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PERSONALITY STUDIES IN DOGS

Doctoral thesis

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“Dogs got personality. Personality goes a long way.”

~ the character Jules in Pulp Fiction

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GENERAL INTRODUCTION

1.1 The concept of personality

Personality is a concept whose meaning is usually apparent to the average person. Indeed, all of us use the term ‘personality’ in our daily lives, and characterize others using personality trait concepts, for example, “*He is a friendly guy*”, or “*Such a coward!*”. What we usually refer to is a characteristic of the person, the way he/she behaves, feels, or thinks.

However, the list of the characteristics that distinguish the behaviour of one human being from that of another (called person variables or person descriptors) is not restricted to personality, it also includes a number of diverse psychological phenomena (e.g. cognitive abilities, physical states, moods, activities, capacities, talents, social roles, expectations, goals, etc., John and Gosling, 2000; John and Srivastava, 1999). The person variables represent a superordinate category of phenomena, encompassing a large number of categories (Scheier and Bridges, 1995). The two types of constructs that are relevant to the current topic are the personality predispositions and the momentary states (e.g. emotions, mood). Personality predispositions represent cognitive, affective, and behavioural tendencies that are relatively stable, consistent across time and context (Costa et al., 1980). These enduring characteristics help to define a person’s identity and help to distinguish one person from another. On the other hand, people also experience a variety of less stable psychological states, e.g. fear, fatigue, excitement, etc. which states may last only a few seconds, or they might persist for days (Scheier and Bridges, 1995). Both types of person variables influence how people think, feel or behave in a given situation (Booth-Kewley and Vickers, 1994), the difference is that the personality predisposition remains a relatively constant source of influence, whereas the momentary states comes and goes more readily (Segerstrom, 2003).

As the researches described in this thesis are focusing on personality, first of all, I have to define this construct. Personality has been conceptualized at various levels of abstraction (e.g. supertraits, traits, facets), therefore only a very broad definition could satisfy all these levels simultaneously. Pervin and John (1997) defined personality as *those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving, across time and context*. In the current thesis, I adopt this definition as it is broad

enough to capture most phenomena studied by both personality psychologists and animal ethologists.

Personality has a hierarchical structure. Personality traits (also called dimensions or factors) represent the broadest level of abstraction (not counting the supertraits), and each trait summarizes a large number of distinct, more specific personality characteristics (called facets). In humans, after decades of research, personality psychologists reached a consensus on a general taxonomy of personality traits. It is widely accepted, that individual differences in human personality can be classified into five broad factors (Five Factor Model FFM, Goldberg, 1992; McCrae and Costa, 1987), namely (1) Neuroticism (including nervousness, jealousy, or anxiety); (2) Extraversion (including energetic, talkative, or assertive); (3) Openness (or Intellect) (including imaginative, artistic, or uncreative); (4) Agreeableness (including cooperative, trustful, or warm) and (5) Conscientiousness (including responsible, systematic or sloppy) (Gosling and Bonnenburg, 1998; John and Srivastava, 1999).

1.2 Personality concept in animals

The importance of animal individual behaviour differences – contrary to that of humans – and the animal personality conception was a question under debate earlier.

Although, the basic level of the Darwinian evolution theory is the individual, researchers initially applied this theory to explain differences between genera, species or sub-species. The intraspecific differences in behaviour were assumed to be non-adaptive variations surrounding the assumed adaptive average (Dall et al., 2004). More recently, however, biologists recognized the importance of studying individual differences within single population, since inter-individual variation in behaviour is often consistent and distributed in a non-random manner (Gosling, 2001; Sih et al., 2004), suggesting that it is likely to have fitness consequences, therefore, it could be a focus for selection (Dall et al., 2004).

While in humans, these consistent individual differences are referred to as personality, in non-human animals the term ‘personality’ is avoided sometimes, just because of the fear of anthropomorphism (Jones and Gosling, 2005). Other terms emerged to describe the same phenomenon, such as temperament, behavioural strategies, syndromes, or types (Bell, 2007; Benus et al., 1989; Ruefenacht et al., 2002; Sih et al., 2004). Behaviour syndromes and behaviour types are the terms most frequently used in behavioural ecology, referring to “*a suite of correlated behaviours reflecting between-individual consistency in behaviour across*

multiple (two or more) situations. [...] Within the syndrome, individuals have a behavioural type (e.g. more aggressive versus less aggressive behavioural types)” (Sih et al., 2004).

In ethology, the terms personality and temperament are preferred, however researches sometimes use them interchangeably (Jones and Gosling, 2005). For the sake of a standardized nomenclature, it must be determined how (or whether) personality differs from temperament. In human psychology, these two terms refer to different components of the consistent individual behaviour (Cloninger, 2002). According to Goldsmith et al. (1987), *temperament* is an early emerging behavioural tendency which is highly heritable and largely independent of the environment. *Personality* is the outcome of the interplay between temperament and environment (e.g. individual experiences). Research on human infants mostly refers to the term temperament whereas personality is restricted for adults. Adapting this distinction for animal personality research, in this thesis I use the term “personality” for adult animals and use “temperament” only when referring to a study explicitly discussing non-adult animals.

In the recent 2–3 decades it became clear that personality exists in a wide range of animal species, from primates to cephalopods (Gosling, 2001; Gosling and John, 1999) and individuals differ in a wide range of personality traits, for example, aggressiveness (Huntingford, 1982; Riechert and Hedrick, 1993), activity (Henderson, 1986; Sih et al., 2003), exploration (Dingemanse et al., 2002), risk-taking (Fraser et al., 2001; Wilson et al., 1994), fearfulness (Boissy, 1995), reactivity (Koolhaas et al., 1997), coping strategy (Benus et al., 1991), etc.

The devoted effort of animal personality researchers is also evident in the several comprehensive reviews which summarize the current knowledge about the personality of animals: (1) Personality can have a large fitness consequence (reviewed in Réale et al., 2007; Sih et al., 2004), for example bolder individuals have increased reproductive success (Smith and Blumstein, 2008). (2) Personality can have a clear genetic basis, and can be heritable (reviewed in Spady and Ostrander, 2008; van Oers et al., 2005), for example the heritability of boldness trait in dogs was 0.27 (Strandberg et al., 2005). (3) Personality often has relationship with physiology or neuroendocrine system (reviewed in Careau et al., 2008; Koolhaas et al., 1999; Wingfield, 2003), for example pigs with ‘proactive’ and ‘reactive’ coping strategies differed in their reaction to apomorphine due to the different hormonal signalisation of these groups (Bolhuis et al., 2000). (4) Personality often relates to other characteristics of individuals (e.g. age) and their environment (e.g. predator risk) (reviewed in Gosling, 2001),

for example in three-spined sticklebacks, aggressiveness, activity and exploratory behaviour correlated positively with each other only in environments where predators were present (Dingemanse et al., 2007).

Studying behavioural variations between individuals could be useful from both theoretical point of view (e.g. understanding of the evolution and development of behaviour, Benus et al., 1991; Wolf et al., 2008) and for applied animal behaviour research (e.g. Cavigelli, 2005; Bolhuis et al., 2006; Lucidi et al., 2005; Slabbert and Odendaal, 1999). Moreover, studying the personality of different animal species could also contribute to our knowledge about the human personality. Several elements of personality are universal in animals and show generality across species (Gosling and John, 1999). For example the shyness–boldness continuum was described in humans and in a range of other species (reviewed in Wilson et al., 1994). Distinct coping strategies (i.e. coping with environmental challenge) were also found in many non-human species (reviewed in Koolhaas et al., 1999). Since animal studies allow greater experimental control, animal models can be used to examine questions that are difficult or impossible in case of humans (Gosling and Vazire, 2002); for example, the biological base and the development and of personality (Mehta and Gosling, 2008), or the associations between personality and different health-related factors (Capitanio et al., 1999; Cavigelli, 2005).

1.3. Personality in the domestic dog

One species which has been emerged in the recent decades as a suitable model in several areas of behavioural research is the domestic dog (*Canis familiaris*).

Dog is the earliest domesticated species, however the time and place of the domestication is still an open question (ranging between 12,000 – 100,000 years ago, Morey, 2014). In recent years dogs have become famous for their human-like socio-cognitive abilities, for example their attachment to the owner (Gácsi et al., 2001; Topál et al., 2005) or their ability to follow human communicative gestures (e.g. pointing – Soproni et al., 2002 or gazing – Lakatos et al., 2014). Dogs are also sensitive to the human attentional state (Gácsi et al., 2004; Virányi et al., 2004) and ostensive cues (eye contact, addressing), which even leads to social bias in object choice tasks (Erdőhegyi et al., 2007; Marshall-Pescini et al., 2012; Topál et al., 2009a). It has been shown that in a large number of socio-cognitive tests, the dogs surpass their closest relatives, the wolves (e.g. Kubinyi et al., 2007; Gácsi et al., 2005), moreover, in some

cognitive abilities dogs even outperform the primates and show considerable similarity to the cognitive skills of young children (e.g. Lakatos et al., 2009). Dogs' special evolutionary history, their special bond to humans, and their complex social behaviour makes them a useful model to investigate the early evolutionary process of humans.

