test to be stressful, how do they cope? Of additional interest is the investigation of early experiences and mother-offspring interactions and how they relate to temperament later in life.

BEHAVIOUR

Behaviour, personality and temperament

First, it should be stated that there is no consensus over what vocabulary to use, or the definition of terms. However, the following description of behaviour is an effort to conceptualise the term, and it will be used throughout the thesis. Behaviour encompasses the observable response of an individual who reacts to a specific signal within a given context, and it may be induced by stimuli or inputs from the environment of internal or external cues. Behaviour may be conscious or unconscious, voluntary or involuntary, but it may also be innate, which means that it may be based on instinct or natural actions. In other words, innate behaviour occurs when a stimulus is encountered for the first time. Instinctive behaviours are a direct result of natural selection (Beilharz, 2007), and an example is the interaction between a mother and her new-born young. Behaviour may also be acquired or learned from previous exposure and experiences, such as training. Genetic factors also play a role. In fact, as mentioned in the Breeding of working dogs section, genes control behaviour (Jensen, 2006), but the genetic contribution to behaviour is excluded from this thesis.

Most empirical and theoretical behaviour research has been done within humans, and research on children and adults tends to use the term "personality", whereas studies of human infants and animals often use "temperament". Unfortunately, the distinction between the terms has been inconsistent, and they are often used interchangeably in the literature (McCrae et al., 2000). From a human perspective, temperament has been defined by some researchers as a rubric for a group of related traits and not a trait itself; others define it as the inherited, early-appearing tendencies that continue through life and serve as the foundation for personality (Goldsmith et al., 1987), thus viewing personality and temperament as two separate entities. Some psychologists that study personality include traits, goals, abilities, physical and bodily states, moods *and* temperament, among other parameters, in their research (Jones and Gosling, 2005). Thus, they make a distinction between personality and temperament and do not consider them to be interchangeable terms. Although researchers do not agree on the definition of temperament in humans, there is even less of a consensus among researchers who study animals (Gosling, 2001). Sometimes, the word temperament seems to be used in animal research to simply avoid the term personality, which some researchers associate with anthropomorphism (Jones and Gosling, 2005). Hence,

no single definition of personality would be satisfactory to all behavioural researchers. Regardless of whether it is termed personality or temperament, the concept is usually defined as a pattern of behaviour that is distinctive to an individual, which is consistent in different situations and across time (Pervin and John, 2001). Although temperament is relatively stable over time, it can still be influenced by a number of external factors, such as early experiences and learning (Diederich and Giffroy, 2006).

Despite the difficulties in defining the term, the concept of personality has been with us at least since the time of the ancient Greeks, and the theory has its roots in their notion of the four fundamental bodily fluids called humours (blood, yellow bile, black bile and phlegm). It was believed that human emotions, moods and behaviours were caused by the mix of humours, and illness by imbalances. The Sanguine personality was linked to the element of air and characterised an optimistic individual. Choleric was linked to fire and an irritable character; Melancholic represented the earth and a depressed character. Finally, Phlegmatic was tied to the element of water and characterised a calm individual (Stelmack and Stalikas, 1991).

The idea that individuals can be categorized based on their behaviour remains valid, and although this ancient type theory no longer has a place in modern psychology or medicine, it most likely laid the foundation for modern thinking and a variety of other approaches. In human psychology, there are theories, such as the psychodynamic theory, of which Sigmund Freud was a great advocate. Further is there the behaviouristic view, whose founder was Watson, although Skinner and Pavlov are perhaps the most recognised advocates. Skinner proposed that differences in our learning experiences are the main reasons to why individuals behave differently in similar situations, and Pavlov demonstrated classical conditioning through his famous work with dogs. There is also the humanistic approach to personality developed by Rogers, who stated that self-actualisation is the force driving behaviour, and Maslow, whose research on basic motivation lead to his hierarchy of needs. Finally, we have the trait theory, in which, broadly speaking, personality traits refer to consistent pattern in the way an individual feels, thinks and behaves. Among the trait theorists is Allport, who categorized three types of traits (cardinal, central and secondary) based on a list of 4000 words used to describe personality. Furthermore, there is Cattell, who narrowed Allport's list to 16 personality traits, and Eysenck, who developed a model of personality based on only three universal trait dimensions: 1) introversion-extraversion, 2) neuroticism-emotional stability, and 3) psychoticism. However, even though Allport, Cattell and Eysenck share the

fundamental view that traits are the proper units to describe personality, the field remains fragmented as to how it should be categorised (Passer and Smith, 2001).

Trait theory and the five-factor model

Based on Cattell's and Eysenck's models, many modern researchers agree that human personalities can be described through a five-factor solution (Pervin and John, 2001), and this five-factor model (FFM) has been shown to possess substantial validity and reliability and has remained relatively stable over time (McCrae and Costa, 1994). Support for the FFM arises from its three main components as follows: 1) a factor analysis of a large set of trait descriptive adjectives, 2) a test of the universality of the trait dimension via cross-cultural research, and 3) the relationship of trait-questionnaires to other questionnaires and ratings (Pervin and John, 2001). The five dimensions yielded by the FFM, forms the acronym OCEAN, which stands for Openness, Conscientiousness, Extraversion, Agreeableness, and Neuroticism (Costa and McCrae, 1992). Interestingly, in a review paper, Gosling and John (1999) found evidence for cross-species generality in four of the five dimensions; it is strongest for Extraversion, Neuroticism and Agreeableness, followed by Openness. Conscientiousness, however, was only found in chimpanzees, the closest relative to humans, but there are also other models that account for personality in animals.

Measuring personality

Although some of the theories were developed using animal models, they were intentionally meant for studies of human personality, but personalities are found in a wide range of animal species (Gosling and John, 1999). Once personality can be described, how to measure it becomes of interest. Human personality can be quantified in a variety of ways, such as with behavioural observations in a normal environment and self-reporting through questionnaires. Each of these techniques has its pros and cons, but how to measure behaviour in animals? You certainly cannot hand out a questionnaire for the animal to complete, but does that mean that questionnaires cannot be used in animal research? On the contrary, a caretaker that knows an animal well may be able to complete a survey, and in human research, this method is known as peer evaluation. It can be done with dogs in numerous ways, and one of the commonly used, if not the most common, questionnaires for dogs is the Canine Behaviour and Research Questionnaire (C-BARQ), which was developed by Hsu and Serpell (2003). The C-BARQ is a comprehensive questionnaire of approximately 100 questions related to a dog's behaviour in everyday situations, and it is one of the methods employed in Paper

III of this thesis. Other questionnaires are also available, such as the Monash Canine Personality Questionnaire (MCPQ), which uses 41 words describing the dog and is measured on a six-point intensity scale (Ley et al., 2009).

However, these methods do not measure an animal's personality directly; instead, a trait or behaviour is measured or observed in a wide range of situations. To be able to say something about personality, other tools are needed, and one useful method is principal component analysis (PCA), which has been applied in all four of the papers in this thesis to reduce the number of variables and determine a smaller number of factors that account for most of the variability.

PCA is a frequently applied tool to animal behaviour research. It is used to reduce the number of dimensions through a correlation matrix that identifies clusters of related behaviours. Behaviours or variables within the same cluster are assumed to represent a single underlying factor (Budaev, 2010). This method is appropriate for identifying a smaller number of theoretical superordinate factors. These are thought to account for individual differences in a set of observed or measured behaviours (Tóth et al., 2008) or other variables, as well as questions if a questionnaire is used.

Verifying behaviour

Personality is considered by many to be a result of psychological, behavioural and physiological parameters (Gosling, 2001), which means that the results of a behaviour test can be verified with results from a questionnaire or by different physiological measurement techniques. Current research suggests that physiological needs and mechanisms can affect an individual's personality; for instance, individuals respond to stress with either a proactive or reactive coping style depending on their personality. Examples of physiological measurements used to detect variability in the stress response are heart rate variability, cortisol levels, and the fairly new and promising technique of infrared thermography (IRT) (Travain et al., 2015). Salivary cortisol sampling is used in Paper IV to achieve a better understanding of the responses of dogs during a standardised behavioural test. Behaviour tests or temperament tests, as it will be referred to throughout the rest of the thesis, is another and commonly used method measuring behaviour.

Temperament tests

A temperament test applies different stimuli to standardised situations to elicit a behavioural response (Serpell and Hsu, 2001), and it often includes different

subtests using different stimuli depending on the purpose of the test. Several different temperament tests have been developed for a number of species; some are more specific and some are more general. Furthermore, there are a number of different temperament tests designed specifically for dogs; many individuals and organisations have created tests for companion dogs, assistance dogs and working dogs. As described in detail by Taylor et al (2006), despite the large variety of temperament tests, of the upmost importance is that a given temperament test must meet five quality criteria; it must be reliable, valid, feasible, purposeful and apply a standardised test procedure.

The most commonly and most objective method for assessing temperament in dogs is the practice of using so called test batteries (Jones and Gosling, 2005), which consists of two components: the actual temperament test itself, which usually consists of several sub tests, and the system for coding or rating the dogs reactions during the test. Several different methods can be used to quantify the reactions of dogs during a test (Sinn et al., 2010), such as a behavioural rating, subjective rating, or behavioural coding (Svartberg, 2007). Rating methods rely on the ability of the human observer to interpret dog behaviour in a standardised and pre-defined test situation. Ratings are usually based on Likert scales; e.g., scores of one to five correspond to a dog's behavioural intensity in a subtest or throughout the entire test depending on the method (Wilsson and Sinn, 2012). A behavioural rating is usually based on observations during a single subtest, whereas subjective ratings are based on the observer's overall perception of the dog's performance in multiple subtests (Wilsson and Sinn, 2012). Rating methods are subject to observer bias because they rely on subjective interpretations, although behavioural ratings are sensitive to a lesser extent.

