Ann-Sofie Sundman
PhD student essay

On how dogs behave themselves:

The why and how of testing dog behaviour

Introduction

Although the when and where of the origin of the domestic dog is continuously challenged by new scientific evidence, the fact that the dog is our first domesticated animal and has lived by our side at least since the rise of agriculture about 14.000 years ago is by now rather undisputable (Savolainen et al., 2002, Pang et al., 2009, Thalmann et al., 2013, Freedman et al., 2014, Skoglund et al., 2015). The fact that we have co-evolved for such a long period of time have also resulted in a unique bond between human and dogs, and dogs seem to have an innate ability to understand us. It has, for example, been shown that the level of oxytocin rises in both humans and dogs as an effect of eye contact between the two, laying a foundation for the strong bond between them (Nagasawa et al., 2015), and dogs are better than both chimpanzees and wolves to understand human pointing gestures (Miklósi et al., 2003, Kirchhofer et al., 2012). Today, dogs are a natural part of society and wherever in the world there are humans there are also dogs. They are highly appreciated for their suitability as pets and their hunting, herding and guarding abilities, not to mention for their important role as police, military, search and rescue and assistance dogs. This also puts pressure on the behaviour of the dogs, and different behaviours are desirable depending on role and owner preferences. Additionally, dogs are an important model animal, for example for genetic studies.

Since its domestication, various types of dogs have developed through adaptation to an environment shared with humans and selective breeding, resulting in a unique within-species variation in morphology and behaviour. The stringent selective breeding we are familiar with today began with the founding of breeding associations and breed standards in the 19th century, giving rise to purebreds with closed gene pools (Parker et al., 2004, Boyko, 2011). From a research point of view, the great variation between breeds and remarkable similarities within a breed, makes them a

fascinating model animal for studies on morphology, physiology, and, of course, behaviour. Since its genetic makeup follows the pattern of the phenotypes with low within-breed variation and high between-breed variation, they are an excellent model for genetic studies. Accordingly, the dog genome was one of the first to be sequenced (Lindblad-Toh et al., 2005).

Being the popular and commonly found animal that they are together with their importance as a model animal, dogs have a high research value. Simply, learning more about dogs is both important and out of great interest to many. Especially, there is an interest to learn more about the behaviour of dogs since this is of such importance to both pet owners, dog trainers and researchers, and of course to the dogs themselves from a welfare perspective.

Interestingly, the dog did not start to interest ethologists until rather late, focus instead being the behaviour ecology of wild animals. During the first decades of the 20th century those that used dogs in research were psychologists who were interested in the process of learning. One of the first and to date one of the most extensive studies on dog behaviour were Scott and Fuller's 20 years long project where they studied behavioural patterns, breed differences in behaviour, developmental stages and the genetics of behaviour (Scott and Fuller, 1965). Studies on dog behaviour became more and more popular. Especially during the last 20 years studies on for example personality, social cognition and behavioural genetics with the dog in focus have increased extensively (e.g. Jones and Gosling, 2005, Hall and Wynne, 2012, Kaminski and Nitzschner, 2013).

In order to test the behaviour of animals in a way that is valid, reliable and comparable there is a need for standardized tests that can be used in different places and by different people. The use of standardized behaviour tests began in medical and pharmacological research where there was a need to test laboratory model animals. One such test is for example the open-field test which was developed in the 1940s and measures an animal's exploratory behaviour and activity (Gould et al., 2009). When it comes to dogs, different behavioural tests have been developed mainly due to a need for unbiased and uniform assessment of dogs' aptitude for different work tasks and for a tool to use in dog breeding to help breeders make sound decisions. For example, behavioural tests have been used to assess shelter dogs' suitability as pets (e.g. Mornement et al., 2014), to assess dogs' aptitude for becoming police and military dogs (e.g. Wilsson and Sinn, 2012), to evaluate the breeding stock of working dogs (e.g. Svartberg and Forkman, 2002) and herding dogs (e.g. Arvelius et al., 2013), and to assess potential guide dogs (e.g. Batt et al., 2008). Behavioural tests are of course also used in gaining more knowledge about the behaviour of dogs, for example the personality of dogs (e.g. Svartberg and Forkman, 2002) or specific behaviours or behavioural traits, like aggression (e.g. van der Borg et al., 2010) and fear (e.g. Ley et al., 2007), and dog's social cognition (e.g. Miklósi et al., 2003).

Concepts

Behavioural tests are often referred to as 'behavioural assessments' or 'temperament tests'. Although some behavioural tests focus on only one specific behaviour, most score several behavioural variables in one or several situations. Behavioural variables that are correlated are assumed to reflect and underlying common trait (Diederich and Giffroy, 2006, Taylor and Mills, 2006). Behaviour traits are commonly extracted by the use of a factor analysis on a larger set of behavioural data. Among other things, this reduces the data set into something more approachable and more readily used in further statistical analysis.

By assessing a dog's behavioural reactions in different situations and/or to different stimuli, many attempt to describe a dog's personality. Personality in any animal is defined as individual behavioural differences that are consistent over time or across situations. This concept is, however, not only known as 'personality', but is used more or less interchangeably with 'temperament' and 'character' within dog research (Jones and Gosling, 2005, Diederich and Giffroy, 2006, Taylor and Mills, 2006). One example of a factor analysis being used to extract behaviour traits was for example done in Svartberg and Forkman (2002) when they studied personality in dogs. They found five different personality traits from 33 behavioural variables scored in a behavioural test. Jones and Gosling (2005) took another approach. Based on behavioural traits described in previous research, an expert panel sorted them into seven broad personality traits, or, to use the concept they themselves use, temperament dimensions. Further, 'super-trait' is a term regarding a higher-order personality trait, representing a broad factor consisting of correlating traits. Svartberg and Forkman (2002) identified one such super-trait, the shy-bold axis, by a second-order factor analysis. Another super-trait would be the coping styles, where proactive and reactive copers differ in a variety of behaviours (Horvath et al., 2007, Blackwell et al., 2010, Starling et al., 2013).