1.3.1 Main aims in dog personality research

Despite the fact, that the first scientific investigations of dog personality started early in the twentieth century, when Ivan Pavlov began a research program designed to identify the basic types of canine personality (Pavlov, 1906 cited in Teplov, 1964), the study of personality in dogs did not become a major area of research. However, as dogs became one of the most frequently owned pets throughout the world, many groups of people became interested in assessing the individual differences in behaviour of the dogs and dog personality became a topic of increased interest during the last decades.

As the “man’s best friend”, dogs share the human niche and are ubiquitous wherever humans live. Dogs play more and more important role in people’s everyday life, and owners spend more and more money on special products or services for them (e.g. health-care or training course) (Cavanaugh et al., 2008; Serpell, 2003). The owners in the Western-cultures generally regard their dog as family member or companion (Bennett and Rohlf, 2007; Marinelli et al., 2007), therefore choosing a puppy suitable for their particular circumstances is important both for owners and for the welfare of dogs. Several studies aimed to help the potential owners by trying to predict the adult behaviour of dogs in early puppyhood (e.g. Riemer et al., 2014), by developing special ‘character tests’ for breeders (e.g. Svartberg and Forkman, 2002) or by analysing the typical behavioural tendencies of dog breeds (e.g. Hart and Miller, 1985).

The widespread interest in pet dogs’ behaviour also facilitated the research of the problematic behaviours (e.g. fear, noise phobia, or separation anxiety, Blackwell et al., 2013; Hsu and Serpell, 2003; O’Farrell, 1997) and the factors affecting them. Aggression is one of the most frequently studied behaviour problems in this line of research, a great number of behaviour tests and questionnaire surveys have been developed to investigate this personality trait and its possible risk factors (Duffy et al., 2008; Kroll et al., 2004; Netto and Planta, 1997; Podberscek and Serpell, 1996, 1997a; van den Berg et al., 2003). As dogs live close to their owners, contact family members, children, and unknown persons/dogs day-to-day, predicting the aggression of the dogs is important not only for ethical reasons, but there can be great medical consequences, too.

Dog personality research has been also motivated by practical concerns. Numerous studies have developed behaviour tests for shelter dogs, aiming to predict the dogs' future behaviour in their new home, or improving the success of the adoption by matching dogs to their potential owners (e.g. De Palma et al., 2005; Stephen and Ledger, 2007). Dogs are also used for very diverse applied functions, such as social therapy for elderly people, guiding visually impaired people, or searching for explosives. The special training methods which are required for such working dogs are usually long and expensive, not surprising therefore, that numerous studies aimed to investigate dog's aptitude for these purposes (Murphy, 1998; Rooney and Bradshaw, 2004; Rooney et al., 2007; Serpell and Hsu, 2001). These surveys can help to select the appropriate dogs for the given purposes in an early state, making their training more effective and less expensive.

Of course, aside from studies with explicit practical purposes, theoretical studies about the structure and concepts of dog personality itself (e.g. Gosling and John, 1999), about general methodological issues (e.g. Taylor and Mills, 2006), about personality \times environment associations (e.g. Kobelt et al., 2003) and about the genetic background of dog personality (e.g. Héjjas et al., 2007b) have been also accumulated.

Taken together, dog personality drew a great scientific interest, it has a wide range of practical applications, and it is a matter of public concern.

1.3.2 Lack of methodological standardization in dog personality research

As mentioned, studies of dog personality have striven to fulfil many goals, from identifying a puppy test that will predict adult behaviour (e.g. Riemer et al., 2014; Slabbert and Odendaal, 1999), to examining the heritability of personality traits (e.g. Strandberg et al., 2005; Wilsson and Sundgren, 1998). These studies are unified by a common interest in dog personality, but their aims and focuses are very different, and the researchers conducting these studies come from a wide variety of research fields (e.g. ethology, psychology, genetics, veterinary medicine, etc.). As a consequence, the number of personality traits and methods designed to measure them escalated exponentially, without an end in sight. The lack of standardization in the methodology and nomenclature makes the comparison between studies nearly impossible. What made matters worse, traits with the same name often measure concepts that are not the same in different studies, and traits with different names often measure concepts that are quite similar.

Several large meta-analyses aimed to bring together these studies, highlighting the methodological and conceptual weaknesses, and emphasising the importance of a standardisation and dog personality research.

Diederich and Giffroy (2006) reviewed the dog personality studies from methodological point of view, pointing out several major gaps in the literature. For example, there are some breeds with large number of scientific investigations (e.g. German Shepherd Dogs or Labrador Retrievers), while other breeds have been rarely or never studied so far (e.g. some companion breeds). There are two predominant testing periods in dog surveys: 1) from the age of 1 to 11 weeks and 2) from the age of 1 to 10 years; but from the central period (3–11 months) only a few studies provided data. The two main criteria of the scientific relevant measurements (reliability and validity) are also rarely provided in dog personality studies and their results are usually inconsistent.

Taylor and Mills (2006) reviewed in detail the subtests and coding systems of the personality test batteries, identifying the most commonly used subtests in personality studies. Some of them were relevant only for specific purposes: for example, a test for working dogs (e.g. police dogs, hunting dogs) may subject the dog to gunfire, prey objects, or mock attacks toward the dog or its handler (e.g. Svartberg, 2002; Wilsson and Sundgren, 1997), while such subtests are of less relevance when trying to identify a potential family pet. Other subtests were common in a large number of tests, both for pet dogs and working dogs (e.g. approach by person, object play, novel room test). However, the authors called the attention to standardization within a subtest, for example, it's not irrelevant for the dog's reaction whether the person approaching him/her is a male or female, familiar or unfamiliar (e.g. Wells and Hepper, 1999). Test batteries also differ in what they measure from the dog's behaviour and how they measure it. Some studies attempted to code all behavioural responses using well defined behavioural variables (Hennessy et al., 2001; Ledger and Baxter, 1997), others assessed the dogs' reaction subjectively, on a range of a priori defined characteristics (e.g. Svartberg and Forkman, 2002), even others aimed only to categorize the dogs' reaction throughout the whole test into a qualitative scale (e.g. 1: no aggression to 5: biting, Netto and Planta, 1997, or pass–fail, Batt et al., 2008).

More recently, Fratkin et al. (2013) carried out a meta-analysis specifically focusing on the temporal consistency in personality traits in dogs. Consistency estimates were significantly different from zero, ranging from 0.28 for Responsiveness to training to 0.50 for Aggression. Their analysis also showed that personality in adults are more consistent in time than the temperament of puppies (in harmony with Goddard and Beilharz, 1986). Consistency

measures in adults (average $r = 0.51$) were 1.7 times higher than in puppies (average $r = 0.30$). In puppies, Fearfulness and Responsiveness to training were the least consistent traits, Aggression and Dominance were the most consistent; in contrast, there was no significant variation in consistency by personality trait among adult dogs. As the test interval increased, the magnitude of consistency decreased. Comparisons of the temporal consistency of behavioural rating versus behavioural coding did not differ from each other. However, there is no consensus about the extent to which personality is temporally consistent in dogs.

1.3.3 The personality structure of dogs

Based on the above mentioned methodological diversity, it is not surprising that contrary to humans, dog personality researchers have yet to develop a common framework for personality taxonomy. For example, in the above mentioned meta-analysis of Fratkin et al. (2013) the reviewed 31 studies reported 213 unique trait names. Although, there were some attempts to organize the personality traits of dogs, currently we are far from a general agreement about the personality structure in dogs.

The first attempt to classify the dogs based on their behaviour was credited to Pavlov (Pavlov, 1906, cited in Teplov, 1964). In his study, he adapted the categories of Hippocrates, dividing the dogs into two main groups: dogs with a “strong” nervous system and dogs with a “weak” nervous system. Dogs with weak nervous system are also called melancholic dogs: they were categorized as shy, inhibited, sensitive and nervous. Dogs with a strong nervous system were divided in three types: choleric dogs were categorized as strong but unbalanced, active and they tend to be aggressive. Sanguine dogs are strong and balanced, active, and reactive to novel stimuli. Finally, phlegmatic dogs were categorized as strong and balanced, but slow. They tend to be quiet, restrained, and persistent (Pavlov, 1906, cited in Teplov, 1964).