In behavioural coding, a dog's reaction is measured according to strict objective criteria, such as the frequency and duration of a behaviour (Svartberg, 2007). Behavioural coding often relies on video analysis, in which a trained observer decodes variables according to an ethogram (Vazire et al., 2007), which is a detailed description of an animal's behaviour. One benefit of behavioural coding is that it can reveal many details of the behaviour and a disadvantage is the time consumption needed. Both rating and coding methods have been used on different data sets in all of the papers included in this thesis, although behavioural coding has only been applied in Papers II and IV.

Temperament tests for dogs

As previously described, temperament in dogs can be investigated using different approaches, e.g., questionnaire-based studies, and temperament test batteries.

Therefore, it is not surprising that, depending on the method, the models may capture different, complementary aspects of dog temperament, which can be useful if the results from one method are to be verified with the results from another; see Paper III. As mentioned above it has been shown that the FFM can be applied on dogs to yield the OCEAN dimensions, except for Conscientiousness (Gosling and John, 1999). Another questionnaire-based method which was used in Paper III, the C-BARQ, results in 14 behavioural dimensions: Stranger-directed aggression, Owner-directed aggression, Dog-directed aggression, Stranger-directed fear, Non-social fear, Dog-directed fear, Separation related behaviours, Attachment- and Attention-seeking behaviours, Trainability, Chasing, Excitability, Touch sensitivity, Energy level, and Dog rivalry (Duffy and Serpell, 2012). However, the most commonly used test in Sweden, according to the Swedish Working dog Association, is a standardised test battery called the Dog Mentality Assessment test (DMA). A study by Svartberg and Forkman (2002) using DMA score sheets included 15,329 dogs of 164 different breeds and yielded five temperament dimensions: Playfulness, Curiosity/Fearlessness, Chase-proneness, Sociability, and Aggressiveness. Depending on the method used, the number of parameters used to describe dog temperament differs.

The FFM, C-BARQ and DMA are all relatively general, but tests can be more specifically in target certain traits depending on the objectives of the test. For instance, temperament tests can be used to measure hunting or herding capabilities or to evaluate service dogs or police- or military working dogs. In Sweden the military K9 unit uses a standardised, evaluative temperament test battery, the SAF T-test, for prospective MWDs.

Temperament tests for MWDs in Sweden

The SAF T-test has been used in its present form since 2005, and more than 1200 dogs have been evaluated to date. All dogs are measured with both behavioural ratings (BR) and subjective ratings (SR). The test consists of 12 different, standardised subtest situations that either measure 25 different behavioural variables or 13 subjective traits. For more details about the test, see Wilson and Sinn (2012), who evaluated the SAF T-test and its value for predicting the success of dogs during subsequent training. Using data reduction, i.e., PCA, the authors found five underlying BR dimensions: Confidence, Physical Engagement, Social Engagement, Aggression, and Environmental Sureness, and three SR dimensions: Engagement, Confidence and Aggression. Both rating methods managed to correctly identify the dogs that did or did not complete the training, so the SAF T-test seems to be able to measure some aspects of dog temperament. PCA of the behavioural rating data has been used in all of the papers included in this thesis,

resulting in the same dimensions or factors, with only minor differences in the composition of the variables.

An interesting question that arises with regard to the SAF T-test is how it is perceived by the dog. One of the main issues in testing prospective MWDs is the ability to discriminate between dogs that show an inappropriate fear response and those that respond in a desirable way. Hence, some of the subtests are designed to potentially frighten the dog in order to observe its reaction to the potentially threatening stimuli. This may induce a stress response in the animal, so this is an interesting topic for investigation.

STRESS

Stress and the stress response

The term "stress" is a very popular and frequently used term in biology, medicine and psychology (Overli et al., 2007), but the definition of stress is subject of debate because something that is perceived to be stressful by one individual, may not be considered stressful by another. The common societal view is to interpret stress as something that has only negative consequences, but biologically, stress may be defined as a state of increased arousal that can be provoked by both aversive and pleasurable conditions (Kim and Diamond, 2002). Nevertheless, stress has been thoroughly investigated with regards to both physiology and behaviour. For instance, animal models are used in the study of stress-related diseases, and stress is an important aspect of animal welfare *per se*.

The capacity to respond to stress is one of the most basic adaptive mechanisms in animals (Meaney et al., 1985). A stress response starts with a potential threat to homeostasis (the regulation of the body towards a balanced state) as a reaction to perceived internal or external stressors, i.e., unpredictable or uncontrollable and sometimes threatening stimuli (Moberg and Mench, 2000) that can be of different origins e.g., physical, psychological or environmental. A stressor can also vary depending on the species, as well as the individual (Grandin, 1997; Moberg and Mench, 2000). The stress response further includes both the physiological and the behavioural responses to the stressor or the coping mechanisms.

The behavioural stress response

The behavioural response may be manifested as moving away from a stressor (Moberg and Mench, 2000), such as seeking shade due to an increased body temperature from sun exposure, or fleeing from an object that suddenly appears in a dog temperament test. Dogs often exhibit avoidance behaviour in response to startling stimuli (King et al., 2003; Ley et al., 2007) and react with fearful behaviours, such as freezing, flight, or low body posture, or aggressive behaviours (Goddard and Beilharz, 1984; Netto and Planta, 1997). Other typical behaviours include vocalisation, altered body posture or freezing depending on the species and the characteristics of the stressor. However, only relying on behavioural responses as indicators of stress may be too crude and subjective.

The physiological stress response

In addition to the behavioural stress response, a physiological stress response also occurs via the autonomic nervous system, which affects a number of biological systems including the metabolic, gastrointestinal, cardiovascular and reproductive systems (Sapolsky, 2002). The responses of the autonomic nervous system are often understood to have an adaptive role called the fight-or-flight response, which was originally described by Cannon (1915). By mobilising energy, and up- or down-regulating various systems, the body allocates its resources to promote survival (Mendl, 1999). This complex neuroendocrine system, i.e., the hypothalamic-pituitary-adrenal (HPA) response to stress, involves the release of many different hormones that act on target cells in the heart, liver, muscles, adrenal glands and brain (Brown, 1994).

The HPA stress response

When a stress stimulus is perceived, the hypothalamus releases corticotropin releasing hormone (CRH) and vasopressin. CRH then acts on the anterior pituitary gland and triggers the release of adrenocorticotropic hormone (ACTH). This stimulates glucocorticoid release (GR) from the adrenal cortex and through sympathetic stimulation, causes the adrenal medulla to release the catecholamines known as adrenaline and noradrenaline (Brown, 1994). Glucocorticoids are steroids, of which cortisol is the dominant form in primates and most mammals, whereas corticosterone is dominant in rodents and birds (Stratakis and Chrousos, 1995). Cortisol then acts as a negative feedback on the hypothalamus and the anterior pituitary (Figure 3).

Together, glucocorticoids and catecholamine mediate most of the changes during the stress response (Sapolsky, 2002). Many studies investigating stress have used cortisol as a biomarker, but there are other techniques, such as measuring heart rate variability and the use of IRT, as mentioned in the Behaviour section. Cortisol concentrations can be measured in plasma, saliva, hair and urine; saliva cortisol measurement is used in Paper IV of this thesis.

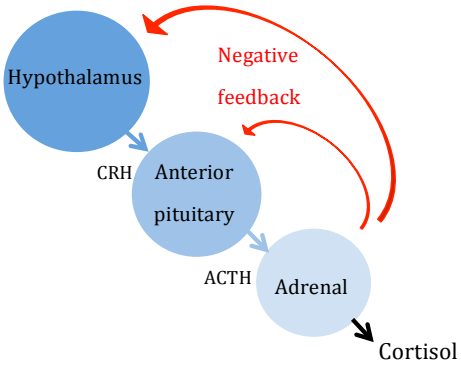

Figure 3. *Schematic and simplified illustration of the HPA axis. When a stressor is perceived, the hypothalamus releases corticotropin releasing hormone, CRH, which acts on the anterior pituitary. This in turn, stimulates the release of cortisol from the adrenal cortex via the release of adrenocorticotropic hormone, ACTH. Cortisol then acts on the hypothalamus and the anterior pituitary to form a negative feedback loop. Figure redrawn from https://en.wikipedia.org/wiki/Hypothalamic–pituitary–adrenal_axis, 2015-07-05.*

The key organ in the stress response is the brain because it is an important target of the stress hormones (i.e., cortisol, CRH and ACTH). The brain determines what is to be perceived as a threat; it orchestrates which coping strategy an individual will use (Koolhaas et al., 1999); and it changes both structurally and functionally as a result of stressful experiences (Meaney et al., 1985; McEwen and Gianaros, 2011). Work by Meaney and colleagues (1985) established the important link between early life experience, handling and the development of the HPA negative feedback system in rodents, another mammalian species just as the dog.

Coping style and stress reactivity.

When facing stressful situations, animals can adopt different behavioural strategies, so-called stress coping strategies or styles (Koolhaas et al., 1999; Korte et al., 2005). Coping styles are characterised by *"a coherent set of behavioural and physiological stress responses that are consistent over time and characteristic for a group of individuals"* (Koolhaas et al., 1999), and have long been described in the literature as two different response patterns, the fight- or- flight response and the conservation-withdrawal response.

According to Koolhaas et al., (1999), the proactive coping style is embodied by individuals that react with territorial control and high aggression and tend to adopt the fight-or-flight response first described by Cannon (1915) when

challenged. Individuals with proactive coping style, besides displaying high levels of aggression, generally exhibit short attack latency and impulsive decision-making and score high in frustration tests. Furthermore, they take risks in the face of potential danger, are usually novelty-seekers (Koolhaas et al., 1999; David et al., 2004; Groothuis and Carere, 2005; Steimer and Driscoll, 2005), and score high for active avoidance (Koolhaas et al., 1999). In the fox experiment, as well as in other studies, it has been shown that the HPA axis response can be down regulated and that this can be linked to selection for less fearful behaviour, such as more exploration of novel environments and a tendency to approach humans (Trut, 1999).