Types of tests and methods of measurement

In their review, Jones and Gosling (2005) recognize four main ways in which dogs' behaviours are tested. Two where the dogs' behaviour is actually observed, namely observational test and test batteries, and two that rely upon information from an informant, namely ratings of individual dogs and expert ratings of breed prototypes.

Observational test is when the dog is observed in a natural environment. For example, Carrier et al. (2013) studied dogs' interactions in a dog park and Mongillo et al. (2014) studied gazing behaviour

between dogs and their owners during their regular dog walk. A test battery will instead test dogs' behaviour across different standardized test situations. One such example is the Socially Acceptable Behaviour (SAB) test based on Netto and Planta (1997). It is used by the Dutch Kennel Club to select against unwanted aggression and fear in breeding animals and has also been the focus of several studies (e.g.Planta and De Meester, 2007, Haverbeke et al., 2009, van der Borg et al., 2010, De Meester et al., 2011). The test consists of 16 subtests such as, among others, approach by unfamiliar persons, sudden visual and sound stimuli and a doll pulled towards the dog and then used to touch and pet the dog.

In contrast to these two methods, in ratings of individual dogs information on a dog's behaviour is gathered from an informant, most commonly its owner or caretaker. The most commonly used questionnaire is the C-BARQ (Canine Behavioral Assessment and Research Questionnaire), developed by Hsu & Serpell (2003). It consists of about 100 questions where the owner describes on a five point rating scale how the dog reacts and behaves in different situations in its everyday life. Based on a factor analysis, the majority of the questions are divided into 14 distinct factors, for example different forms of aggression and fear (Duffy and Serpell, 2012). It has, for example, been used to evaluate trainability (Serpell and Hsu, 2005) and aggression (Duffy et al., 2008), and can predict success in both young guide and service dogs (Duffy and Serpell, 2012) and military working dogs (Foyer et al., 2014). While rating of individual dogs is commonly used, expert ratings of breed prototypes have been scarcely used in research recent years. The informants in this method are deemed experts on dogs, such as veterinarians, dog trainers and judges in dog sports (Jones and Gosling, 2005).

Questionnaires are able to capture dogs' behaviour over a longer time span than observational tests and are less influenced by daily fluctuations, seasonal effects and the dogs' conditions before the test. Test batteries only capture the behaviour during the time in which the test takes place. However, questionnaires might be influenced by the subjectivity of the informant. There are studies that have used both questionnaires and test batteries and tested the accordance between the two. For example, Svartberg (2005) found correlation between traits such as fearfulness, playfulness and sociability and corresponding traits measured by the C-BARQ. There was, however, no correlation found between aggression as measured by the different tests. Similarly, Mirkó et al. (2013) found some but not all expected correlations between the test battery FIDO personality test and the questionnaire Dog Personality Questionnaire, for example for aggressive behaviour. Aggression being a strongly loaded term, this could be because owners are reluctant to score their dogs high in that category, or because the tests fail to measure the aspect that is shown in dogs' everyday behaviour.

For test batteries and observational data, there are different methods of measurement. The ones mainly used are behavioural coding, subjective or observer rating and behaviour rating. Behavioural coding refers to the, within ethology, classic ethogram-based method of observation, where the behaviours are objectively described and then scored and quantified into, for example, frequencies and/or numbers (Svartberg, 2007). Haverbeke et al. (2009) used this method of measurement when they studied aggression in military working dogs. During a test battery, behaviours coupled to aggression described in an ethogram were observed and the total number of the aggressive behaviours in the different subtests is presented. In the two rating methods, the behaviour of the dog is instead scored on a pre-described rating scale. In subjective rating, this scale commonly consists of how high expression the dog shows of certain traits, for example aggression or fear, over multiple observations. A subjective rating is thus based on the observer's overall interpretation of the dog's reactions and therefore rather subjective, hence the name (Svartberg, 2007). Behaviour rating, on the other hand, is more objective and is used in specific situations to score certain behaviours. The scale consists of descriptions of specific behavioural reactions belonging to the same behavioural category and is usually ordered in intensity.

Both subjective and behaviour rating are used in the standardized behaviour test used by the Swedish armed forces to find suitable dogs. During the subtests, the reactions are scored according to behaviour rating. For example, in the retrieving sub-test, the rating regards the dog's interest in the object (behavioural category) and the dog is rated according to a five-point-scale with the following descriptions of its behaviour: 1) Does not take ball. 2) Grabs ball but let's go immediately. 3) Grabs ball, carries less than 5 s. 4) Grabs ball, carries. 5) Grabs ball intensely, carries. Based on all the sub-tests, the observer will then make a subjective rating of certain behavioural traits, among others courage and sharpness. This is done on a scale from 1 to 5 where one is low expression and five is high expression (Wilsson and Sinn, 2012). When comparing the two methods, Wilsson and Sinn (2012) concluded that both behaviour and subjective rating predicted what dogs that would not complete training, although it seems that they identified different aspects of some traits. According to Svartberg (2007), although behavioural coding and behaviour rating will be more objective methods, subjective rating might capture an overall behavioural dispositions that the others might miss.