Later, Gosling and John (1999) attempted to characterize the personality in non-human animals following the structure of the human five-factor model. They reviewed the structural studies of personality in many species, ranging from chimpanzees to octopuses. The authors found evidence for several basic dimensions that recurred across species, with strong cross-species evidence for three of the human five factors: Neuroticism (in animals: Anxiety/Nervousness), Extraversion (in animals: Sociability) and Agreeableness (in animals: Aggression). Openness to experiences (or Intellect) and Conscientiousness were found as a relevant trait only in primates, and a mixture of these two traits might be relevant also in dogs. Regarding the most widely used measurements, the largest dog personality questionnaire, the Canine Behavioural Assessment and Research Questionnaire (C-BARQ, Hsu and Serpell,

2003), proposes eleven personality traits (Stranger-directed aggression, Owner-directed aggression, Stranger-directed fear, Non-social fear, Dog-directed fear or aggression, Separation-related behaviour, Attachment or attention seeking, Trainability, Chasing, Excitability, Pain sensitivity). The largest behaviour test battery, the Dog Mentality Assessment test (DMA, Svartberg and Forkman, 2002) proposes five traits (Playfulness, Curiosity/Fearlessness, Chase-proneness, Sociability, and Aggressiveness).

Taking a meta-analytical approach, Jones and Gosling (2005) reviewed 51 dog personality surveys, collecting all the articles which mention the term of “dog” and “personality” or “dog” and “temperament” in the title, list of keywords, or abstract. They aimed to identify which traits have received the most cross-study support. All traits from the collected studies were given to nine judges who independently classified them and sorted them into categories. This method yielded six (or seven) broad dimensions: Reactivity and/or Fearfulness, Sociability, Responsiveness to Training, Aggression, Dominance and Activity (an additional category “Other” included traits not necessarily related to dog personality).

Reactivity was related to the approach/avoidance of novel objects, raised hackles, and activity in novel situations. Related traits were found in 39 studies and were labelled as “excitability” or “nerve stability”. This dimension highly overlapped with Fearfulness which latter related, for example, to tendency to avoid unfamiliar people/dogs and was labelled also as “courage”, “self-confidence” or “boldness”. Traits related to Fearfulness were found in 43 studies.

Sociability was indexed by such behaviours as initiating friendly interactions with people or other dogs. Related traits were found in 31 studies, labelled also as “extraversion” or “affability”.

Responsiveness to training was related to behaviours like working with people, learning quickly in new situations and playfulness. Related traits were found in 34 studies, also labelled as “problem solving”, “willingness to work” or “cooperative”.

Aggression was categorized by behaviours such as biting, growling, and snapping at people or other dogs. Aggressive behaviour was sometimes divided into subcategories on the basis of the cause of the aggression (e.g. “territorial aggression”) or of the target of aggressive behaviour (e.g. “stranger-directed aggression”). Related traits were found in 30 studies.

Activity has often been assessed by activity in open-field or open-field-like tests, often labelled as “activity” or “locomotor activity”. Related traits were found in 15 studies.

Dominance was reflected in such behaviours as refusing to move out of a person’s path, could be judged by observing which dogs bully others, and which guard food areas or feed first. There is some debate about whether the Dominance should be considered independent

personality trait (Gosling and John, 1999), however traits related to this dimension were found in 16 studies, which support the relevancy of this personality trait in dogs.

In sum, there is great diversity in most features of the dog personality research, including the goals, methods, and disciplinary bases of the studies. Both the methodology issues and the taxonomy/nomenclature of the dog personality are far from reaching consensus. Researchers usually develop their own devices to measure a certain part of the dog personality they are interested in, usually not taking into consideration if their methods are replicable or if their results are comparable with other studies on similar fields.

1.4 Main methods in dog personality assessment

1.4.1 Personality concept from methodological point of view

In human psychology, the concept of personality has a theoretical background; the term ‘personality trait’ was defined as “*correlations of internal factors that cause consistent individual differences in behaviour*” (Eysenck, 1994). In animal personality research (including dogs), personality is rather a statistical construct, based on the observed behavioural pattern of the animals in different situations. However in both cases, we hypothesize and aim to find some underlying factors which control the behaviour in different situations and over specific time period. Personality traits in animals can be defined as a quantity of behavioural reactions that are correlating among themselves (Svartberg, 2003) or in other words, a suite of behaviours correlated across contexts and over time (Fratkin et al., 2013; Sih et al., 2004). This concept assumes that measuring the individuals’ (dogs’) behaviour in a certain number of situations allows us for predicting their behaviour in future situations. For example, when a dog was friendly towards a stranger in a controlled (and repeated) test situation we may hypothesize that this dog has a general tendency to react with affiliative behaviours whenever meeting strangers, therefore he/she will be also friendly when meeting strangers in the future.

There are three main methods by which dog personality can be assessed: 1) Test batteries: dog is subjected to a series of standardized (and controlled) situations; 2) Observational tests: describes the dogs’ spontaneous behaviour in naturalistic or semi-naturalistic environment; 3) Ratings of individual dogs: the owner or other person familiar with the dog rates its behaviour on different behaviour scales.

The two most frequently used (and most relevant in the current thesis) are the test batteries and ratings of individual dogs (questionnaires).

1.4.2 Test battery

The aim of test batteries is to assess the dogs' reactions to a series of specific stimuli. The tests are performed by presenting various stimuli to a dog and record its reaction. Thus, test batteries had two components: the list of its subtests and the method used for coding the dogs' reaction. In a general test battery, the dogs are subjected to a series of situations (usually aiming to replicate everyday situations, such as meeting a stranger, encountering a novel object, etc.) in a standard manner; the dogs' behaviour is described in durations (time %), latencies, and frequencies of different behavioural elements (e.g. time % of locomotion, latency of approaching a stranger, or the frequency of looking at the owner).

This method is often referred as 'objective', since the behaviour is directly observed and the variables are clearly defined not leaving much space to subjectivity. However, reducing a suite of behaviours to raw behavioural elements may cause the overall quality of the dog's behaviour to be lost (Taylor and Mills, 2006; Wemelsfelder and Farish, 2004). In many cases, the dogs' behavioural reaction can be evaluated only by the combination of the raw behavioural elements. For example, when people meeting a dog on a street, they take into account the combination of a number of behaviour variables (e.g. tail wagging, general body posture, ear position, types of vocalization, usually without consciously thinking about it) before they decide if it's safe to approach this dog. Different combination of these elements may mean different motivation behind the dog's reaction, therefore different outcome for the person approaching it. For example, jumping up at the end of the leash with intense tail wagging, low body posture, and whining means it's safe to pet this dog, while a dog jumping up without tail wagging, erected body position, while growling is better to be avoided. A low body posture while retreating behind the owner, maybe accompanied by a soft growling means, again, a third thing. Statistically, these behavioural elements not necessarily correlate with each other, especially when other test situations are also included in the analysis. So, when coding raw behavioural elements, although doing so may reduce observer bias, we may lose in the details, not seeing the general pattern and the apparent function of the behaviour.

Therefore, in many behaviour test batteries the researchers developed a scoring system, when (professional) coders observe the dogs' whole reaction to a given stimuli then score the behaviour on different scales (e.g. based on the intensity of the reaction, Svartberg and Forkman, 2002; van der Borg et al., 1991; Wilsson and Sundgren, 1997). However, the

objectivity of such measures can be called into question as the assessment of the dogs' behaviour is now based on a coder's subjective judgment.

As a disadvantage of test batteries, the actual behavioural reaction to a given stimuli is influenced by several factors other than the personality, e.g. recent experiences, physical states (e.g. tired or hungry), weather, etc. The dogs (as well as humans) do not react the same way to a given stimuli in every single case, several similar situation would be needed to test in order to assess the average reaction which might reflect the background personality. However, the number of the situations which could be tested in a row is limited (the dog could easily get tired after encountering 15–20 new stimuli).

Moreover, there are some traits, like fearfulness or aggression, which are hard to measure with behaviour tests because the dogs in “normal” experimental situations (which more or less try to replicate everyday situations in standardized circumstances) very rarely show such behaviours (e.g. Duffy et al., 2008; Klausz et al., 2014). The situations which would evoke such severe fear or aggression are sometimes questionable by ethical and welfare standards (and the owners of aggressive or seriously fearful dogs are less likely to voluntarily participate in such tests).

1.4.3 Individual rating (questionnaire)

The other type of personality measures – ratings of individual dogs or questionnaire – relies on the owners' or care-takers experience of the dogs' behaviour instead of the actual observation. Questionnaire is a widely used method in the human personality research, and nowadays more and more researchers accept that the owner's rating is a useful tool in dog personality studies, as well. The rationale of the questionnaire rating methods is, that the person (most of the time, the owner) who knows the dog for a considerable time had the opportunity to observe its behaviour in a range of different situations, therefore he/she could reliably evaluate its behaviour (e.g. how the dog usually reacts, when meeting another dog, or in unfamiliar situations, or when the vacuum cleaner is turned on). The owners are usually provided a list of adjectives, short sentences or detailed situations, and they rate whether or not, or how often, his/her dog shows a specified behaviour (e.g. in a 5–point Likert scale, from 1: never to 5: always).

The subjectivity of such measures cannot be questioned, since each owner judges or interprets the dogs' behaviour differently. The subjectivity originates from two different sources: 1) how the owner defines a given behaviour (e.g. what is considered as “*aggressive*” reaction); and 2)

how the owner defines the points of the rating scale (e.g. what is “rarely” or “sometimes”). These factors can vary from owner to owner.