On the other hand, individuals that adopt the conservation-withdrawal type of response, which was originally described by Engel and Schmale (1972), are considered to have a reactive coping style (Koolhaas et al., 1999). These individuals exhibit less mobility and lower levels of aggression, long attack latency, low active avoidance, and higher reactivity in the HPA-axis system (Koolhaas et al 1999).

Koolhaas et al., (2010) also note the confusion around the terminology used in the literature and try to clarify the concepts with a two-tier model (Figure 4). They emphasise that the coping style axis reflects the quality of the response stressor, i.e., how an animal responds to a challenge, whereas the emotional reactivity axis quantitatively reflects the strength of the response, which is expressed as the duration and/or intensity of behaviour and/or the plasma levels of stress hormones or other physiological measurements.

In the model, four different labels, one for each quadrant, represent four extreme characteristics. Koolhaas et al., (2010) choose to use the terms shy and bold although, as they rightfully note, these terms have not been well defined. However, the authors state that these words seem to include both qualitative and quantitative aspects of the differential behavioural responses to environmental challenges.

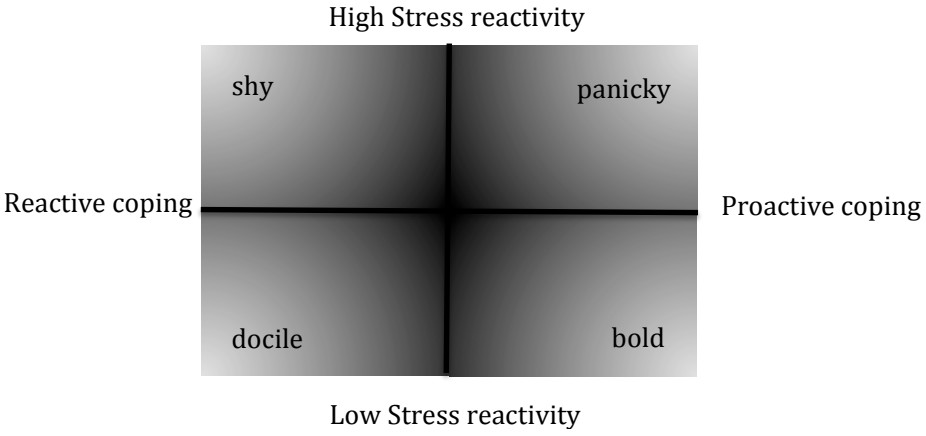

Figure 4. *The two-tiered model proposed by Koolhaas et al., (2010) with stress coping style and stress reactivity as two independent dimensions of stable trait characteristics (e.g., aggression). The four quadrants indicate the type of animal when the two dimensions vary simultaneously.*

The terms shy and bold have also been used to describe dogs; shy individuals are described as generally being cautious, timid and evasive in both novel social and non-social situations, whereas bolder individuals are more social, spontaneous and exploratory, according to Svartberg and Forkman (2002). Svartberg (2002) observed a clear interaction between Boldness and Trainability and found that bold dogs were more likely to perform well in situations requiring persistence. Both Trainability and working persistence are desirable traits in an MWD, and a correlation between Trainability and performance was found when investigating the SAF T-test in Paper III. It may be tempting to assume that MWDs are all bold individuals that respond to threats with low stress reactivity, i.e., low cortisol levels, and in a proper behavioural manner. However, a study by Horváth et al (2007) of experienced police working dogs suggests that dogs can be divided into three groups (fearful, aggressive and ambivalent) depending on their coping style and cortisol levels and that even experienced dogs show signs of fear. They found that the group containing individuals with a proactive coping style, i.e., those responding with aggression, did not experience a significant increase in cortisol, whereas the group that had a reactive coping style (fearful) displayed a small but significant increase in cortisol. There seems to be a link between coping style and the physiological stress response, as measured by cortisol levels in this study by Horváth et al (2007). Therefore, the behaviour and perception of dogs during the performance of the SAF T-test was further investigated in Paper IV of this thesis.

EARLY EXPERIENCE

As described in the Behaviour section of this thesis, behaviour may be evaluated with temperament tests. Behaviours may be innate or acquired by experiences, such as training, but may also come from early experiences during ontogenesis (the development of an individual from birth to death). The results of previous studies have shown that events occurring early in life can have significantly affect behaviour and physiology later in life (Meaney, 2001; Maestripieri et al., 2005), which may, in part, be explained by the way that the nervous system and, ultimately, the behaviour of an animal, or human for that matter, develop. Many altricial (offspring that require care or nursing after birth) mammalian species, such as the dog, are born in a state of large neural immaturity, but the nervous system develops rapidly. During this development, the individual is particularly vulnerable to various influences, and this dynamic developmental process is largely dependent on the individual´s interactions with its environment before and after birth (Gazzano et al., 2008). Additionally, environmental influences can also have a profound and lasting effect on an animal's behavioural repertoire (Rosenzweig, 1984). Therefore, it is reasonable to suggest that there may be a "window of opportunity" during the neonatal phase (newly born) for influences, such as stress, that can lead to phenotypic alterations in the adult animal.

Much of the empirical research on early experiences has been carried out in the field of stress research (Meaney, 2001). For instance, stress influences cognitive function, such as memory and attention, and mild or moderate concentrations of stress hormones can enhance memory formation, whereas high concentrations or prolonged elevation can lead to memory disruption (Mendl, 1999). Many of these stress studies are classified as prenatal (before birth) or postnatal (after birth) research, depending on when the stressor is presented. In many cases, it has been shown that the effect on behaviour and physiology in response to pre- and postnatal induced stress may vary depending on the timing.

Prenatal stress

There is evidence that prenatal stress can influence behaviour and HPA regulation in offspring. Vallée et al., (1997) showed that prenatally stressed adult rats (whose mothers were restrained in an illuminated environment for 3x45 minutes per day during the last week of pregnancy) exhibited a high degree of anxiety-like behaviour, which was expressed as an escape response to novelty, and that this correlated with high corticosterone secretions in response to stress.

Champagne et al (2003) also examined how stress during pregnancy in rats affected maternal behaviour in previously defined High- and Low-licking and grooming and arch-back nursing (LG-ABN) mothers. They found that High LG-ABN mothers exposed to restraint stress during the last half of pregnancy decreased their frequency of maternal licking/grooming and arch-back nursing, whereas the Low LG-ABN mothers did not. They also found that the effect was fully evident in the third generation, even in the absence of any further stressor, reflecting a potent, trans-generational effect.

Postnatal experience

Various postpartum circumstances, such as physical stress, diseases, naturally occurring variations in maternal behaviour i.e., licking, grooming and nursing, and experimentally neonatal handling (short but repeated daily sessions of separation from the mother) can all contribute to altered neurological development (Chapillon et al., 2002) and are important factors in the HPA-axis stress response in rodents. Among the first to demonstrate this was Levine et al (1967), who showed that neonatal handled rats were less reactive, more explorative and more emotionally stable as adult compared with controls and that these early separated animals showed a lower plasma corticosterone levels over time compared with non-handled animals. Vallée et al (1997) also found that adult rats handled as neonates displayed a low degree of anxiety-like behaviours, which was expressed as high exploratory behaviour correlated with low corticosterone secretion in response to novelty (i.e., a proactive coping style). However, longer periods of daily separations from the mother can increases the fear and stress response in adult offspring (Plotsky and Meaney, 1993; Macrí et al., 2004). In a study of dog handling, handling was found to have a positive effect on the emotional development; handled pups were calmer (Gazzano et al., 2008).

It was long believed that the handling procedure *per se* led to these alterations, but more recent studies have revealed that neonatally handled rat pups received more maternal care than their non-handled counterparts (Liu et al., 1997; Meaney, 2001; Macrí et al., 2004). Macrí and Würbel (2007) demonstrated that small changes in the maternal environment (food location) modified the pattern of maternal behaviour and nest attendance, which also resulted in altered behavioural and HPA responses to stressors in the adult offspring.

Thus, both the behaviour and physiology of offspring may change as a consequence of differences in the pattern and amount of maternal care received, leading to for instance modifications of the HPA response and altered behaviour in rodents. However, does this also hold true for dogs? In a study by Gazzano et al

(2008), the authors assumed that the consequences resulted from handling, but if dogs are comparable to rodents from this perspective, it would make more sense to measure mother-pup interactions. Furthermore, it is uncertain if the difference observed between handled vs. non-handled puppies remains consistent into adulthood because the puppy test was conducted on 8-week-old puppies with no follow-up studies. Wilson and Sundgren (1997) found that the correlation between the results of a puppy test and later adult performance was negligible, and Riemer et al (2014) found only weak support for behavioural consistency in a longitudinal study from neonates to adults in Border Collies. The only trait that was significantly correlated between the puppy and adult tests was exploratory behaviour.

Hence, whether *i)* there are any naturally occurring variations in maternal care in dogs, and *ii)* if so, do they influence the behaviours of puppies later in life are the questions investigated in Paper II in this thesis.

Breeding, denning and parental care

For female wolves, maternal behaviour starts before the pups are born when she is selecting and preparing a den (Johnson and Aamodt, 1985), which are behaviours that can also be seen in various dog species, including the domestic dog. Even first-time mothers seem to know how to provide for their young, and this innate behaviour is hormonally driven, for example, by progesterone, which is released from the ovaries, and prolactin, which is released from the anterior pituitary gland. Immediately after birth, the mother licks her pups dry and clean and bites through the umbilical cord while the pups instinctively search for the nipple to begin nursing (Lindholm et al., 2015).