Reliability and validity

Reliability and validity are two concepts regarding the efficiency of an experimental design, where reliability concerns the degree of measurement errors and validity concerns how well the test setup measures a given behaviour and how relevant the result is.

A high reliability means a low degree of measurement errors and thus high repeatability of and consistency in the experimental design. There are mainly three types of reliability estimates, namely intra-observer, inter-observer and test-retest reliability (Jones and Gosling, 2005, Diederich and Giffroy, 2006, Taylor and Mills, 2006). Intra-observer reliability measures the consistency of one observer. In Kim et al. (2010) this was for example tested by letting the observer re-rate the videos. Inter-observer reliability is instead the consistency between several observers. Carrier et al. (2013) tested this by letting a second observer rate 20 % of the same videos that the main observer had rated. Although high agreement on most behavioural categories, one was found where low agreement existed. To increase the reliability of the study, both observers rated the videos and where the rating differed they discussed the incident and reached a consensus decision. Lastly, test-retest reliability tests the consistency in the test itself; will the dog react in the same way tested on another occasion and/or a different place? By repeating a questionnaire six month after the first filling in, Ley et al. (2009) could assess the test-retest reliability of the same.

Two types of validity ought to be addressed. Internal validity regards such things as how well a test measures both specific behaviour and a broader construct and if it measures all aspects of it, while external validity concerns the generality of the results, for example how well what the test measures predicts behaviour in other situations (Taylor and Mills, 2006, Miklósi, 2015). Valsecchi et al. (2011) tested how valid a temperament test for shelter dogs was by comparing scores from the temperament test to the case history on the dogs made by police and veterinarians, e.g. on their aggression level. This relates to how well the test can predict behaviour in other situations. They also performed a factor analysis, in which variables described in different subtests designed to describe aspects of the same behaviour also should correlate.

The lack of reliability and validity measures for behaviour tests for dogs has been a concern in previous reviews (Jones and Gosling, 2005, Diederich and Giffroy, 2006, Rayment et al., 2015). According to Jones and Gosling (2005), though, those studies that do report reliability and validity show promising results of tests being both reliable and valid, although authors note that more should report this. Diederich and Giffroy (2006) argue that instead of inventing more and more general behaviour tests that needs to be tested for reliability and validity, there should be standardized tests

already tested that can be chosen. With a focus on tests used in shelters, Rayment et al. (2015) points out the importance of high quality behaviour tests for dogs where they decide whether the dog may be rehomed or not. Even so, authors write that few protocols have been shown to accurately test dog behaviour.

Testing fear, aggression and sociability in dogs

Behaviour tests for dogs exist testing several behaviours and behavioural traits. Three of the most common are fearful behaviours, aggressive behaviours and social behaviours.

Boissy (1995) defines fear, and anxiety, as "emotional states that are induced by the perception of any actual danger (fear state) or potential danger (anxiety state) that threatens the well-being of the individual", and continues with that fearfulness can be considered "a personality or temperament trait defining the general susceptibility of an individual to react to a variety of potentially threatening situations". In behaviour tests for dogs, a dogs reaction to potential threatening stimuli is tested, often a novel object or a startle test. For example, Sherman et al. (2015) tests dogs reactions in a battery of potential threatening situations in the Emotional Reactivity Test. Among other things, dogs are handled by a stranger and walked up and down an open riser stair, a big bag suddenly dropped in front of the dog, a remote-controlled vehicle moves towards the dog and a gunshot is fired. Both the dogs' initial reactions are scored as well as their willingness to approach the stimuli. This is a common way of testing fearfulness (Jones and Gosling, 2005). Fearful behaviours may for example be avoidance, crouching, barking, hiding and seeking support from handler (Foyer et al., 2016). A low fearfulness is sometimes labelled curiosity (Svartberg and Forkman, 2002), and Wilsson and Sundgren (1997) uses the concept courage as the ability to overcome fear.

Aggression is another commonly studied trait in dogs. Aggressive behaviours include for example biting, growling and snapping, directed at either people or other dogs (Jones and Gosling, 2005). Aggressive behaviours are often divided depending on either the recipient, for example owner, stranger or dog, or the motivation for the behaviour, for example fear, dominance or prey. Many times similar stimuli that are used to test fear reactions are also used to test aggressive reactions. For example, the dog mentality assessment used in Svartberg and Forkman (2002) do not only measure fear behaviours during the visual startle test but also aggressive behaviours such as threats, attacks and bites. In a study by Netto and Planta (1997), 98 % of included dogs showed signs of aggression during a behaviour test with several subtests that got increasingly more threatening and trying for the dogs (for example a stranger approaching the dog yelling and making kicking movement towards the dog, being cornered by three barking dogs and owner being attacked by a test person).

Aggressive behaviour is a natural part of a dogs behaviour repertoire, but at the same time considered a problem if being too pronounced. Due to the difficulty of standardizing a test another dog as a stimulus to test for dog-dog aggression, a commonly reported problem among pet dogs, dummy dogs may be used. However, Shabelansky et al. (2015) failed to show an agreement between aggressive behaviour toward a real and a fake dog, raising concern if this is a valid test design.

A quite unique trait for dogs is their interspecies sociability. Their social behaviour towards people is also something that is regularly tested as it is an important behaviour for a pet dog. Other concepts used for sociability are affability and extraversion (Jones and Gosling, 2005). One way of measuring the social behaviour is by studying the dogs' reaction towards an approaching stranger. For example, in Roth and Jensen (2015), a novel person approached the dogs and the dogs' behaviours towards the stranger was recorded, as well as their behaviour towards their owner. Another way of studying human-directed social behaviour is by presenting the dogs with a problem-solving situations, either unsolvable or difficult to solve. Studies have shown that dogs, but not wolves, will seek contact with humans in this context (Miklósi et al., 2003, Udell, 2015). Persson et al. (2015) used this test setup when investigating the heritability of human-directed social behaviour.