The first types of subjectivity can be reduced by giving detailed behavioural descriptions instead of broad adjective-based questions (e.g. “*My dog growls or barks when encountering a stranger on a street*”, instead of “*My dog is aggressive towards strangers*”). The second type of subjectivity is harder to control for. For example, some owners have a tendency to give only the extreme scores (in a 5 point scale they give only 1–3–5), other owners never use the two extremes, restricting their rates to the 2–3–4 scores. However, Block (1961) showed that the combined ratings of observers are largely independent of the idiosyncrasies of any single observer, so, by combining the ratings of a larger number of owners, their individual subjective judgement bias can be, more or less, overcome.

Questionnaire rating method also offers some advantages, for example, it allows the researchers to collect a considerably larger and more diverse sample than with behaviour tests (Jones, 2008). In some traits, the owners’ ratings may reflect more to the dogs’ everyday behaviour as the observation of several similar situations allows the owners to generalize the dogs’ reactions to such situations. Moreover, with questionnaire, the number of situations investigated could be higher than with behaviour test.

1.4.4 Obtaining personality traits

As mentioned above, the aim of these personality measures at the end is to define broader behavioural constructs (i.e. scales) which combines the dogs’ reaction in a number of situations. Although researchers may have some hypotheses about which aspects of personality they aim to measure, the actual traits are usually not defined *a priori* (but see e.g. De Palma et al., 2005), but using specific statistical methods (e.g. principal component analysis). In the latter case, the raw behavioural variables/questionnaire answers are subjected to data-reduction methods which statistically identify correlated sets of variables/items within the whole database and place them into components (also called factors) (Goodloe and Borchelt, 1998).

Interestingly, the structure of the dog personality traits derived from behavioural test batteries and those derived from questionnaire ratings are not necessarily similar. Traits derived from behavioural tests are usually harder to interpret than those derived from questionnaires, the latter more likely to resemble the structure of the human personality. It may not be surprising since questionnaires are filled out by humans who may tend to project their own personality structure onto dogs (e.g. Kwan et al., 2008). (On a side note, several questionnaires used in

dog personality research originate from human questionnaires adapted for dogs, e.g. the Dog-ADHD questionnaire, Vas et al., 2007 or the Canine Big Five, Gosling et al., 2003), hence such structural similarity is understandable). In behavioural tests, however, researchers are more likely to capture more dog-specific traits which structure are not necessarily similar to the human personality, and therefore might be harder to interpret.

1.4.5 Reliability, validity

Two requirements should be met to consider a measurement relevant and accurate: reliability and validity (see in detail in George et al., 2003; Martin and Bateson, 1993).

Reliability regards to consistency and stability of the measurement (Gosling and Vazire, 2002; Taylor and Mills, 2006), the three frequently used methods to estimate it are: (1) Intra- and inter-observer agreement (consistency within and between observers or raters): it concerns the degree to which the measurement and the coding/scoring system are free from errors and are replicable. (2) Internal consistency (consistency within components of measures designed to assess the same behaviour): it is the reliability of the created scales (or traits), usually assessed by Cronbach's alpha coefficients. (3) Test-retest reliability (stability of the measurement over time): reflecting to the temporal consistency. The assessment of the internal consistency (consistency across situations) and test-retest reliability (consistency over time) are what differentiate a personality measurement from a 'normal' behavioural assessment.

Validity reveals how well the test or questionnaire measures what it is meant to measure (Gosling and Vazire, 2002; Taylor and Mills, 2006). In case of validity, there are two subtypes: internal and external validity. The former relates to the validity of the measurement, the latter reflects the degree to which results can be generalized across studies. Within the confines of internal validity there are three different categories. Content validity refers to the measurement's scientific relevancy, for example the questionnaire contains only items which are relevant to its aims. Construct validity investigates the degree to which the current measurement correlates with others to which it is theoretically related (convergent validity) and whether it is independent from others to which it is not related (discriminant validity). Criterion validity refers to the predictive ability of the measurement, e.g. whether the newly developed measurement leads to similar results as a previously validated instrument.

Unlike reliability, validity assessments for personality tests and questionnaires are usually fraught with difficulty, because it is unlikely that any measurement will be wholly predictive of a dog's behavioural reaction in any given circumstance. For example, the correlation

between two different measurements (construct validity) in human personality questionnaires are between $r = 0.2\text{--}0.3$ (Gosling, 1998); similar results was found in dogs, too (Gosling et al., 2003; Svarthberg, 2005).

Jones and Gosling (2005) also reviewed the reliability and validity assessments provided in the papers, concluding that some issues of reliability had been rarely addressed (e.g. intra-rater reliability), and validity was low for behaviour tests, especially those conducted on young dogs.

In sum, both behavioural test series and questionnaire ratings are adequate tools (if the necessary reliability and validity measures are provided) for assessing the personality in dogs. The best would be, if it is possible, to combine the two methods and compare their results (e.g. Kubinyi et al., 2014). Since researchers usually must evaluate dog personality using limited resources, the actual aims and opportunities of the study define which is the better suited for the purpose.

1.5 General aims

As mentioned above, the difference between temperament and personality is that the former is largely affected by genetic factors, while the latter is the outcome of the interplay between temperament and environment (including individual experiences). Based on this, numerous biological, environmental, and evolutionary influences affect the personality in dogs. The general aims of the four studies described in this thesis are to develop reliable ethological methods for measuring personality traits in dogs and to identify both environmental (*Study I and II*) and genetic factors (*Study III and IV*) in association with these traits.

In several studies researchers aim to explain the variation in personality by the means of demographic and environmental factors. It can be assumed that factors like the owner's general attitude towards dogs (e.g. the dog is just a pet, a play-mate, or a family member), the dog-keeping practices (e.g. how much time the owner spends with the dog, how much training the dog receives, etc.), the characteristics of the household (e.g. the dog lives alone or with other dogs, whether there are children in the household, etc.), and the dogs' own biological characteristics (e.g. sex, age, neutering) influence what kind of experiences the dog

could gather during its life, which, in turn, could affect not only the actual behaviour but could also contribute to the development of the dogs' personality.

The difficulty of such studies is that the number of potential influencing factors is practically endless and the direction of the associations is not always clear. For example, is the dog more trainable because he/she participated in a large number of professional training courses or, on the contrary, the owner decides to attend a larger number of training courses with the dog because the dog is more trainable? Moreover, these above mentioned factors do not necessary act independently in the behaviour (e.g. neutering can have a different behavioural outcome in male and female dogs, Podberscek and Serpell, 1996).

In *Study I*, analysing a large number of dogs ($N > 10,000$ individuals) we aimed to explore not only the most relevant demographic and environmental factors in association with four dog personality traits but we also investigated their complex interactions.

In *Study II*, we focused on the personality of the owner as a special environmental factor affecting the dogs' personality. As similarity in personality profile was described in various human relationships, we expected a similar positive association between the owners and dogs personality profile.

Since the dog genome has been sequenced (Kirkness et al., 2003; Lindblad-Toh et al., 2005), dogs became a widely used model species also in behavioural genetics (Spady and Ostrander, 2008; Sutter and Ostrander, 2004). Dogs' great morphological and behavioural diversity, their unique genetic make-up (i.e. more than 300 genetically isolated breeds – Shearin and Ostrander, 2010) and the fact that several human psychiatric disorders have an analogue in dogs (Overall, 2000; Parker et al., 2010) makes them ideal candidates for this kind of research, as well. The heritability of the different personality traits of dogs is a frequently investigated topic, (e.g. Ruefenacht et al., 2002; Strandberg et al., 2005; Wilsson and Sundgren, 1998) probably because of the possible breeding consequences. Recently, many studies also aimed to survey the allelic variations of candidate genes in dogs (Héjjas et al., 2007a; Niimi et al., 2001; Takeuchi et al., 2005), and to associate these variations with behaviour and personality (Héjjas et al., 2007b; Ito et al., 2004; Jones et al., 2008).

The phenotyping methods in many of these studies are based solely on breed stereotypes (e.g. Chase et al., 2009; Jones et al., 2008). This method is based on the assumption that, since dog breeds are genetically isolated populations, behavioural differences between them are predominantly due to genetic differences. However, the discriminative potential of the behaviour traits among breeds is variable (Hart, 1995; Lit et al., 2010b); some traits are

characteristic on breed level, while in others, the individuals' behaviour differ more within breeds than between breeds.

In *Study III*, our aims were threefold: 1) we investigated the discriminative potential of four personality trait among dog breeds; 2) we characterized dog breeds based on their typical behaviour; and 3) investigated whether the earlier function of the breeds or the genetic relatedness between breeds affect their behaviour.