As in all mammals, the brain of the mother dog coordinates maternal behaviour, and the smell, sight and touch of nursing pups activates the release of various hormones from the pituitary gland, including two hormones vital for generating and maintaining maternal behaviour, oxytocin and prolactin. Oxytocin is responsible for milk letdown and the formation of the mother-pup bond, whereas prolactin controls milk production (Vander et al., 2001). During the first two weeks, the mother must also stimulate urination and defecation in her pups through anogenital licking. The mother dog is kept busy feeding, nursing and licking her pups, but even though this "knowledge" is innate, results from rodent studies indicate the existence of naturally occurring variations in the amount of maternal care provided (Caldji et al., 2000; Francis et al., 2000; Champagne et al., 2001). As described in the Early experience section, this may influence the behaviour of adult offspring. Primates also show evidence of differences in maternal style (Fairbanks, 1996), and this was found for dogs in Paper II. Apart from individual differences in maternal style, maternal behaviour declines during the first three weeks (Figure 5).

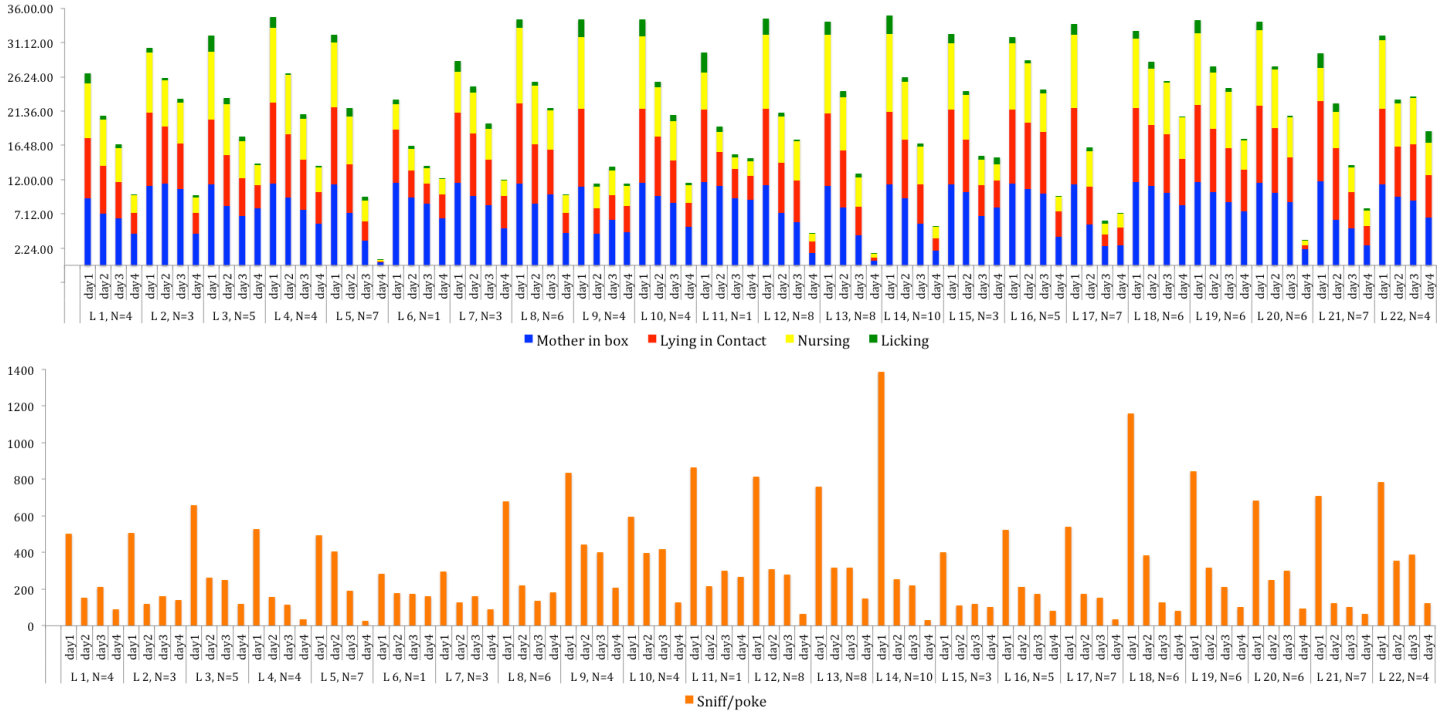

Figure 5. *Individual differences in female maternal behaviour, observed in 22 litters during four observational days for three weeks postpartum. a) Duration (in hours) of the following behaviours:* Mother in Box, Lying in Contact, Nursing *and* Licking. *b) The frequency of* Sniff/poke. *Data from Paper II*

Maternal behaviour

Maternal behaviour is defined as the behaviour shown by the mother toward her offspring, and it varies depending on the species. In precocial (young that are able to move and forage at a very early stage) mammalian species like the horse, where the foal is able to follow the mare just hours after being born, the maternal behaviour primarily consists of providing food and protection against predators. In the altricial dog, the maternal behaviour is more extensive. Like wolf or rat pups, dog puppies are helpless at birth; they are born blind and deaf with a very immature olfactory (smell) system and limited movement abilities. Furthermore, they are unable to maintain their own body temperature; therefore, for the first weeks of their lives, they depend entirely on their mothers for food, warmth and protection and do little but eat and sleep (Lindholm et al., 2015).

However, dog pups develop quickly, changing from helpless to active and curious pups in just four or five weeks. Within a few weeks, dogs complete some of their most important developmental processes in life (Jensen, 2007), which are often divided into four periods: the neonatal period (0-13 days), the transition period (13-20 days) followed by the socialisation period (3-12 weeks) and the juvenile period (3-20 months) (Lindholm et al., 2015). Additionally, the prenatal period may also be included because, as described in the Early experience section, events such as prenatally induced stress could also affect offspring behaviour and physiology later in life, but prenatal effects are excluded from this thesis. However, early experiences include far more than just maternal-offspring interactions, and this issue is addressed in Paper I. Other environmental influences that have the potential to influence the development of temperament in dogs were investigated. Such early environmental experience may include litter size, the sex ratio of the litter and date of birth.

Puppy development

During the neonatal phase, pups require constant attention from their mother. Their loco-motor abilities are constrained to crawling and head oscillations to locate their mother and siblings, and they need their mother to obtain food and dispose of waste products (Jensen, 2007). Furthermore, pups cannot thermo-regulate themselves; therefore, in nature, the den floor is often slightly concave to keep the puppies in physical contact with each other as they crawl around (Fält, 2003). When breeding domestic dogs, it is not unusual to place the whelping box on a plain floor in a well-lighted area at room temperature. In this case, pups will crawl away from their siblings if the temperature is too high, thereby missing out

on tactile stimulation, which has been shown to have positive effects on the emotional development (Gazzano et al., 2008).

At the end of the second week, the eyes start to open, which marks the beginning of the Transition period that continues for about a week (Fält, 2003). The reason that dog pups cannot see from birth is probably in part an inheritance from their wolf ancestor. In the darkness of the den, the visual cues are limited, so vision is of limited value. Furthermore, to the mind of the author, the brain is also still underdeveloped, so it might not yet be able to process any visual signals. However, the brain and nervous system develop rapidly, particularly during the transition period (Gazzano et al., 2008). By the end of the Transition period, the pups begin to walk, play-fight with their siblings and wag their tails (Fält, 2003). Eliminative behaviour no longer requires maternal anogenital licking, so the mother's licking gradually transitions to social licking instead (Wilsson, 1997). By the end of the third week, pups can maintain their own body temperature, and the ear channels start to open, which marks the end of the Transition period. However, the ability to see and hear remains poor for the next few weeks (Fält, 2003). In Paper II, mother-pup interactions were monitored for 24 hours a day, 7 days a week during these first three weeks of life and were later evaluated to examine the presence of naturally occurring variation in maternal care.

Even though most mother dogs take good care of their litters and spend much time with their pups, particularly during the first two weeks, there are occasions when something truly goes wrong, and seemingly dysfunctional mothers even kill their own pups (infanticide). This phenomenon is not understood, but it could be stress-related.

The following weeks (weeks 3-12) are the socialisation period, during which the pups start to display several adult behaviour patterns (Jensen, 2007). It is now that the wolf pup leaves the den for the first time to meet other members of the pack (Johnson and Aamodt, 1985), so it is during this time that the pup begins to recognise its conspecifics and other social networks, which would include humans for dogs. If a dog pup is deprived of human contact during this phase, it may become more difficult to tame and train (Jensen, 2007) despite being domesticated. Additionally, the first signs of fear can be observed during this time period. The process of socialisation involves the introduction of a gradually higher levels of complexity into pups' lives (Hubrecht, 1995) through a variety of objects such as toys, sounds, novel objects, and handling by humans of both sexes and various ages. Pups progressively become more active, explorative and independent, and the transition from milk to solid food begins (Lindholm et al., 2015). In wolves, the mother and other pack members regurgitate food in

response to the pups licking the lips of the adult animal (Johnson and Aamodt, 1985), and this behaviour sometimes occurs in domestic dogs (Malm, 1995). By the end of the socialisation period, the dog pups are weaned and ready to move to their human families. Paper I is concerned with how different environmental experiences during this time frame, i.e., the neonatal and transition periods and part of the socialisation period, affect later behaviour and temperament.

The juvenile period (3-12 months) is characterised by the gradual maturation and development of the dog, both cognitively and physically. This is the time when the young dog learns the cues related to living in human society. It is an important time, and the young dog must be introduced to different environments and circumstances to develop into a confident and secure individual (Lindholm et al., 2015). Such enrichment typically involves exposure to a variety of novel and exciting opportunities for investigation, as well as interaction with objects and humans and members of other species. In many respects, enrichment is an extension of socialisation (Battaglia, 2009); pups that are not exposed to enrichments would typically be fearful of unfamiliar objects and generally prefer to withdraw rather than investigate, which corresponds with a high stress reactivity pattern. The adolescence period coincides with the juvenile period, during which behavioural changes may occur (Diederich and Giffroy, 2006). When a dog reaches one year of age, it has become sexually mature, whereas the wolf becomes sexually mature at approximately two years of age (Johnson and Aamodt, 1985). In the third paper in this thesis, the lives of dogs during the juvenile period were investigated, including whether there were any variables associated with experiences during this time frame and later success in the evaluative temperament test.