Physiological measurements

Behavioural reactions are of course coupled to physiological reactions and by measuring physiological aspects as well as behavioural we are able to understand the behaviour even further as well as getting a better understanding of the emotional state. Those physiological aspects that have been the main focus for researchers are physiological measurements of stress. One measurable physiological reaction is cortisol which is the product of the hypothalamic–pituitary–adrenal (HPA) axis that is activated in response to a stressor. Hydbring-Sandberg et al. (2004) measured plasma cortisol levels in response to gunshot and dogs displaying a high fear behavioural reaction also showed increase cortisol levels. While plasma and saliva cortisol measurements measures the acute stress reactivity, cortisol can also be measured in a hair sample to get a more long-term measure of cortisol secretion. Using this method, Siniscalchi et al. (2013) found that hair cortisol levels correlated to fear-related behaviours in response to sounds such as thunderstorms and barks from strangers.

Another regularly used physiological measurement is cardiac activity in forms of heart rate and heart rate variability. The sympathetic nervous system is activated for example by a stressor and will increase the heart rate. In addition to the increased cortisol levels, noise phobic dogs in the study by Hydbring-Sandberg et al. (2004) mentioned previously also showed an increase in heart rate. Heart rate variability, beat-to-beat alterations of the heart rate, represents the balance between

parasympathetic and sympathetic nervous system where a low variability represents an increased sympathetic cardiac control. For example, Wormald et al. (2017) found that dogs with anxiety-related behaviour problems had a reduced heart rate variability in comparison to control group.

Breed differences

While there is a variation in behaviour between individual dogs, there are also differences between breeds. During domestication, the predatory motor patterns have been modified through selection and often differ distinctively between groups of dog breeds. In retrievers, the behaviours of orienting and grabbing prey are hypertrophied while crushing or killing is suppressed. In border collies, on the other hand, eye, stalk and chase have been hypertrophied (Coppinger and Coppinger, 1996, Mehrkam and Wynne, 2014). Behavioural differences has been found also in behavioural traits such as boldness, playfulness, sociability and aggression (Svartberg, 2006, Duffy et al., 2008, Starling et al., 2013). In a study by Eken Asp et al. (2015), the C-BARQ is used to study breed differences and found that breed have a significant effect on most of the behavioural categories. The biggest difference found was in human-directed play interest where Belgian Malinois had the highest scores and Bernese mountain dog, Rhodesian ridgeback and Chihuahuas hade the lowest.

In their review on breed behavioural differences, Mehrkam and Wynne (2014) conclude that there are breed differences, but also note that there are substantial within-breed differences in behaviour that should not be neglected. Indeed, golden and Labrador retrievers bred for different purposes (show and hunting) show significant behavioural differences between the types for several behavioural traits (Sundman et al., 2016). For example, hunting bred dogs of both breeds showed higher playfulness.

Behaviour and genetics

The fact that breeds are both genetically distinct and show high diversity in phenotypic traits puts the dog in the position of being a good genetic model. Many breeds were created through a small number of founders, a small population size and high levels of inbreeding has caused big genetic variation between breeds while the variation is small within breeds. As a result, purebred dogs can for example be assigned to the correct breed based on genotype data (Parker et al., 2004, vonHoldt et al., 2010). Taking advantage of the breed differences in both phenotypic traits and genetics, genes have been found for morphological trait such as size (Hoopes et al., 2012), colour (Kaelin and Barsh, 2013) and coat length and texture (Cadieu et al., 2009), and genes underlying both Mendelian and complex diseases have been identified in dogs, many of which have human analogies (Boyko, 2011).

Within behavioural genetics, however, the genes have proven to be more elusive. Behaviours are both complex and difficult to phenotype. Behaviours are thought to be mainly polygenic and with environment having an effect, explaining the difficulties in pinpointing specific genes as responsible for specific behaviours (Ilska et al., 2017).

Studies show that the variation in behaviour in many cases has a significant genetic factor shown by narrow-sense heritability estimates (Saetre et al., 2006, Liinamo et al., 2007, Arvelius et al., 2013). Narrow-sense heritability is an estimate of the proportion of the variation in a trait that is caused by additive genetic factors. For example, Arvelius et al. (2014) found that in a population of rough collies the heritability for sociability as measured in the dog mentality assessment was 0.22.

In candidate gene approaches, associations has been made for example between genes and the behaviours aggression, fearlessness and activity levels (Takeuchi et al., 2009a, Takeuchi et al., 2009b, Våge et al., 2010, Lee et al., 2008, Lit et al., 2013). Additionally, Kis et al. (2014) studied the oxytocin receptor gene and found that SNPs in the regulatory region of the gene were associated to stranger-directed behaviours.

Few genome-wide association analyses have reached genome-wide statistical significance. Two that have are studies on obsessive-compulsive behaviour with the approach of using breeds prone to obsessive-compulsive behaviour, for example compulsive tail chasing, and control breeds that are not (Tang et al., 2014, Dodman et al., 2010). That is, they have used clinical disorders that can be clearly defined. However, there are studies that have found associations to common traits as well. For example, a genome-wide association study on a population of beagle dogs found three significant SNPs for human-directed social behaviour during a problem solving task (Persson et al., 2016). Additionally, Ilska et al. (2017) found several associations between SNPs and behavioural traits measured by the C-BARQ, many in or close to genes known to regulate neurological or behavioural functions.