However, as belonging to a certain breed account for 27% of total genetic variation among individuals (Parker et al., 2004), there are large within-breed differences not only in behaviour but also in genetics. Since the effect of a single allele on the behaviour is relatively small, individual-based methods are more preferable than breed comparisons in studies aiming to assess direct genotype-phenotype associations.

In *Study IV*, we aimed to develop reliable, individual-based phenotyping tools for characterizing the behaviour and used the candidate gene approach to explore the associations between the gene polymorphisms in the dopamine and oxytocin systems and certain personality traits in dogs.

STUDY I.

Demographic and environmental factors in association with dog personality traits¹

1. Introduction

Every dog's behaviour results from the interactions between its genetic make-up, environment, and past experiences (Borchelt and Voith, 1982; Reisner et al., 2005; Serpell and Jagoe, 1995). In this sense, factors relating to the dog, like the environment in which the dog is kept, the way in which the owner interacts with it, or the owner's management choices can have a significant effect on the dog's behaviour.

Previous studies in this field have been largely focusing on factors associated with the development and risk factors of behaviour problems in dogs (e.g. Bennett and Rohlf, 2007; Jagoe and Serpell, 1996; Kobelt et al., 2003; Takeuchi et al., 2001). Researchers identified several factors in association with problematic behaviours, for example, improper early socialization (Podberscek and Serpell, 1997b; Serpell and Jagoe, 1995) or the lack of proper training (Bennett and Rohlf, 2007; Jagoe and Serpell, 1996; Kobelt et al., 2003; Voith et al., 1992). In other factors, the results were more contradictory. For example, O'Farrell (1997) found positive associations between 'spoiling' the dog (i.e. letting the dog sleep on the owner's bed, feeding it from the table, etc.) and dominance aggression; Jagoe and Serpell (1996) found that sleeping close to the owner was associated with an increased prevalence of competitive aggression and separation-related problems. Contrary to it, no association was found between allowing the dog on the bed and separation anxiety (Flannigan and Dodman, 2001); Voith et al. (1992) also found no relationship between the owner's tendency to 'spoil' the dog and the dog's behaviour.

Only a few studies addressed the associations between the demographic, environmental and management factors and the dog's everyday behaviour or personality. For example, Tami et al. (2008) found that dogs living in the house with the owner showed significantly higher prevalence of friendliness toward approaching strangers and unknown dogs, and they were also more obedient than kennel-living dogs, but house-living was also associated with increased fear of loud noises.

¹ this chapter is based on: Kubinyi, E., **Turcsán, B.**, Miklósi, Á., 2009. Dog and owner demographic characteristics and dog personality trait associations. *Behavioural Processes*, 81, 392–401.

Some of the most frequently investigated factors (age, sex, neutering) have a biological basis, thus influence the behaviour through genetic and hormonal pathways. Other variables are more likely to affect the behaviour indirectly, through past experiences (e.g. when and from where the owner acquired the dog), and current lifestyle (e.g. time spent with the owner, where the dog is kept).

Studies aimed to explore the effect of influencing factors meet three difficulties: 1) there are numerous factors relevant to investigate; 2) the effect of a given factor could be small and overshadowed by other factors; 3) although, such factors are referred as “independent variables”, but they are usually not independent from each other. Previous studies pointed out several associations between factors related to the dog, owner or environment that influenced dog keeping practices. For example, neutering the dog was associated with increased walking frequency (Masters and McGreevy, 2008), larger dogs were more likely to receive formal training (Kobelt et al., 2003), and dogs living in the house are more likely to live with other dogs than those living in kennels (Tami et al., 2008). Thus, these variables not necessarily act independently on the behaviour, and any associations found could still be an indirect one affecting the behaviour through another, probably undetected background factor. Studying the interactions of demographic and environmental variables might reveal yet uncovered associations.

Our study’s central objective was to identify not only the main effects but also the complex interactions of demographic and environmental factors on certain personality traits of dogs.

For such exploratory investigation a huge sample size and diverse sample are needed, which can be most easily achieved using the questionnaire method. We used the Internet to collect the data because of the many potential benefits compared to the conventional, paper-based method (Gosling et al., 2004). The owners are motivated, since they are self-selected and receive an immediate feedback in contrast to the traditional method. The questionnaire spreads widely, thus the Internet samples are more diverse and can be larger than those with traditional questionnaire method. The data collecting is also simpler, inexpensive and efficient (i.e. no experimenter is needed to administer the data collection), moreover, web-based data collection also removes the necessity of entering the data (therefore the risk of data entry mistakes). Another potential benefit of the Internet emphasized in the human psychological research is the anonymity of the responders (subjects more readily answer intimate questions). In animal personality surveys, the anonymity may reduce the probability of the social desirability bias (when respondents answer the questions in a socially desirable manner, independently of the actual observation, Ley et al., 2009). Moreover, Gosling et al. (2004) and

Duffy et al. (2008) showed that results obtained using online questionnaire do not differ from those obtained by traditional questionnaire method. Naturally, online questionnaires have potential disadvantages, too. The most occurring is that the responders (owners) complete the questionnaire several times or another owner completes the questionnaire for the same dog. The effect of “repetitions” should be minimalized.

In sum, in this study we used an online questionnaire to reveal associations between dog personality traits and both dog and owner demographic variables in a large sample of dogs. The novelty of our investigation is the statistical method we applied in order to identify the most relevant factors for each personality trait and to analyse the effect of multi-level interactions between these variables.

2. Method

2.1. Subjects

In this study we collected owner’s reports on 14,004 dogs. Owners filled in an online questionnaire in German which was advertised in the “Dogs” magazine (published by Living at Home Multi Media GmbH, Hamburg, August 2007 issue) and the magazine’s website (www.dogs-magazin.de). It was accompanied by a short article and was available from the end of August 2007 to the beginning of January 2008. Incomplete questionnaires (N = 783) were excluded from the analysis, repetitions (more questionnaires about the same dog, N = 201) were used only in assessing reliability (see in later in 2.3). As we aimed to assess personality, dogs younger than 1 year old (N = 2690) were also excluded from this sample. After these corrections, the final sample size was N = 10,330.

2.2. Questionnaires

The owners were asked to complete two different questionnaires.

1. A quantitative questionnaire (“Demography Questionnaire”) was designed to address the demographic information and management practices. The questions were selected based on available literature, the owners reported about their own demographic attributes and those of the dog, their typical shared activities and management practices (14 variables, Table 1.1a).

2. The “Personality Questionnaire” was based on a 48-item Human Big Five Inventory adapted for dog behaviour by Jesko Wilke, freelancer journalist (Table 1.1b). This

questionnaire consisted of 24 items in which owners are asked to score their dogs using a 3–point scale (not at all agree; neither agree, nor disagree; completely agree).

Table 1.1 Questionnaires applied in the study

a) Demography Questionnaire

Dog's characteristics
1) name, 2) breed, 3) age, 4) sex (male, female), 5) neutered status (intact, neutered), 6) age at acquisition (bred by the owner, 2–12 weeks, 3–13 months, >1 year), 7) training experience (nothing, puppy class, basic class, obedience, assistance dog, guarding, agility, other)
Owner's characteristics
1) gender (man, woman), 2) age (< 18, 19–30, 31–60, > 60 years), 3) education (elementary school, high school, college, university), 3) number of people in the household, 4) number of other dogs in the household (0, 1, 2, > 2 dogs), 5) purpose of keeping the dog (family member, hobby, guarding, work, breeding), 6) number of previous dogs; 7) hours spent with the dog (< 1 hour, 1–3 hours, > 3 hours / day), 8) frequency of playing with the dog (once, 2–3, 4–5, 6–7 times / week)

b) Personality Questionnaire

The dog... (answers: <i>fit</i> , <i>partly fit</i> , <i>not fit</i>)	
1. is ingenious, inventive when seeks hidden food or toy	14. is unassertive, aloof when unfamiliar persons enter the home*
2. is sometimes distressed, desolate*	15. is emotionally balanced, not easy to rile
3. is calm, even in ambiguous situations	16. is passionless and holds him/herself apart*
4. fights with conspecifics frequently*	17. often does not understand what was expected from him/her during playing*
5. is active, eager	18. is sometimes fearful, awkward*
6. is stubborn, energetic	19. is cool-headed even in stressful situations
7. can be stressed easily*	20. is bullying with conspecifics*
8. is ready to share toys with conspecifics	21. is not much interested except in eating and sleeping*
9. is intelligent, learns quickly	22. is very self-confident
10. is rather cool, reserved*	23. is sometimes anxious and uncertain*
11. is shy with conspecifics	24. gets on well with conspecifics
12. is not hostile with people	
13. is very easy to warm up to a new toy	

* scoring was reversed

2.3 Reliability of the questionnaire

As mentioned above, one inconvenience of the web-based questionnaire method is that it allows subject to fill out the questionnaire more than once. Such repetitions could bias the results (however, with large sample size, such biases can be minimized). We used these

repetitions to investigate the test–retest reliability and the inter–rater reliability of the questionnaire.