SUMMARY OF PAPERS

Paper I

Early experiences modulate stress coping in a population of German Shepherd dogs.

Foyer, P., Wilsson, E., Wright, D., Jensen, P. (2013). Applied Animal Behaviour Science 146, 79–87.

Background and Aim

In many mammalian species, the neonatal period is a time of significant social interaction and brain development, which includes the organization of the central nervous system. Therefore, it is an important time for the development of the expression of social behaviour and the adult stress response. Understanding how personality is affected by early experiences is important as it may alter the phenotypic expression and the development of temperament in an animal. These differences can persist through adulthood and may have a profound impact on animal welfare. Previous studies have concluded that specific variables in the neonatal environment, such as litter size, litter composition, parity, i.e., previous maternal experience, season of birth and other environmental, genomic or intrinsic factors, can all shape long-term behaviour in a variety of species. Records from dogs within the SAF breeding program and score sheets from the SAF T-test were used to investigate which, if any, maternal and/or litter effects correlate with different behavioural traits and later temperament in a population of prospective MWDs.

Results and Conclusions

Using a standardised evaluative temperament test, we found that some factors in the early environment have effects on the dogs' behaviour measured approximately at one and a half years. The Confidence of the offspring was affected by parity, sex and litter size, and Physical Engagement was affected by parity, growth rate, litter size and season of birth. Social Engagement was affected by growth rate and sex, but Aggression was affected only by sex in this study. The result indicates that some early experiences seem to affect later temperament in this population.

Paper II

Levels of maternal care in dogs affect adult offspring temperament

Foyer, P., Wilsson, Erik., Jensen, P. Submitted manuscript.

Background and Aim

Various postpartum circumstances including diseases, food shortages, physical stress or naturally occurring variation in mother-offspring interactions, such as nursing or licking and grooming, can all contribute to altered neurological development and behaviour in rodents and other mammalian species. The first objective of this study was to assess the differences in maternal behaviour in dogs, which was defined in terms of specific tactile and non-tactile interactions. The second objective was to investigate the behavioural differences in the puppies resulting from differences in mother-pup interactions.

Results and Conclusions

The results clearly show that mother dogs differ in the amount and distribution of maternal behaviour during the first three weeks of motherhood and that these behaviours declined over time in a rather consistent fashion. Furthermore, differences in maternal care impacted pup behaviour and temperament on a litter level as measured by the standardised temperament test (SAF T-test) at approximately one and a half years of age. Maternal care was positively correlated to Physical Engagement, Social Engagement and Aggression, but Confidence was unaffected in this study. That both Physical and Social Engagement are affected by maternal care is interesting because they, together with Confidence, have been recognized as predictors of suitability as an MWDs. Further knowledge about this effect may be helpful in the breeding and selection processes of the MWD breeding programs.

Paper III

Behaviour and experiences of dogs during the first year of life predict the outcome in a later temperament test

Foyer, P., Bjällerhag, N., Wilsson, E., Jensen, P. (2014). Applied Animal Behaviour Science 155, 93-100.

Background and Aim

Several studies of early experiences and how they may affect the behaviour of adult animals have been carried out in recent years to understand the mechanisms behind phenotypic, genomic and behavioural variations. In addition to prenatal and early postnatal experiences, environmental factors may have an impact on an animal's future behaviour; later experiences may exert an influence as well. Therefore, we investigated whether events during the juvenile period could predict behaviour and temperament in dogs later in life using the Canine Behavioural and Research Questionnaire (C-BARQ) and the results from the standardised evaluative temperament test (SAF T-test) used by the Swedish Armed Forces K9 department.

Results and Conclusions

Dogs that were approved by the evaluative temperament test scored significantly higher in the C-BARQ category *Trainability* and C-BARQ items *Hyperactivity/Restlessness, Difficulties in Settling Down* and *Chasing/Following Shadows or Light Spots* and were left at home for longer times compared with non-approved dogs. Furthermore, non-approved dogs scored significantly higher in different fear-related C-BARQ categories. These findings indicate that the experiences and behaviour of the dogs during their first year of life can, in part, determine their suitability to become MWDs. This knowledge could potentially be used to improve selection procedures for working dogs.

Paper IV

Behaviour and Cortisol Responses of Dogs Being Approved in a Standardised Temperament Test for Military Working Dogs

Foyer, P., Svedberg, A-M., Nilsson, E., Wilsson, E., Faresjö, Å., Jensen, P. Accepted manuscript.

Background and Aim

Stress can be seen as a state of increased arousal that may be provoked by both aversive and pleasurable stressors, and a stressor may vary depending on the species, as well as the individual. Therefore, it is an individual's perception of the stimulus that determines if the stressor should be considered stressful and potentially harmful if prolonged or frequent or if it merely elicits excitement and positive emotions. Regardless of whether a stressor is considered positive or negative, there will most likely be both a behavioural and physiological response. When a stressor arouses an animal, one physiological reaction is the controlled pathway for cortisol secretion, known as the hypothalamic-pituitary-adrenal (HPA) response. In this study, we investigated the responses of dogs in a standardised temperament test to assess the activity of the HPA axis and its relationship to a dog being approved for further training.

Results and Conclusions

Approved dogs displayed high emotionality, which is a possible fear-related behaviour, in the subset of the test conditions that were evaluated. Furthermore, approved dogs showed significantly higher levels of salivary cortisol secretion, both prior to and after the completion of the temperament test, than non-approved dogs. Although these results were in accordance with results from other studies that have shown that reactivity and fearfulness often overlap, they were surprising; therefore, there is a need for further investigation, including the verification of the cortisol response with other physiological measurements. The higher levels of cortisol in approved dogs, even prior to the test, may indicate that these dogs have a higher overall energetic level than non-approved dogs, which is in line with the results in Foyer et al., (2014) (Paper III).

GENERAL DISCUSSION

The aim of this thesis is to investigate the parameters that can influence behaviour and help us understand the complexity of the underlying temperament, or personality, of MWDs. If variables in the early environment can be identified and knowledge about how they influence later behaviour can be obtained, it may also be possible to apply this knowledge and, by changing some of these variables, alter the phenotypic expression in the dogs in a favourable way.

Many studies of early experiences and mother-offspring interactions have been carried out with rodents under laboratory conditions (Mendl and Paul, 1991; Francis et al., 1999; Champagne et al., 2003; Macrí and Würbel, 2007). Laboratory settings are advantageous due to the standardised conditions and the possibility to obtaining a large amount of reliable data from a large population with a relatively short generation time. One important difference when studying dogs is that the opportunity to study such phenomena, such as early experiences, under strict and regulated settings similar to those offered by a laboratory is rare. There is an obvious risk of ending up with either very small sample sizes, different breeds, or the same breed but from different breeders and kennels. In studies with small sample sizes, such as Malm (1995), and Malm and Jensen (1997), it may be difficult to obtain significant results and draw any strong conclusions. The use of different breeds may also be confounding as development and behavioural reactions may be breed-specific (Morrow et al., 2015). However, sometimes, such as when developing a test or questionnaire to describe a dog in general terms, validating the test using a large number of breeds may be beneficial and provide more reliable test results. Therefore, depending on the objective, it is sometimes advantageous to use more than one breed. Differences in management routines and the local environments of different kennels may further confound the results (Blaustein, 2011). Hence, using the SAF K9 breeding facility, with its standardised conditions and single breed, to study early experiences has been of great value and has ensured the reliability of the results. Nevertheless, there are still a number of variables that are difficult to control, e.g., prenatal effects and the experiences of the dogs with the foster families. Furthermore, as is often the case in science, there are many other factors beyond the control of researchers, such as behavioural and physiological impacts of a nearby construction site, that may compromise the results of even carefully controlled experiments, even under laboratory conditions (Blaustein, 2011).

In all of the four papers in this thesis, the central theme is the examination of temperament using various methods in a range of different contexts and over different time periods to generate different pieces of information. As described earlier, the psychological, physiological and behavioural aspects of temperament or personality can be studied, but different approaches are required depending on the specific research question. Thus, the results from the different approaches in this thesis can be combined to yield a broader foundation of knowledge about the development of temperament that can then be used in the selection of and management routines for MWDs.

This thesis, like most research on the development of temperament or behavioural profiles, has focused on early life phases. However, unlike many others studies, I did not study prenatal effects, although parity was used as a variable in Papers I and II. However, it is possible that prenatal stress affects the offspring within the breeding program. The females live their lives with their human families in ordinary homes but are transferred to the kennel approximately three weeks prior to their estimated whelping date, and this transfer and the relative isolation during quarantine and in the whelping facility may subject some females to stress, which may have an effect on the puppies. One suggestion for future research is to investigate whether this transfer is perceived by the females to be stressful and if this affects the offspring. With a growing number of breeding animals which have been recruited from within the program, so their temperament profiles will be known, there will be more opportunities for future studies, such as an examination of prenatal effects and heritability. Whereas some studies of dogs have certainly investigated and described the temperament of adult animals (Goddard and Beilharz, 1984; Svartberg and Forkman, 2002; Horváth et al., 2007; Haverbeke et al., 2009), others have used temperament tests as aptitude tests to match dogs to specific tasks, such as police dogs (Slabbert and Odendaal, 1999), guide dogs for the blind (Duffy and Serpell, 2012), MWDs (Wilsson and Sundgren, 1997), or other working dogs (Svartberg, 2002), similar to Papers I and III. However, to my knowledge, none have attempted to evaluate the effects of maternal care during the first weeks postpartum, i.e., to study the maternal behavioural factors that matter and their links to the future ability of working dogs, as performed in Paper II of this thesis.