To conclude…

Dog behaviour has been in focus for many studies up to date and the number will most likely continue to increase due to the dogs' position as an appreciated pet and model animal. Critique has been raised that tests are not tested for reliability and validity and always when coming across a behavioural test it is important to be careful not to interpret more than what the test design allows. Although there are plenty behavioural tests out there already, the search for genetic architecture

behind behaviours will continue will require even more specific and specialized behavioural tests to be able to pinpoint the exact genetics behind a behavioural reaction.

Reference list

ARVELIUS, P., ASP, H. E., FIKSE, W. F., STRANDBERG, E. & NILSSON, K. 2014. Genetic analysis of a temperament test as a tool to select against everyday life fearfulness in Rough Collie. *J Anim Sci,* 92**,** 4843-55.

ARVELIUS, P., MALM, S., SVARTBERG, K. & STRANDBERG, E. 2013. Measuring herding behavior in Border collie-effect of protocol structure on usefulness for selection. *Journal of Veterinary Behavior-Clinical Applications and Research,* 8**,** 9-18.

BATT, L. S., BATT, M. S., BAGULEY, J. A. & MCGREEVY, P. D. 2008. Factors associated with success in guide dog training. *Journal of Veterinary Behavior-Clinical Applications and Research,* 3**,** 143-151.

BLACKWELL, E. J., BODNARIU, A., TYSON, J., BRADSHAW, J. W. S. & CASEY, R. A. 2010. Rapid shaping of behaviour associated with high urinary cortisol in domestic dogs. *Applied Animal Behaviour Science,* 124**,** 113-120.

BOISSY, A. 1995. Fear and fearfulness in animals. *Q Rev Biol,* 70**,** 165-91.

BOYKO, A. R. 2011. The domestic dog: man's best friend in the genomic era. *Genome Biology,* 12.

CADIEU, E., NEFF, M. W., QUIGNON, P., WALSH, K., CHASE, K., PARKER, H. G., VONHOLDT, B. M., RHUE, A., BOYKO, A., BYERS, A., WONG, A., MOSHER, D. S., ELKAHLOUN, A. G., SPADY, T. C., ANDRE, C., LARK, K. G., CARGILL, M., BUSTAMANTE, C. D., WAYNE, R. K. & OSTRANDER, E. A. 2009. Coat Variation in the Domestic Dog Is Governed by Variants in Three Genes. *Science,* 326**,** 150-153.

CARRIER, L. O., CYR, A., ANDERSON, R. E. & WALSH, C. J. 2013. Exploring the dog park: Relationships between social behaviours, personality and cortisol in companion dogs. *Applied Animal Behaviour Science,* 146**,** 96-106.

COPPINGER, R. & COPPINGER, L. 1996. Biologic Bases of Behavior of Domestic Dog Breeds. *In:* VOIRTH, V. L. & BORCHELT, P. L. (eds.) *Readings in Companion Animal Behavior.* Trenton, New Jersey: Veterinary Learning Systems.

DE MEESTER, R. H., PLUIJMAKERS, J., VERMEIRE, S. & LAEVENS, H. 2011. The use of the socially acceptable behavior test in the study of temperament of dogs. *Journal of Veterinary Behavior-Clinical Applications and Research,* 6**,** 211-224.

DIEDERICH, C. & GIFFROY, J. M. 2006. Behavioural testing in dogs: A review of methodology in search for standardisation. *Applied Animal Behaviour Science,* 97**,** 51-72.

DODMAN, N. H., KARLSSON, E. K., MOON-FANELLI, A., GALDZICKA, M., PERLOSKI, M., SHUSTER, L., LINDBLAD-TOH, K. & GINNS, E. I. 2010. A canine chromosome 7 locus confers compulsive disorder susceptibility. *Molecular Psychiatry,* 15**,** 8-10.

DUFFY, D. L., HSU, Y. Y. & SERPELL, J. A. 2008. Breed differences in canine aggression. *Applied Animal Behaviour Science,* 114**,** 441-460.

DUFFY, D. L. & SERPELL, J. A. 2012. Predictive validity of a method for evaluating temperament in young guide and service dogs. *Applied Animal Behaviour Science,* 138**,** 99-109.

EKEN ASP, H., FIKSE, W. F., NILSSON, K. & STRANDBERG, E. 2015. Breed differences in everyday behaviour of dogs. *Applied Animal Behaviour Science,* 169**,** 69-77.

FOYER, P., BJÄLLERHAG, N., WILSSON, E. & JENSEN, P. 2014. Behaviour and experiences of dogs during the first year of life predict the outcome in a later temperament test. *Applied Animal Behaviour Science,* 155**,** 93-100.

FOYER, P., SVEDBERG, A.-M., NILSSON, E., WILSSON, E., FARESJÖ, Å. & JENSEN, P. 2016. Behavior and cortisol responses of dogs evaluated in a standardized