In the first step we identified dogs with more than one evaluation. For this, we investigated the demographic and environmental characteristics of the dogs (the dogs' name, sex, neutering status, breed, age, training level) and some characteristics of the household (the number of people and dogs in the household). If these filter variables had the same values in more than one questionnaire response, we marked these questionnaire–pairs as repeated data about the same dog. Altogether 201 such pairs were collected.

In the second step we investigated the demographic characteristics on the owners (gender, age, education level) in this pairs to decide whether the same or different owner evaluated the dog in both times. In $N = 137$ of these cases, the second questionnaire was filled out by the same owner, in the other $N = 64$ cases, by another person.

The first sample was used to analyse the test–retest reliability, the second sample to assess the inter–rater reliability.

2.4 Statistical analyses

To condense the items of the Personality Questionnaire, we used principal component analysis (PCA). This data–reduction method is based on the assumption that variables (in our case, questionnaire items) relating to the same background factor (personality trait) correlate each other more than those related to different factors. The statistic investigates the correlation pattern between the items clustering them around several hypothetical axes, called principal components. These components can be used in further analyses hereby reducing the number of statistical comparisons (*Type I* error). Our aim was to find independent axes which explain the majority of the whole individual variance, therefore we used the Varimax method to rotate these hypothetical axes. Each individual item correlates with each component (represented by the loadings which values vary between 0 and 1). Items not correlating with any component (threshold loading was < 0.4 , Hair et al., 1998) or correlating with more than one component with a similar loading were excluded to ensure the independency of the components. The number of extracted components was decided after visual inspection, using the rules of the Scree test (Cattell, 1966). The component scores were calculated automatically by the SPSS software using the Regression method.

The stability of the component structure was tested on a subsample of dogs. We have randomly chosen 25 individuals from each breed with at least 25 representatives ($N = 1425$) and principal component analysis with the same parameter settings was run on this sample

(e.g. Svartberg and Forkman, 2002). To investigate the internal consistency of the scales derived from the PCA we calculated Cronbach's alpha coefficients for each component (DeVellis, 1991). The test-retest and inter-rater reliability were investigated using Intraclass correlation (one-way random measures).

We carried out four regression tree analyses, one for each component, to examine the associations between the demographic variables and the behaviour. Regression trees are ideal for analyzing complex numeric and/or categorical data and detecting non-linear relationships in the structure of the data (Karels et al., 2004; Low et al., 2006). We decided to use this method, because the large number of explanatory variables used in this study does not facilitate the revealing of complex interactions by the generally used univariate analyses. The tree is constructed by dividing data into mutually exclusive groups, called nodes. In one node, individuals have similar values for the dependent variable. The output is a tree diagram with a parent node at the top containing the entire data set. The parent node is split into child nodes based on the explanatory variable (environmental variable) that reduces the most total variation within the dependent variable (component scores). Having considered all possible splits, the most suitable split is retained. The process is repeated on the next grouping level. The number of data divisions is determined using a cross-validation procedure by randomly drawing samples from the data set to evaluate the predictive error of the tree (De'Ath and Fabricius, 2000). According to Yamauchi et al. (2001), the resulting tree model resembles a human judgment process. We used the CHAID statistical technique (Kass, 1980). CHAID uses an F test if the variable is continuous (e.g. the dog's age in our case) and χ^2 test if the variable is categorical (e.g. gender of the owner). In order to facilitate interpretation, we specified the minimum number of cases as 2000 for parent nodes and 1000 for child nodes. SPSS 13.0 was used for the analyses.

3. Results

3.1 Descriptive statistics

The descriptive statistics of the sample are presented in Table 1.2.

The mean age of the dogs in the sample was 4.2 years (ranging from 1 year to 18 years). A bit more than 50% of the dogs were males, were acquired before the age of 12 weeks, and almost 50% of them were neutered. Approximately one-third of the dogs had not participated in any kind of professional training courses. The respondents were mainly female, the majority of

them were between 31 and 60 years old, most of them had secondary education and two-thirds of them had previous experience with dogs. The majority of the respondents resided in a two-person household and owned only one dog. Family member was marked as the most common purpose of keeping the dog and most respondents claimed to spend more than 3 hours with the dog per day and playing with it every day.

Table 1.2 Descriptive statistics of the owners and dogs in the present study (N= 10,330)

Dog's characteristics		Owner's characteristics	
Age	mean \pm SD = 4.2 ± 3.1	Age	< 18 years: 5.3%
Sex	male: 56.1%		19–30 years: 26.9%
	female: 43.9%		31–60 years: 64.9%
Neutered status	intact: 56.9%		> 60 years: 2.9%
	neutered: 43.1%	Gender	man: 20.4%
Age at acquisition	bred by the owner: 1.9%		woman: 79.6%
	2–12 weeks: 53.7%	Education	elementary school: 22.3%
	3–12 months: 22.6%		high school: 40.3%
	>1 year: 21.7%		college: 26.0%
Training	nothing: 35.3%		university: 11.4%
	1 type: 23.3%	People in the household	mean \pm SD = 2.8 ± 1.4
	2 types: 21.5%	Dogs in the household	no other dog: 66.9%
	3 types: 11.6%		1 other dog: 20.6%
	4 or more types: 8.3%		2 other dogs: 7.7%
			> 2 other dogs: 4.8%
		Purpose of the dog	family member only: 45.1%
			family member + other: 48.2%
			not family member: 6.7%
		N of previous dogs	mean \pm SD = 1.2 ± 2.2
		Time spent with the dog	0–1 hour/day: 3.2%
			1–3 hours/day: 27.0%
			> 3 hours/day: 69.8%
		Playing with the dog	1 time/week: 3.3%
			2–3 times/week: 9.5%
			4–5 times/week: 10.6%
			6–7 times/week: 76.6%

3.2 Principal component analysis

17 of the 24 items were grouped into four components that accounted for 58% of the total variance in item scores (Table 1.3). The component structure on the subsample of N = 1425 dogs was exactly the same as on the original sample and the item-loadings were very similar (the maximum difference in the loadings were 0.02) which confirmed the stability of the analysis.

Items loading on a component higher than 0.4 were used for the interpretation; the components were given the following labels: calmness, trainability, dog sociability, and boldness.

Table 1.3 Component structure, explained variance, Cronbach's alpha values and Eigenvalues of components. Loadings > 0.4 are in bold

Variables <i>The dog...</i>	Calmness	Trainability	Dog sociability	Boldness
is cool-headed even in stressful situations	0.820	−0.043	−0.153	0.033
is emotionally balanced, not easy to rile	0.787	−0.058	−0.162	−0.038
is calm, even in ambiguous situations	0.784	0.006	−0.109	0.069
is sometimes anxious and uncertain*	0.729	−0.070	−0.054	−0.331
can be stressed easily*	0.709	−0.051	−0.183	−0.218
is intelligent, learns quickly	−0.095	0.721	0.034	−0.138
often does not understand what was expected from him/her during playing*	−0.159	0.709	0.013	−0.012
is very easy to warm up to a new toy	0.044	0.684	0.067	0.226
is inventive when seeks hidden food or toy	−0.063	0.642	−0.036	0.063
is not much interested except in eating/sleeping*	0.104	0.621	0.126	0.175
gets on well with conspecifics	−0.185	0.076	0.821	0.011
fights with conspecifics frequently*	−0.152	0.021	0.808	−0.080
is bullying with conspecifics*	−0.090	0.064	0.762	0.191
is ready to share toys with conspecifics	−0.098	0.018	0.545	−0.086
is rather cool, reserved*	0.084	0.188	0.038	0.769
is unassertive, aloof when strangers enter the home*	−0.116	−0.049	0.002	0.706
is sometimes fearful, awkward*	−0.325	0.150	−0.086	0.704
Explained variance	23.807%	13.859%	11.412%	8.596%
Cronbach's alpha	0.849	0.711	0.738	0.642
Eigenvalue	4.047	2.356	1.940	1.461

* scoring was reversed

3.3 Reliability

Three out of the four Cronbach's alpha values were above 0.7, but the value for the boldness was lower (0.642), indicating that more related items would need to be added (Table 1.3). However, values above 0.6 are usually considered as satisfactory (e.g. Hsu and Serpell, 2003). The test–retest reliability of the questionnaire was found to be high; the Intraclass correlation between the first and second filling was > 0.7 in all traits (calmness: 0.839; trainability: 0.735; dog sociability: 0.916; boldness: 0.837, $p < 0.001$ for all).

The inter-rater reliability of the questionnaire was a bit lower but still acceptable. The Intraclass correlation between the two raters was 0.688 for calmness; 0.720 for trainability; 0.724 for dog sociability; and 0.800 for boldness ($p < 0.001$ for all).

As the Cronbach's alpha values and the test-retest reliability of the derived behaviour scales confirmed that they are consistent across situations and over time, in the following we will refer to them as personality traits.

3.4 Regression trees

3.4.1. Calmness

Figure 1.1 shows the regression tree model predicting calmness.