As reported in Paper I, previous studies have mainly been performed on rodents, and the results have shown that different early environmental factors such as litter size, litter composition and parity could all contribute to the alteration of offspring behaviour. However, since most of the previous work has been done on rodents and primates, its generalizability to dogs is limited, but there are a few previous studies that have investigated early environmental effects in dogs. For

instance, van der Waaij et al., (2008) reported significant heritable effects on single traits from sex, age, season of birth, testing and litter size from a behaviour test. Therefore, Paper I investigated which, if any, maternal and/or litter effects during the neonatal, transition and part of the socialisation period (more precisely from birth to 8 weeks) correlate with different, broader behavioural traits and later temperament, i.e., factors derived from the PCA of the SAF T-test, in prospective MWDs. The results from Paper I demonstrate that the early environmental experiences of dogs have a lasting effect on their. However, isolating an eight-week time period and correlating the environmental factors with the results of a temperament test taken approximately one and a half years later has its limitations. Experiences during other time periods also influence the animal, but including all of the factors from birth, or even before birth, until the time of the evaluative temperament test takes place to try and disentangle the results appears to be a monumental task. For practical reasons, it is more reasonable to divide the project into different time frames, each with its own research questions. This means that attention is also given to other time periods and other variables that may interact with the development of the temperament profile.

Papers I and II both consider early experiences during the first weeks postpartum and how they relate to offspring temperament later in life. However, Paper II is concentrated on the consequences of mother-pup interactions during the neonatal and transition periods. The interactions between mother and pup have been studied before, such as by Wilsson (1984), although that study was focused on the time period from three weeks to weaning and was mainly concerned with how social and aggressive behaviours were influenced by conflict during weaning. In Paper II, only the time period from birth to the end of the third week was studied, and there are no apparent conflict of interests between mother and pup during this time period, so the study is focused on maternal care. First, it had to be established that female dogs differed in their maternal style similar to other species, e.g., rodents (Liu et al., 1997; Francis et al., 2000; Meaney, 2001), and the results show that the females differ in their level of maternal care in a consistent manner. This difference significantly affected the behaviours of adult offspring, mainly those classified as belonging to Physical and Social Engagement and Aggression, whereas Confidence was unaffected by differences in maternal care. According to Wilsson and Sinn (2012), Confidence and Engagement are the most important predictors of the suitability of dogs to become MWDs, so it is very interesting that the results in Paper II clearly demonstrates that as more maternal care is received by the pups, the litter means for both Physical and Social Engagement become higher. Although it is impossible to draw any conclusions

about behavioural effects on an individual level based on litter-level data, I believe that there are strong reasons to assume that mother-pup interactions also have implications for offspring behaviour and temperament in individual dogs. Therefore, future research should emphasise the individual level and concentrate on finding the variables in the early environment, or the handling and management regimes that affect Confidence. Identifying such variables and implement changes where needed may lead to further improvement of the breeding program.

In Paper III, different variables and experiences during the time period from weaning to adult (i.e., the time that the puppies stay in their foster homes) and how they connect to and predict the outcome of the future evaluative temperament test were investigated. This was done by comparing the answers from a questionnaire, about the dog's behaviour in home environment, with later performance on the temperament test. Questionnaires or test batteries or a combination of the two are common techniques for evaluating dog behaviour, but the goal in many cases seems to focus only describing the dogs' temperament profile (Serpell and Hsu, 2001; Svartberg and Forkman, 2002), or evaluating how different characteristics in the environment or dog/man dyads affects temperament (Kobelt et al., 2003; Kubinyi et al., 2009). However, the management regime also seems to be an important factor in determining how temperament develops in young dogs. In a study of Swiss MWDs, Fuchs et al (2005) found that dogs who had frequent contact with school-aged children had higher trait defence drive scores, and the authors further observed that the dogs that had participated in puppy/young dog training achieved higher scores for nerve stability and self-confidence. Hence, techniques that can make use of data, such as the use of questionnaires, and apply the results for predictive purposes may be implemented to improve the selection procedure for MWDs. The results in Paper III that makes use of an extended C-BARQ showed that, above all, Trainability could predict whether dogs would be rated as approved or not approved in the SAF T-test.

Other studies have linked Trainability to Boldness (Svartberg, 2002), but Boldness was not specifically investigated in our survey. However, if the model proposed by Koolhaas (2010), which is described in the Stress section, is correct, there would be a greater probability that approved dogs that score high on Trainability would also be bold and have a tendency to act with low stress reactivity, e.g., exhibit low levels of cortisol. However, the opposite result was found in Paper IV, which investigated how the dogs responded to a potentially stressful test situation. The results showed that the dogs that were approved in the SAF-T-test had higher salivary cortisol levels, both before and after

performing the temperament test, compared with non-approved dogs. This indicates that these dogs may not perceive the SAF T-test as being particularly stressful but that they are what could be described as being high in temper i.e., energetic, lively and easily aroused. This is consistent with the results from Paper III, in which caretakers had described the approved dogs as being very active and having difficulty settling down prior to testing. As previously noted, these dogs were also rated as being highly trainable, which is one of the preferred traits in working dogs. According to Weiss and Greenberg (1997), the preferred characteristics for a search and detection dog include energy and endurance, strength and mobility, curiosity, sociability, and keen senses, in addition to high trainability. Therefore, results in Papers III and IV suggests that the characteristics in approved dogs, i.e., dogs with high stress resilience, which are energetic dogs with high stress reactivity that are also highly trainable, may be the result of successful breeding within the SAF breeding program. However, further investigation is needed to confirm this conclusion, and breeding dogs with high stress resilience must be monitored because there may eventually be negative consequences for welfare if the dogs' ability to relax is lowered or lost.

Continuing the discussion about maternal care, dogs may not differ biologically as much from their wild ancestors as we like to think when designing our breeding facilities, thereby providing an environment that might actually prevent the females from attending to their young in an optimal way. For instance, rooms may be kept too warm so that the females prefer to lay outside the whelping box instead of being in physical contact with their pups. Thus, mimicking nature and identifying the environmental variables in current breeding practices, such as temperature or the flooring material in the whelping box, that can be altered and could potentially trigger the females to take "better" care of their young might yield more offspring with preferred temperament profiles.

Temperament tests provide useful information about an individual's suitability and success as a working dog, particularly if used with other relevant assessment tools. Even though new genetic technologies, which might be able to predict certain aspects of dog temperament, are likely to be developed in the future (Olson et al., 2004), I believe that valid temperament tests and matched behavioural descriptions will continue to be necessary to provide essential information to breeding programs and should be further investigated to reach their full potential.

Even though questions remain regarding the early experiences of dogs and how they relate to later temperament, the results from the papers included in this thesis provide some answers. Two traits of particular interest for an MWD are

Confidence and Engagement, and these traits are affected by early experiences, such as parity, sex, litter size and season of birth, as shown in Paper I. Engagement, Aggression, and to a lesser extend Confidence, are also affected by the amount of maternal care, as shown in Paper II, and these results further demonstrate that dogs vary in the amount of maternal care that they provide. Future studies should investigate if females can be influenced into taking greater care of their pups. Of value to breeding programs is the ability to accurately predict future success early, preferably before dogs are put through training. Hence, developing methods that can provide this information is extremely valuable, and the results of Paper III, showed that some C-BARQ categories and items could predict later success in temperament tests. This information can therefore be applied to the breeding program. Results in paper IV, suggests that although dogs approved in the SAF T-test show higher stress reactivity than non-approved dogs, i.e., higher salivary cortisol levels, this might be a result of conscious breeding. Results from each study in this thesis add pieces of information, which contributes to the conditions for an improved knowledge-based selection with a potential to recruit more dogs with preferred temperament to become an MWD.

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REFERENCES

Axelsson, E., Ratnakumar, A., Arendt, M.L., Maqbool, K., Webster, M.T., Perloski, M., Liberg, O., Arnemo, J.M., Hedhammar, A., Lindblad-Toh, K., 2013. The genomic signature of dog domestication reveals adaptation to a starch-rich diet. Nature 495, 360-364.

Battaglia, C.L., 2009. Periods of Early Development and the Effects of Stimulation and Social Experiences in the Canine. J Vet Behav 4, 203-210.

Beilharz, R.G., 2007. Evolutionary Aspects on Breeding of Working Dogs, in: Jensen, P. (Ed.), The Behavioural Biology of Dogs, CABI, Oxfordshire, pp. 166-181.

Berg, L., Wilsson, E., 2014. FM Avelsprogram 2014-2018 och produktionsresultat 2005-2013, Livgardet, Sollefteå, pp. 1-22.

Blaustein, J.D., 2011. Nearby Construction Influences the Physiology of Research Animals: Beyond Stress Hormones. Endocrinology 152, 1197-1198.

Brown, R.E., 1994. An introduction to euroendocrinology. Chapters 1-4, Cambridge University Press, p.1-55.

Budaev, S.V., 2010. Using Principal Components and Factor Analysis in Animal Behaviour Research: Caveats and Guidelines. Ethology 116, 472-480.

Caldji, C., Diorio, J., Meaney, M.J., 2000. Variations in maternal care in infancy regulate the development of stress reactivity. Biological Psychiatry 48, 1164-1174.

Cannon, W.B., 1915. Bodily Changes in Pain, Hunger, Fear and Rage: an account of recent researchers into the function of emotional excitement. D. Appleton and Company, New York.

Champagne, F., Diorio, J., Sharma, S., Meaney, M.J., 2001. Naturally occurring variations in maternal behaviour in the rat are associated with differences in estrogen-inducible central receptors. PNAS 98, 12736-12741.

Champagne, F.A., Francis, D.D., Mar, A., Meaney, M.J., 2003. Variations in maternal care in the rat as a mediating influence for the effects of environment on development. Physiology and Behavior 79, 359-371.

Champagne, F.A., Meaney, M.J., 2006. Stress During Gestration Alters Postpartum Maternal Care and the Development of the Offspring in a Rodent Model. Biological Psychiatry 59, 1227-1235.