temperament test for military working dogs. *Journal of Veterinary Behavior: Clinical Applications and Research,* 11**,** 7-12.
FREEDMAN, A. H., GRONAU, I., SCHWEIZER, R. M., ORTEGA-DEL VECCHYO, D., HAN, E., SILVA, P. M., GALAVERNI, M., FAN, Z., MARX, P., LORENTE-GALDOS, B., BEALE, H., RAMIREZ, O., HORMOZDIARI, F., ALKAN, C., VILÀ, C., SQUIRE, K., GEFFEN, E., KUSAK, J., BOYKO, A. R., PARKER, H. G., LEE, C., TADIGOTLA, V., SIEPEL, A., BUSTAMANTE, C. D., HARKINS, T. T., NELSON, S. F., OSTRANDER, E. A., MARQUES-BONET, T., WAYNE, R. K. & NOVEMBRE, J. 2014. Genome Sequencing Highlights the Dynamic Early History of Dogs. *PLoS Genet,* 10**,** e1004016.
GOULD, T. D., DAO, D. T. & KOVACSICS, C. E. 2009. The open field test. *Mood and anxiety related phenotypes in mice: Characterization using behavioral tests***,** 1-20.
HALL, N. J. & WYNNE, C. D. L. 2012. The canid genome: behavioral geneticists' best friend? *Genes, Brain, and Behavior,* 11**,** 889-902.
HAVERBEKE, A., DE SMET, A., DEPIEREUX, E., GIFFROY, J. M. & DIEDERICH, C. 2009. Assessing undesired aggression in military working dogs. *Applied Animal Behaviour Science,* 117**,** 55-62.
HOOPES, B. C., RIMBAULT, M., LIEBERS, D., OSTRANDER, E. A. & SUTTER, N. B. 2012. The insulin-like growth factor 1 receptor (IGF1R) contributes to reduced size in dogs. *Mammalian Genome,* 23**,** 780-790.
HORVATH, 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.
HYDBRING-SANDBERG, E., VON WALTER, L. W., HOGLUND, K., SVARTBERG, K., SWENSON, L. & FORKMAN, B. 2004. Physiological reactions to fear provocation in dogs. *Journal of Endocrinology,* 180**,** 439-448.
ILSKA, J., HASKELL, M. J., BLOTT, S. C., SÁNCHEZ-MOLANO, E., POLGAR, Z., LOFGREN, S. E., CLEMENTS, D. N. & WIENER, P. 2017. Genetic Characterisation of Dog Personality Traits. *Genetics*.
JONES, A. C. & GOSLING, S. D. 2005. Temperament and personality in dogs (Canis familiaris): A review and evaluation of past research. *Applied Animal Behaviour Science,* 95**,** 1-53.
KAELIN, C. B. & BARSH, G. S. 2013. Genetics of Pigmentation in Dogs and Cats. *Annual Review of Animal Biosciences, Vol 1,* 1**,** 125-156.
KAMINSKI, J. & NITZSCHNER, M. 2013. Do dogs get the point? A review of dog-human communication ability. *Learning and Motivation,* 44**,** 294-302.
KIM, Y. K., LEE, S. S., IL OH, S., KIM, J. S., SUH, E. H., HOUPT, K. A., LEE, H. C., LEE, H. J. & YEON, S. C. 2010. Behavioral Reactivity of Jindo Dogs Socialized at an Early Age Compared with Non-Socialized Dogs. *Journal of Veterinary Medical Science,* 72**,** 405-410.
KIRCHHOFER, K. C., ZIMMERMANN, F., KAMINSKI, J. & TOMASELLO, M. 2012. Dogs (Canis familiaris), but not chimpanzees (Pan troglodytes), understand imperative pointing. *PloS one,* 7**,** e30913.
KIS, A., BENCE, M., LAKATOS, G., PERGEL, E., TURCSAN, B., PLUIJMAKERS, J., VAS, J., ELEK, Z., BRUDER, I., FOLDI, L., SASVARI-SZEKELY, M., MIKLOSI, A., RONAI, Z. & KUBINYI, E. 2014. Oxytocin Receptor Gene Polymorphisms Are Associated with Human Directed Social Behavior in Dogs (Canis familiaris). *Plos One,* 9.
LEE, C., KIM, C., SHIN, S., SHIN, D., KANG, J. & PARK, C. 2008. The dopamine D4 receptor polymorphism affects the canine fearfulness. *Animal Cells and Systems,* 12**,** 77-83.

LEY, J., COLEMAN, G. J., HOLMES, R. & HEMSWORTH, P. H. 2007. Assessing fear of novel and startling stimuli in domestic dogs. *Applied Animal Behaviour Science,* 104**,** 71-84.

LEY, J. M., MCGREEVY, P. & BENNETT, P. C. 2009. Inter-rater and test-retest reliability of the Monash Canine Personality Questionnaire-Revised (MCPQ-R). *Applied Animal Behaviour Science,* 119**,** 85-90.

LIINAMO, A. E., VAN DEN BERG, L., LEEGWATER, P. A. J., SCHILDER, M. B. H., VAN ARENDONK, J. A. M. & VAN OOST, B. A. 2007. Genetic variation in aggression-related traits in Golden Retriever dogs. *Applied Animal Behaviour Science,* 104**,** 95-106.

LINDBLAD-TOH, K., WADE, C. M., MIKKELSEN, T. S., KARLSSON, E. K., JAFFE, D. B., KAMAL, M., CLAMP, M., CHANG, J. L., KULBOKAS, E. J., ZODY, M. C., MAUCELI, E., XIE, X. H., BREEN, M., WAYNE, R. K., OSTRANDER, E. A., PONTING, C. P., GALIBERT, F., SMITH, D. R., DEJONG, P. J., KIRKNESS, E., ALVAREZ, P., BIAGI, T., BROCKMAN, W., BUTLER, J., CHIN, C. W., COOK, A., CUFF, J., DALY, M. J., DECAPRIO, D., GNERRE, S., GRABHERR, M., KELLIS, M., KLEBER, M., BARDELEBEN, C., GOODSTADT, L., HEGER, A., HITTE, C., KIM, L., KOEPFLI, K. P., PARKER, H. G., POLLINGER, J. P., SEARLE, S. M. J., SUTTER, N. B., THOMAS, R., WEBBER, C., LANDER, E. S. & PLAT, B. I. G. S. 2005. Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature,* 438**,** 803-819.