The dog's age, the age at acquisition, neutering status and training experience had the most significant effect on the calmness trait. The regression method separated the whole sample into four subgroups by age ($F_{3,10515} = 89.72$, $p < 0.001$).

Dogs older than 6.9 years were subdivided by the age at acquisition ($F_{1,2177} = 8.88$, $p < 0.001$); acquisition at a younger age was associated with higher calmness.

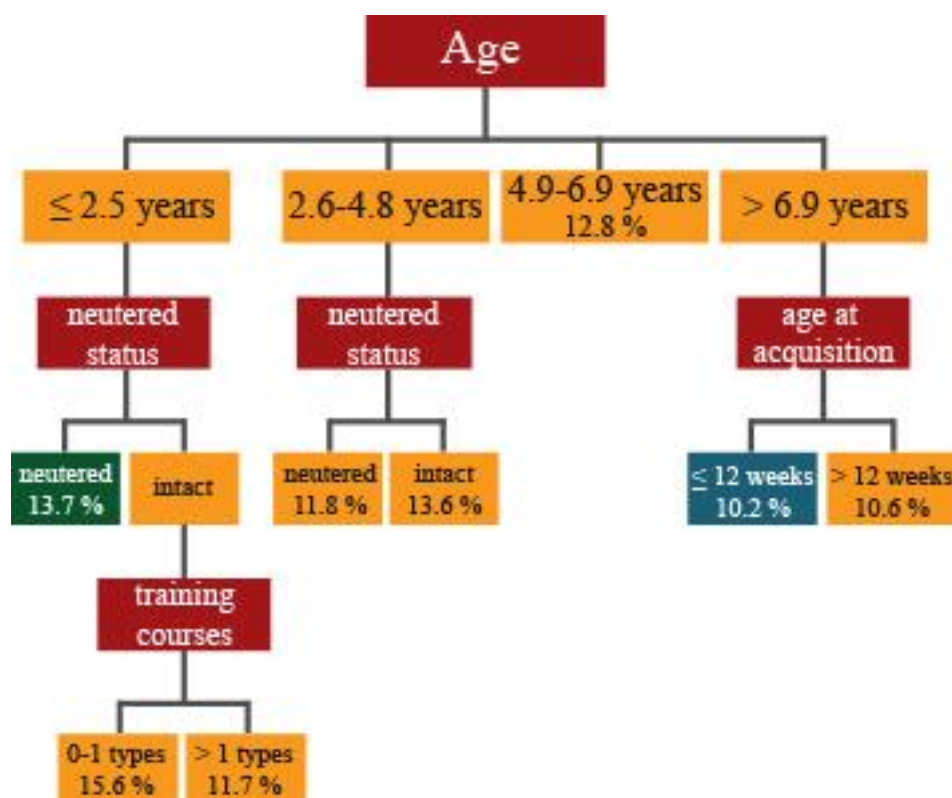


Fig. 1.1 Regression tree model for calmness. Numbers in the end nodes represent the proportion of the sample. Blue background highlights the highest mean, green background the lowest mean

The 1–2.5-year-old and 2.6–4.8-year-old subgroups were subdivided by neutering status ($F_{1,4318} = 81.86$, $p < 0.001$; $F_{1,2668} = 36.30$, $p < 0.001$, respectively). Intact dogs had higher mean calmness in both subgroups.

The node of unaltered dogs younger than 2.5 years were further divided; the split was according to the dog's training experience ($F_{1,2875} = 14.54$, $p < 0.001$). Dogs without any or with one type of training courses (e.g. obedience, agility) had lower calmness score than dogs receiving two or more training types.

Dogs older than 6.9 years and acquired before the age of 12 weeks had the highest mean calmness in the sample (this node consisted 10.2% of the dogs). Dogs younger than 2.5 years old that were neutered had the lowest mean calmness (this node consisted of 13.7% of the sample).

In short, older dogs were calmer than their younger counterparts, and neutering was related to lower calmness score. Earlier acquisition of the dog was reported to enhance its calmness.

3.4.2 Trainability

The regression tree model for predicting the trainability of dogs is illustrated in Figure 1.2. Number of professional training courses the dogs has received (e.g. puppy class, obedience, agility), the age of the dog and purpose of keeping the dog have the most significant effect on the trainability score. The first split was predicated on training experience ($F_{3,10515} = 220.13$, $p < 0.001$).

The group of dogs without professional training experience was further split into two child nodes based on the age of the dog ($F_{1,3707} = 123.88$, $p < 0.001$); older dogs were assessed as less trainable.

Dogs in the one type of training experience group was divided to two terminal nodes based on the purpose of keeping the dog ($F_{1,2463} = 9.10$, $p < 0.01$). Dogs described as the member of the family without any special purpose had lower mean scores on trainability than those dogs that had more specific function in addition (e.g. work, guarding, etc.).

The two types of training experience group, similarly to the untrained dog-group, was split based the age of the dog ($F_{1,2259} = 40.19$, $p < 0.001$). The 2.5-year-old or younger dogs were reported to be more trainable than older dogs with similar types of training experience.

The subgroup of dogs who attended at least three types of professional training courses had the highest mean trainability (this group consisted of 19.8% of the sample). Untrained dogs which were older than 3 years had the lowest mean trainability in the sample (this node consisted of 18.1% of the dogs).

In short, according to the regression tree, the most important factor related to the trainability is the training experience of the dog. Additionally, younger dogs were generally reported to be more trainable than older dogs.

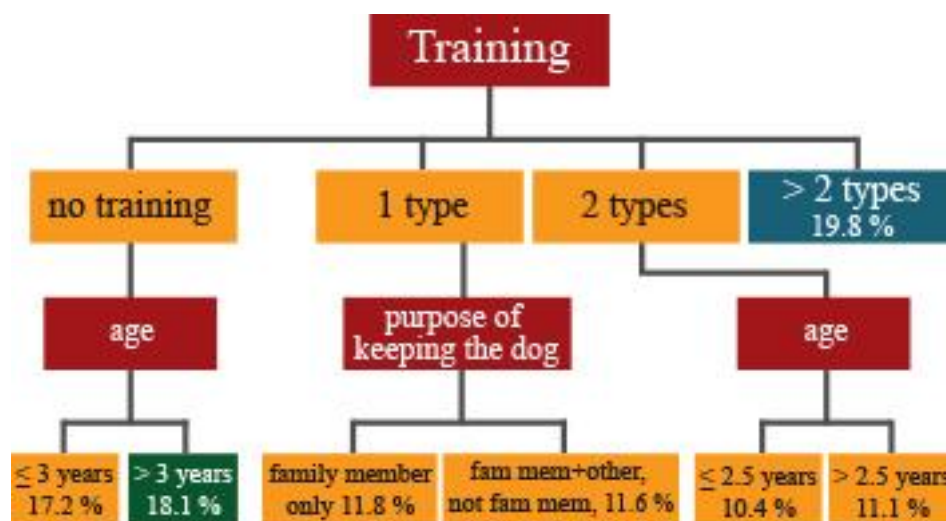


Fig. 1.2 Regression tree model for trainability. Numbers in the end nodes represent the proportion of the sample. Blue background highlights the highest mean, green background the lowest mean

3.4.3 Dog sociability

The regression tree of dog sociability trait can be seen in Figure 1.3.

The dog's age, the time spent together with the owner and the sex of the dog had the most significant effect on the dog sociability trait. The first split on the sample was determined by the age of the dog ($F_{4,10514} = 195.69$, $p < 0.001$); five age groups were formed.

The oldest age group (dogs above 4.8 years) was divided into subgroups by the hours spent together with the owner daily ($F_{1,3527} = 24.06$, $p < 0.001$). More time together with the dog was associated with higher sociability towards other dogs.

Dogs that spent more than 3 hours with the owners were subdivided again by the sex of the dog ($F_{1,2437} = 20.37$, $p < 0.001$). Females were found to be more sociable toward their conspecifics than males.

The youngest group (dogs under or around the one and a half year) had the highest sociability toward other dogs (this node consisted of 20.1% of the dogs). The least sociable dogs were older than 4.8 years and spent less than 3 hours together with the owner (this group consisted of 10.4% of the sample).

In short, older dogs and males were less sociable towards other dogs and time spent together with the dog enhanced its sociability.