Chapillon, P., Patin, V., Roy, V., Vincent, A., Caston, J., 2002. Effects of pre- and postnatal stimulation on developmental, emotional, and cognitive aspects in rodents: A review. Developmental Psychobiology 41, 373-387.

Clutton-Brock, J., 1995. Origins of dog: domestication and early history., in: Serpell, J.A. (Ed.), The Domestic Dog, its Evolution, Behaviour, and Interactions with People, Cambridge University Press, Cambridge, pp. 7-20.

Cobb, M., Branson, N., McGreevy, P., Lill, A., Bennett, P., 2015. The advent of canine performance science: Offering a sustainable future for working dogs. Behav Process 110, 96-104.

Coppinger, R., Schneider, R., 1995. Evolution of working dogs, in: Serpell, J.A. (Ed.), The Domestic Dog: its Evolution, Behaviour and Interactions with People, Cambridge University Press, Cambridge, pp. 21-47.

Costa, P.T., Jr., McCrae, R.R., 1992. NEO-PI-R: Professional Manual. Psychological Assessment Resources, Odessa, FL.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection. Murray, London.

David, J.T., Cervantes, M.C., Trosky, K.A., Salinas, J.A., Delville, Y., 2004. A neural network underlying individual differences in emotion and aggression in male golden hamsters. Neuroscience 126, 567-578.

Diederich, C., Giffroy, J.-M., 2006. Behavioural testing in dogs: A review of methodology in search for standardisation. Appl Anim Behav Sci 97, 51-72.

Duffy, D.L., Serpell, J.A., 2012. Predictive validity of a method for evaluating temperament in young guide and service dogs. Appl Anim Behav Sci 138, 99-109.

Engel, G.L., Schmale, A.H., 1972. Conservation-withdrawl: a primary regulatory process for organismic homeostasis, in: Porter, R., Knight, J. (Eds.), Ciba Foundation Symposium 8 - Physiology, Emotion and Psychosomatic Illness

Fairbanks, L.A., 1996. Individual Differences in Maternal Style: Causes and Consequences for Mothers and Offspring, in: Rosenblatt, J.S., Snowdon, C.T. (Eds.), Advances in the Study of Behavior.

Fält, L., 2003. Beteendeboken. Om valpens tidiga beteendeutveckling. Sellin & Partner Bok och Idé AB, Stockholm.

Francis, D., Diorio, J., Liu, D., Meaney, M.J., 1999. Nongenomic transmission Across generation of Maternal Behaviour and Stress Responses in the Rat. Science 286, 1155.

Francis, D.D., Champagne, F.C., Meaney, M.J., 2000. Variations in maternal behaviour are associated with differences in Oxytocin receptor levels in the Rat. Journal of Neuroendocrinology 12.

Fuchs, T., Gaillard, C., Gebhardthenrich, S., Ruefenacht, S., Steiger, A., 2005. External factors and reproducibility of the behaviour test in German shepherd dogs in Switzerland. Appl Anim Behav Sci 94, 287-301.

Galibert, F., Quignon, P., Hitte, C., Andre, C., 2011. Toward understanding dog evolutionary and domestication history. Cr Biol 334, 190-196.

Gazzano, A., Mariti, C., Notari, L., Sighieri, C., McBride, E.A., 2008. Effects of early gentling and early environment on emotional development of puppies. Appl Anim Behav Sci 110, 294-304.

Goddard, M.E., Beilharz, R.G., 1984. A factor analysis of fearfulness in potential guide dogs. Appl Anim Behav Sci 12, 253-265.

Goldsmith, H.H., Buss, A.H., Plomin, R., Rothbart, M.K., Thomas, A., Chess, S., Hinde, R.A., Mccall, R.B., 1987. Round-Table - What Is Temperament 4 Approaches. Child Dev 58, 505-529.

Gosling, S., 2001. From mice to Men: What can we learn about Personality From Animal Research? Psycholigical Bulletin 127, 45-86.

Gosling, S., John, O., 1999. Personality Dimensions in Nonhuman Animals: A Cross-species Review. Current Directions in Psychological Science 8, 69-75.

Grandin, T., 1997. Assessment of stress during handling and transport. Journal of Animal Science 75, 249-257.

Groothuis, T.G.G., Carere, C., 2005. Avian personalities: characterization and epigenesis. Neuroscience and Biobehavioral Reviews 29, 137-150.

Groothuis, T.G.G., Müller, W., Nikolaus Engelhardt, v., Carere, C., Eising, C., 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. Neuroscience and Biobehavioral Reviews 29, 329-352.

Haverbeke, A., Smet, A.D., Depiereux, E., Giffroy, J.-M., Diederich, C., 2009. Assessing undesired aggression in military working dogs. Appl Anim Behav Sci 117, 55-62.

Horváth, Z., Igyarto, B.Z., Magyar, A., Miklosi, A., 2007. Three different coping styles in police dogs exposed to a short-term challenge. Hormones and Behavior 52, 621-630.

Hsu, Y.Y., Serpell, J.A., 2003. Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. J Am Vet Med Assoc 223, 1293-1300.

Hubrecht, R.C., 1995. Enrichment in Puppyhood and Its Effects on Later Behavior of Dogs. Lab Anim Sci 45, 70-75.

Jensen, P., 2006. Domestication - from behaviour to genes and back again. Appl Anim Behav Sci 97, 3-15.

Jensen, P., 2007. Mechanisms and Function in Behaviour, in: Jensen, P. (Ed.), The Behavioural Biology of Dogs, CABI, Oxfordshire, pp. 61-75.

Jensen, P., 2014. Behavior Genetics and the Domestication of Animals. Annu Rev Anim Biosci 2, 85-104.

Johnson, S.A., Aamodt, A., 1985. Wolf Pack. Tracking Wolves in the Wild. Lerner Publications Company, Minneapolis.

Jones, A.C., Gosling, S.D., 2005. Temperament and personality in dogs: a review and evaluation of past research. Appl Anim Behav Sci 95, 1-53.

Kikusui, T., Nakamura, K., Mori, Y., 2008. A review of the behavioral and neurochemical consequences of early weaning in rodents. Appl Anim Behav Sci 110, 73-83.

Kim, J.J., Diamond, D.M., 2002. The stressed hippocampus, synaptic plasticity and lost memories. Nat Rev Neurosci 3, 453-462.

King, T., Hemsworth, P.H., Coleman, G.J., 2003. Fear of novel and startling objcecys in domestic dogs. Appl Anim Behav Sci 82, 45-64.

Kobelt, A.J., Hemsworth, P.H., Barnett, J.L., Coleman, G.J., 2003. A survey of dog ownership in suburban Australia - conditions and behaviour problems. Appl Anim Behav Sci 82, 137-148.

Koolhaas, J.M., de Boer, S.F., Coppens, C.M., Buwalda, B., 2010. Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. Front Neuroendocrin 31, 307-321.

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 behavior and stress-physiology. Neuroscience and Biobehavioral Reviews 23, 925-935.

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 & Biobehavioral Reviews 29, 3-38.

Kubinyi, E., Turcsan, B., Miklosi, A., 2009. Dog and owner demographic characteristics and dog personality trait associations. Behav Process 81, 392-401.

Levine, S., Haltmeyer, G.C., Karas, G.G., Denenberg, V.H., 1967. Physiological and Behavioral Effects of Infantile Stimulation. Physiology and Behavior. 2, 55-59.

Ley, J., Coleman, G.J., Holmes, R., Hemsworth, P.H., 2007. Assessing fear of novel and startling stimuli in domestic dogs. Appl Anim Behav Sci 104, 71-84.

Ley, J.M., Bennett, P.C., Coleman, G.J., 2009. A refinement and validation of the Monash Canine Personality Questionnaire (MCPQ). Appl Anim Behav Sci 116, 220-227.

Lindblad-Toh, K., al, e., 2005. Genome sequence comparative analysis and haplotype structure of the domestic dog. Nature 438, 803-819.

Lindholm, Å., Linde Forsberg, C., Blixt, I., 2015. Hunduppfödning i teori och praktik. Svenska Kennelklubben, Spånga.

Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., Sharma, S., Pearson, D., Plotsky, P.M., Meaney, M.J., 1997. Maternal care, Hippocampal Glucocorticoid Receptors and Hypothalamic-Pituitary-Adrenal responses to Stress. Science 277, 1659.

Macrí, S., Mason, G.J., Würbel, H., 2004. Dissociation in the effect of neonatal maternal separations on maternal care and the offspring´s HPA and fear responses in rats. Eur. J. Neurosci. 20, 1017-1024.

Macrí, S., Würbel, H., 2007. Effects of variation in postnatal maternal environment on maternal behaviour and fear and stress responses in rats. Animal Behavior 73, 171-181.

Maejima, M., Inoue-Murayama, M., Tonosaki, K., Matsuura, N., Kato, S., Saito, Y., Weiss, A., Murayama, Y., Ito, S.i., 2007. Traits and genotype may predict successful training of drug detection dogs. Appl Anim Behav Sci 107, 287-298.

Maestripieri, D., Lindell, S.G., Ayala, A., Gold, P.W., Higley, J.D., 2005. Neurobiological characteristics of rhesus macaque abusive mothers and their relation to social and maternal behavior. Neuroscience & Biobehavioral Reviews 29, 51-57.

Malm, K., 1995. Behaviour of parents and offspring in two canids, Institutionen för husdjurshygien, Sveriges Lantbruksuniversitet.

Malm, K., Jensen, P., 1997. Weaning and parent-offspring conflict in the domestic dog. Ethology 103, 653-664.

McCrae, R.R., Costa, P.T., 1994. The Stability of Personality - Observations and Evaluations. Current Directions in Psychological Science 3, 173-175.

McCrae, R.R., Costa, P.T., Jr., Ostendorf, F., Angleitner, A., Hrebickova, M., Avia, M.D., Sanz, J., Sanchez-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.