LIT, L., BELANGER, J. M., BOEHM, D., LYBARGER, N. & OBERBAUER, A. M. 2013. Differences in Behavior and Activity Associated with a Poly(A) Expansion in the Dopamine Transporter in Belgian Malinois. *Plos One,* 8.

MEHRKAM, L. R. & WYNNE, C. D. L. 2014. Behavioral differences among breeds of domestic dogs (Canis lupus familiaris): Current status of the science. *Applied Animal Behaviour Science*.

MIKLÓSI, Á. 2015. *Dog behaviour, evolution, and cognition,* Oxford, Oxford University Press.

MIKLÓSI, Á., KUBINYI, E., TOPÁL, J., GÁCSI, M., VIRÁNYI, Z. & CSÁNYI, V. 2003. A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology,* 13**,** 763-766.

MIRKÓ, E., DÓKA, A. & MIKLÓSI, Á. 2013. Association between subjective rating and behaviour coding and the role of experience in making video assessments on the personality of the domestic dog (Canis familiaris). *Applied Animal Behaviour Science,* 149**,** 45-54.

MONGILLO, P., ADAMELLI, S., PITTERI, E. & MARINELLI, L. 2014. Reciprocal attention of dogs and owners in urban contexts. *Journal of Veterinary Behavior: Clinical Applications and Research,* 9**,** 158-163.

MORNEMENT, K. M., COLEMAN, G. J., TOUKHSATI, S. & BENNETT, P. C. 2014. Development of the behavioural assessment for re-homing K9's (B.A.R.K.) protocol. *Applied Animal Behaviour Science,* 151**,** 75-83.

NAGASAWA, M., MITSUI, S., EN, S., OHTANI, N., OHTA, M., SAKUMA, Y., ONAKA, T., MOGI, K. & KIKUSUI, T. 2015. Oxytocin-gaze positive loop and the coevolution of human-dog bonds. *Science,* 348**,** 333-336.

NETTO, W. J. & PLANTA, D. J. U. 1997. Behavioural testing for aggression in the domestic dog. *Applied Animal Behaviour Science,* 52**,** 243-263.

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. *Molecular Biology and Evolution,* 26**,** 2849-2864.
PARKER, H. G., KIM, L. V., SUTTER, N. B., CARLSON, S., LORENTZEN, T. D., MALEK, T. B., JOHNSON, G. S., DEFRANCE, H. B., OSTRANDER, E. A. & KRUGLYAK, L. 2004. Genetic structure of the purebred domestic dog. *Science,* 304**,** 1160-1164.
PERSSON, M. E., ROTH, L. S., JOHNSSON, M., WRIGHT, D. & JENSEN, P. 2015. Human - directed social behaviour in dogs shows significant heritability. *Genes, Brain, and Behavior,* 14**,** 337-344.
PERSSON, M. E., WRIGHT, D., ROTH, L. S., BATAKIS, P. & JENSEN, P. 2016. Genomic regions associated with interspecies communication in dogs contain genes related to human social disorders. *Scientific reports,* 6.
PLANTA, J. U. D. & DE MEESTER, R. H. W. M. 2007. Validity of the Socially Acceptable Behavior (SAB) test as a measure of aggression in dogs towards non-familiar humans. *Vlaams Diergeneeskundig Tijdschrift,* 76**,** 359-368.
RAYMENT, D. J., DE GROEF, B., PETERS, R. A. & MARSTON, L. C. 2015. Applied personality assessment in domestic dogs: Limitations and caveats. *Applied Animal Behaviour Science,* 163**,** 1-18.
ROTH, L. S. & JENSEN, P. 2015. Assessing companion dog behaviour in a social setting. *Journal of Veterinary Behavior: Clinical Applications and Research*.
SAETRE, P., STRANDBERG, E., SUNDGREN, P. E., PETTERSSON, U., JAZIN, E. & BERGSTROM, T. F. 2006. The genetic contribution to canine personality. *Genes, Brain, and Behavior,* 5**,** 240-248.
SAVOLAINEN, P., ZHANG, Y. P., LUO, J., LUNDEBERG, J. & LEITNER, T. 2002. Genetic evidence for an East Asian origin of domestic dogs. *Science,* 298**,** 1610-1613.
SCOTT, J. P. & FULLER, J. L. 1965. *Genetics and the Social Behavior of the Dog,* Chicago, University of Chicago Press.
SERPELL, J. A. & HSU, Y. Y. 2005. Effects of breed, sex, and neuter status on trainability in dogs. *Anthrozoos,* 18**,** 196-207.
SHABELANSKY, A., DOWLING-GUYER, S., QUIST, H., D'ARPINO, S. S. & MCCOBB, E. 2015. Consistency of shelter dogs' behavior toward a fake versus real stimulus dog during a behavior evaluation. *Applied Animal Behaviour Science,* 163**,** 158-166.
SHERMAN, B. L., GRUEN, M. E., CASE, B. C., FOSTER, M. L., FISH, R. E., LAZAROWSKI, L., DEPUY, V. & DORMAN, D. C. 2015. A test for the evaluation of emotional reactivity in Labrador retrievers used for explosives detection. *Journal of Veterinary Behavior: Clinical Applications and Research,* 10**,** 94-102.
SINISCALCHI, M., MCFARLANE, J. R., KAUTER, K. G., QUARANTA, A. & ROGERS, L. J. 2013. Cortisol levels in hair reflect behavioural reactivity of dogs to acoustic stimuli. *Research in Veterinary Science,* 94**,** 49-54.
SKOGLUND, P., ERSMARK, E., PALKOPOULOU, E. & DALÉN, L. 2015. Ancient Wolf Genome Reveals an Early Divergence of Domestic Dog Ancestors and Admixture into High-Latitude Breeds. *Current Biology*.
STARLING, M. J., BRANSON, N., THOMSON, P. C. & MCGREEVY, P. D. 2013. "Boldness" in the domestic dog differs among breeds and breed groups. *Behavioural Processes,* 97**,** 53-62.
SUNDMAN, A. S., JOHNSSON, M., WRIGHT, D. & JENSEN, P. 2016. Similar recent selection criteria associated with different behavioural effects in two dog breeds. *Genes, Brain, and Behavior,* 15**,** 750-756.