McEwen, B.S., Gianaros, P.J., 2011. Stress- and allostasis-induced brain plasticity. Annual Review of Medicine 62, 431-445.

Meaney, M.J., 2001. Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. Annu. Rev. Neurosci. 24:1, 161-192.

Meaney, M.J., Aitken, D.H., Shari R. Bodnoff, Iny, L.J., Tatarewicz, J.E., Sapolsky, R.M., 1985. Early Postnatal Handling Alters Glucocorticoid Receptor Concentrations in Selected Brain Regions. Behavioral Neuroscience 99, 765-770.

Mendl, M., 1999. Performing under pressure: stress and cognitive function. Appl Anim Behav Sci 65, 221-244.

Mendl, M., Paul, E.S., 1991. Litter composition affects parental care, offspring growth and the development of aggressive behaviour in the wild house mice. Behaviour 116, 90-108.

Miklósi, A., 2008. Dog Behaviour, Evolution, and Cognition. Oxford University Press, Oxford, UK.

Moberg, G.P., Mench, J.A. (Eds.), 2000. Biological respons to stress: Implications for animal welfare. CABI, Oxon.

Morrow, M., Ottobre, J., Ottobre, A., Neville, P., St-Pierre, N., Dreschel, N., Pate, J.L., 2015. Breed-dependent differences in the onset of fear-related avoidance behavior in puppies. J Vet Behav 10, 286-294.

Netto, W.J., Planta, D.J.U., 1997. Behavioural testing for aggression in the domestic dog. Appl Anim Behav Sci 52, 243-263.

Olson, P.N., Hall, M.F., Peterson, J.K., Johnson, G.S., 2004. Using genetic technologies for promoting canine health and temperament. Anim Reprod Sci 82-3, 225-230.

Overli, O., Sorensen, C., Pulman, K.G., Pottinger, T.G., Korzan, W., Summers, C.H., Nilsson, G.E., 2007. Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. Neuroscience and biobehavioral reviews 31, 396-412.

Pang, J.F., Kluetsch, C., Zou, X.J., Zhang, A.B., Luo, L.Y., Angleby, H., Ardalan, A., Ekstrom, C., Skollermo, A., Lundeberg, J., Matsumura, S., Leitner, T., Zhang, Y.P., Savolainen, P., 2009. mtDNA Data Indicate a Single Origin for Dogs South of Yangtze River, Less Than 16,300 Years Ago, from Numerous Wolves. Mol Biol Evol 26, 2849-2864.

Passer, M.W., Smith, R.E., 2001. Psychology:Frontiers and Applications. 1st ed. McGraw-Hill, New York.

Pervin, L.A., John, O.P., 2001. Personality: theory and research. Eighth ed. Wiley New York.

Plotsky, P.M., Meaney, M.J., 1993. Early, postnatal experience alters hypothalamic corticotropin-releasing factor (CRF) mRNA, median eminence CRF content and stress-induced release in adult rats. Molecular Brain Research 18, 195-200.

Price, E.O., 1999. Behavioral development in animals undergoing domestication. Appl Anim Behav Sci 65, 245-271.

Riemer, S., Muller, C., Viranyi, Z., Huber, L., Range, F., 2014. The Predictive Value of Early Behavioural Assessments in Pet Dogs - A Longitudinal Study from Neonates to Adults. Plos One 9.

Rosenzweig, M.R., 1984. Experience, memory, and the brain. Am Psychol 39, 365-376.

Sapolsky, R.M., 2002. Endocrinology of Stress Response. Chapter 11 in J. B. Becker, M. Breedlove, D. Crews, M. M. McCarty, Behavioural Endocrinology. 2nd ed. MIT Press, London, UK.

Schapiro, S.J., Bloomsmith, M.A., Suarez, S.A., Porter, L.M., 1995. Maternal behavior of primiparous rhesus monkeys: effects of limited social restriction and inanimate environmental enrichment. Appl Anim Behav Sci 45, 139-149.

Serpell, J.A., Hsu, Y., 2001. Development and validation of a novel method evaluating behaviour and temperament in guide dogs. Appl Anim Behav Sci 72, 347-364.

Sinn, D.L., Gosling, S.D., Hilliard, S., 2010. Personality and performance in military working dogs: Reliability and predictive validity of behavioral tests. Appl Anim Behav Sci 127, 51-65.

Skoglund, P., Ersmark, E., Palkopoulou, E., Dalen, L., 2015. Ancient wolf genome reveals an early divergence of domestic dog ancestors and admixture into high-latitude breeds. Curr Biol 25, 1515-1519.

Slabbert, J.M., Odendaal, J.S.J., 1999. Early prediction of adult police dog efficiency, a longitudinal study. Appl Anim Behav Sci 64, 269-288.

Slabbert, J.M., Rasa, A.E., 1997. Observational learning of an acquired maternal behaviour pattern by working dog pups: an alternative training method? Appl Anim Behav Sci 53, 309-316.

Steimer, T., Driscoll, P., 2005. Inter-individual vs line/strain differences in psychogenetically selected Roman High-(RHA) and Low-(RLA) Avoidance rats: neuroendocrine and behavioural aspects. Neuroscience and biobehavioral reviews 29, 99-112.

Stelmack, R.M., Stalikas, A., 1991. Galen and the humour theory of temperament. Personality and Individual Differences 12, 211-328.

Stratakis, C.A., Chrousos, G.P., 1995. Neuroendocrinology and pathophysiology of the stress system. Ann N Y Acad Sci 771, 1-18.

Svartberg, K., 2002. Shyness–boldness predicts performance in working dogs. Appl Anim Behav Sci 79.

Svartberg, K., 2007. Individual Differences in Behaviour - Dog Personality, in: Jensen, P. (Ed.), The Behavioural Biology of Dogs, CABI, Oxfordshire, pp. 182-206.

Svartberg, K., Forkman, B., 2002. Personality traits in the domestic dog (*Canis familaris*). Appl Anim Behav Sci 79, 133-155.

Taylor, K.D., Mills, D.S., 2006. The development and assessment test for adult companion dogs. Journal of Veterinary Behavior 1, 94-108.

Tóth, L., Gácsi, M., Topál, J., Miklósi, A., 2008. Playing styles and possible causative factors in dogs' behaviour when playing with humans. Appl Anim Behav Sci 114, 473-484.

Travain, T., Colombo, E.S., Heinzl, E., Bellucci, D., Previde, E.P., Valsecchi, P., 2015. Hot dogs: Thermography in the assessment of stress in dogs (Canis familiaris)-A pilot study. J Vet Behav 10, 17-23.

Trut, L.N., 1999. Early canid domestication: The farm-fox experiment. Am Sci 87, 160-169.

Valleé, M., Mayo, W., Dellu, F.o., Moal, M.L., Simon, H., Maccari, S., 1997. Prenatal Stress Induces High Anxiety and Postnatal Handling Induces Low Anxiety in Adult Offspring: Correlation with Stress- Induced Corticosterone Secretion. The Journal of Neuroscience 17, 2626-2636.

van der Waaij, E.H., Wilsson, E., Strandberg, E., 2008. Genetic analysis of results of Swedish behaviour test on German Shepherd Dogs and Labrador Retrievers. Journal of Animal Science 86, 2853-2861.

Vander, A., Sherman, J., Luciano, D., 2001. Human Physiology. The Mechanisms of Body Function. Eight ed. McGraw-Hill, New York.

Vazire, S., Gosling, S.D., Dickey, A.S., Schaprio, S.J., 2007. Measuring personality in nonhuman animals. , in: Robins, R.W., Fraley, R.C., Krueger, R. (Eds.), Handbook of Research Methods in Personality Psychology, Guilford, New York, pp. 190-206.

vonHoldt, B.M., Pollinger, J.P., Lohmueller, K.E., Han, E.J., Parker, H.G., Quignon, P., Degenhardt, J.D., Boyko, A.R., Earl, D.A., Auton, A., Reynolds, A., Bryc, K., Brisbin, A., Knowles, J.C., Mosher, D.S., Spady, T.C., Elkahloun, A., Geffen, E., Pilot, M., Jedrzejewski, W., Greco, C., Randi, E., Bannasch, D., Wilton, A., Shearman, J., Musiani, M., Cargill, M., Jones, P.G., Qian, Z.W., Huang, W., Ding, Z.L., Zhang, Y.P., Bustamante, C.D., Ostrander, E.A., Novembre, J., Wayne, R.K., 2010. Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. Nature 464, 898-U109.

Wang, G.D., Xie, H.B., Peng, M.S., Irwin, D., Zhang, Y.P., 2014. Domestication Genomics: Evidence from Animals. Annu Rev Anim Biosci 2, 65-84.

Weiss, E., Greenberg, G., 1997. Service dog selection tests: Effectiveness for dogs from animal shelters. Appl Anim Behav Sci 53, 297-308.

Wilsson, E., 1984. The social interaction between mother and offspring during weaning in German shepherd dogs: individual differences between mothers and their effects on offspring. Appl Anim Behav Sci 13, 101-112.

Wilsson, E., 1997. Maternal Effects on Behaviour of Juvenile Adult Dogs, Department of Zoology, Stockholm University, Stockholm.

Wilsson, E., 2013. Personal Communication.

Wilsson, E., Sinn, D., 2012. Are there differences between behavioral measurement methods? A comparsion of the predictive validity of two rating methods in a working dog program. Appl Anim Behav Sci 141, 158-172.

Wilsson, E., Sundgren, P.-E., 1997. The use of a behaviour test for selection of dogs for service and breeding I: Methods of testing and evaluating test results in the adult dog, demands on different kinds of service dogs, sex and breed differances. Appl Anim Behav Sci 53, 279-295.

Wilsson, E., Sundgren, P.-E., 1998. Effects of weight and litter size and parity of mother on the behaviour of the puppy and the adult dog. Appl Anim Behav Sci 56, 245-254.

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