SVARTBERG, K. 2005. A comparison of behaviour in test and in everyday life: evidence of three consistent boldness-related personality traits in dogs. *Applied Animal Behaviour Science,* 91**,** 103-128.
SVARTBERG, K. 2006. Breed-typical behaviour in dogs - Historical remnants or recent constructs? *Applied Animal Behaviour Science,* 96**,** 293-313.
SVARTBERG, K. 2007. *In:* JENSEN, P. (ed.) *The behaviourial biology of dogs.* Wellington: Cabi.
SVARTBERG, K. & FORKMAN, B. 2002. Personality traits in the domestic dog (Canis familiaris). *Applied Animal Behaviour Science,* 79**,** 133-155.
TAKEUCHI, Y., HASHIZUME, C., ARATA, S., INOUE-MURAYAMA, M., MAKI, T., HART, B. L. & MORI, Y. 2009a. An approach to canine behavioural genetics employing guide dogs for the blind. *Animal Genetics,* 40**,** 217-224.
TAKEUCHI, Y., KANEKO, F., HASHIZUME, C., MASUDA, K., OGATA, N., MAKI, T., INOUE-MURAYAMA, M., HART, B. L. & MORI, Y. 2009b. Association analysis between canine behavioural traits and genetic polymorphisms in the Shiba Inu breed. *Animal Genetics,* 40**,** 616-622.
TANG, R. Q., NOH, H. J., WANG, D. Q., SIGURDSSON, S., SWOFFORD, R., PERLOSKI, M., DUXBURY, M., PATTERSON, E. E., ALBRIGHT, J., CASTELHANO, M., AUTON, A., BOYKO, A. R., FENG, G. P., LINDBLAD-TOH, K. & KARLSSON, E. K. 2014. Candidate genes and functional noncoding variants identified in a canine model of obsessive-compulsive disorder. *Genome Biology,* 15.
TAYLOR, K. D. & MILLS, D. S. 2006. The development and assessment of temperament tests for adult companion dogs. *Journal of Veterinary Behavior-Clinical Applications and Research,* 1**,** 94-108.
THALMANN, O., SHAPIRO, B., CUI, P., SCHUENEMANN, V. J., SAWYER, S. K., GREENFIELD, D. L., GERMONPRE, M. B., SABLIN, M. V., LOPEZ-GIRALDEZ, F., DOMINGO-ROURA, X., NAPIERALA, H., UERPMANN, H. P., LOPONTE, D. M., ACOSTA, A. A., GIEMSCH, L., SCHMITZ, R. W., WORTHINGTON, B., BUIKSTRA, J. E., DRUZHKOVA, A., GRAPHODATSKY, A. S., OVODOV, N. D., WAHLBERG, N., FREEDMAN, A. H., SCHWEIZER, R. M., KOEPFLI, K. P., LEONARD, J. A., MEYER, M., KRAUSE, J., PAABO, S., GREEN, R. E. & WAYNE, R. K. 2013. Complete Mitochondrial Genomes of Ancient Canids Suggest a European Origin of Domestic Dogs. *Science,* 342**,** 871-874.
UDELL, M. A. 2015. When dogs look back: inhibition of independent problem-solving behaviour in domestic dogs (Canis lupus familiaris) compared with wolves (Canis lupus). *Biology letters,* 11**,** 20150489.
VALSECCHI, P., BARNARD, S., STEFANINI, C. & NORMANDO, S. 2011. Temperament test for re-homed dogs validated through direct behavioral observation in shelter and home environment. *Journal of Veterinary Behavior-Clinical Applications and Research,* 6**,** 161-177.
VAN DER BORG, J. A. M., BEERDA, B., OOMS, M., DE SOUZA, A. S., VAN HAGEN, M. & KEMP, B. 2010. Evaluation of behaviour testing for human directed aggression in dogs. *Applied Animal Behaviour Science,* 128**,** 78-90.
WILSSON, E. & SINN, D. L. 2012. Are there differences between behavioral measurement methods? A comparison of the predictive validity of two ratings methods in a working dog program. *Applied Animal Behaviour Science,* 141**,** 158-172.
WILSSON, E. & SUNDGREN, P.-E. 1997. The use of a behaviour test for the selection of dogs for service and breeding, I: Method of testing and evaluating test results in

the adult dog, demands on different kinds of service dogs, sex and breed differences. *Applied Animal Behaviour Science,* 53**,** 279-295.

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.

WORMALD, D., LAWRENCE, A. J., CARTER, G. & FISHER, A. D. 2017. Reduced heart rate variability in pet dogs affected by anxiety-related behaviour problems. *Physiology & Behavior,* 168**,** 122-127.

VÅGE, J., WADE, C., BIAGI, T., FATJO, J., AMAT, M., LINDBLAD-TOH, K. & LINGAAS, F. 2010. Association of dopamine- and serotonin-related genes with canine aggression. *Genes, Brain, and Behavior,* 9**,** 372-378.