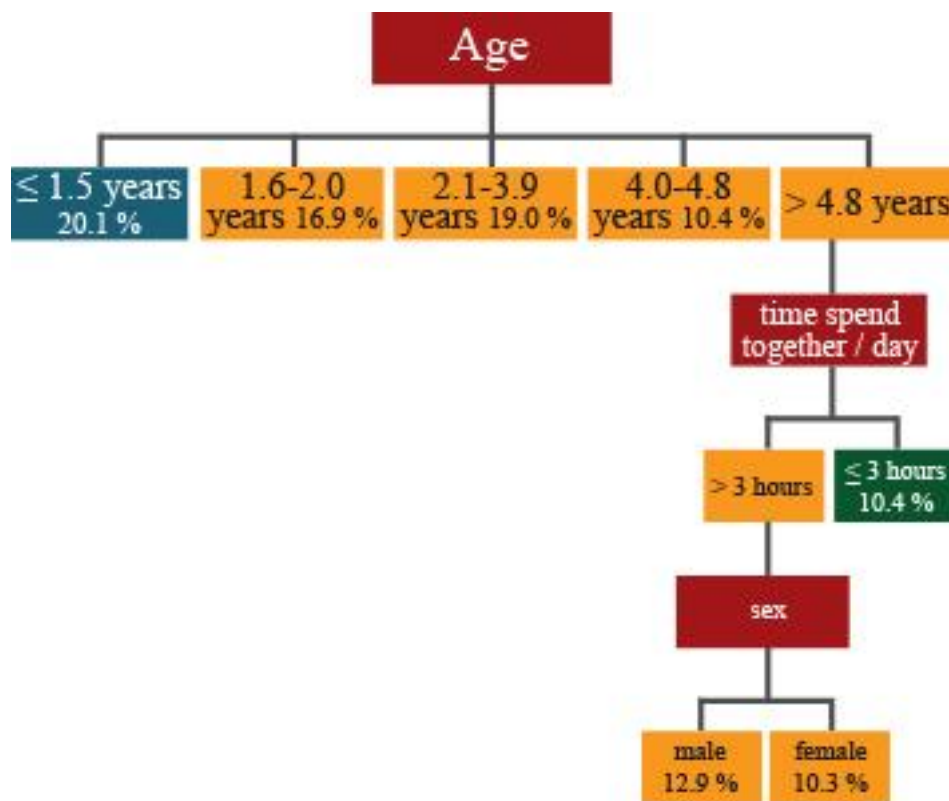


Fig. 1.3 Regression tree model for dog sociability. Numbers in the end nodes represent the proportion of the sample. Blue background highlights the highest mean, green background the lowest mean

3.4.4 Boldness

Figure 1.4 presents the regression tree model of boldness.

The sex of the dog, the age at acquisition, and age of the dog had the most significant effect on the boldness trait. The first split was related to the dogs' sex ($F_{1,10517} = 196.59$, $p < 0.001$). Males were divided into three subgroups ($F_{2,5898} = 28.97$, $p < 0.001$) based on their age at acquisition. Dogs acquired at a younger age received higher boldness score.

Dogs acquired at the age of 2–12 weeks were further subdivided by the dogs' ages ($F_{1,3179} = 39.51$, $p < 0.001$); younger dogs (≥ 2 years) were bolder than older dogs.

Females, similarly to males, were divided by the age at acquisition ($F_{2,4616} = 51.23$, $p < 0.001$). The first node consisted of dogs either bred by the owner or acquired > 1 years of age, the second node consisted of dogs acquired between 2 weeks and 12 months.

This latter node was further subdivided by the dogs' ages ($F_{1,3526} = 34.59$, $p < 0.001$); younger dogs (≥ 2 years) were bolder.

The boldest dogs were males, acquired between 2–12 weeks of age, and were younger than 2 years old (12.3% of the sample). The least bold dogs were females either acquired after the age of 1 year or were bred by the owner (10.4% of the sample).

In short, males were bolder than females and younger dogs were bolder in both sexes. Males were bolder if acquired in younger age, females were less bold if they were either bred by the owner or acquired after the age of their first year.

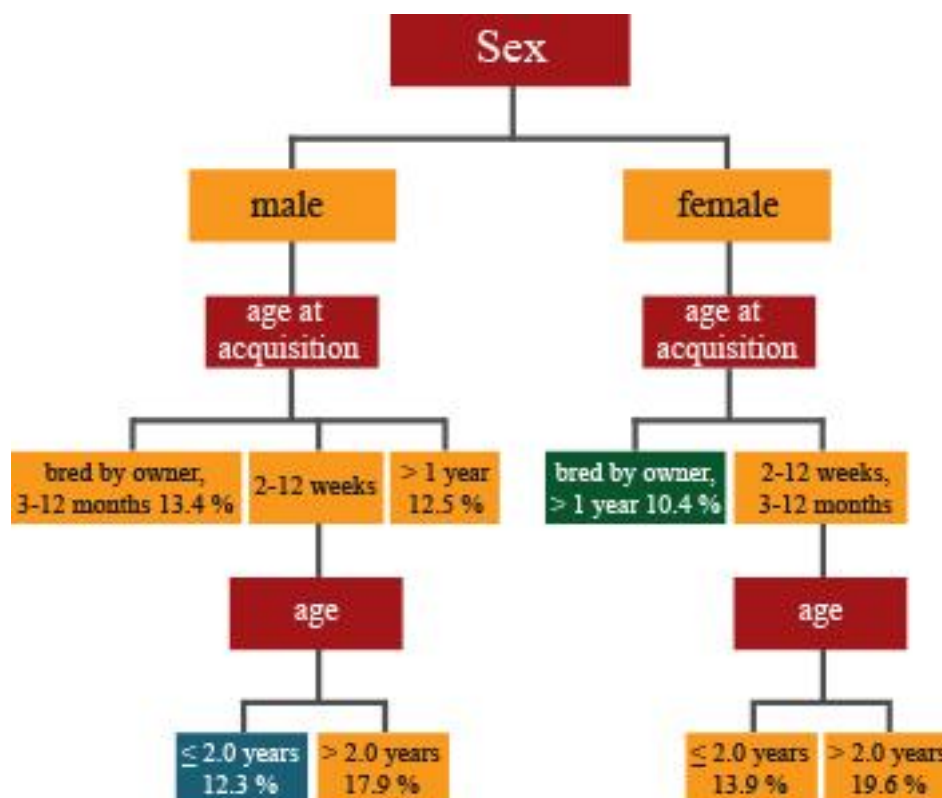


Fig. 1.4 Regression tree model for boldness. Numbers in the end nodes represent the proportion of the sample. Blue background highlights the highest mean, green background the lowest mean

4. Discussion

In this study we analysed the questionnaire responses about more than 10,000 dogs to reveal associations between dog personality traits and demographic, environmental, and dog management variables. We applied regression trees to identify the most relevant factors for each personality trait and to analyse the effect of multi-level interactions between these variables.

We derived four dog personality traits from the questionnaire using principal component analysis and labelled them as calmness, trainability, dog sociability and boldness. These

personality traits showed convincing internal consistency (Cronbach's $\alpha = 0.642\text{--}0.849$), the mean test–retest correlation in our study (0.836) was similar to those reported in previous studies (e.g. Goddard and Beilharz, 1986 in fearfulness: 0.460; Svartberg et al., 2005: mean of the five traits: 0.766; Netto and Planta, 1997 in aggression: 0.770; Jones, 2008: mean of the five traits: 0.753). The mean inter–rater reliability (0.728) also corresponded to the literature (e.g. Gosling et al., 2003: mean of the five traits: 0.620; Vas, 2007: mean of three traits: 0.599; Duffy et al., 2008 in aggression: 0.760).

The calmness trait described the dogs' behaviour in stressful/ambiguous situations. A low score on this trait indicated stressed and anxious behaviour in these situations, while a high score referred to calm and emotionally stable dogs, according to the owner. Dogs that scored low regarding the trainability trait were described by their owners as uninventive and not playful, whereas dogs that scored high on this trait were regarded as intelligent and playful. Dog sociability referred to their behaviour toward conspecifics, with a low score indicating a high tendency for bullying or fighting and inversely high scores related to a low tendency. Finally, boldness was related to fearful and aloof behaviour with a low score corresponding to a high degree of fearfulness/aloofness, and vice versa. The four traits and their converses were described previously by several authors (e.g. Ley et al., 2008) and our four traits also fit into the meta–analytical framework of Jones and Gosling (2005). Their reactivity trait is similar to our calmness, trainability corresponds to the responsiveness to training, dog sociability refers to a specific part of two traits, the sociability and aggression, and our boldness trait is the converse of their fearfulness trait. However, our study did not touch upon the activity and dominance traits in dogs.

We used the regression tree statistical method for investigating the behaviour–environment associations. Regression trees are ideal for analyzing complex numeric and/or categorical data and detecting non–linear relationships in the structure (Breiman et al., 1984). As far as we know, this method has not been used to analyze large data sets in personality research on dogs, despite the fact that the method shows some advantages over other statistical approaches. Although it is not included in this thesis, we also investigated the behaviour \times environment associations using more traditional GLM models which led to similar results (Kubinyi et al., 2009).

The most important factors affecting the personality traits were the age of the dog, the sex and neutering status, the training level and the dog's age at acquisition. Note that the characteristics of dogs in the present study were reported by the owners, and in most

associations it is not possible to determine the cause – effect relationships (except in some cases, where the behaviour cannot affect the demographic characteristics, e.g. gender or age). The age of the dog had been found to influence all the four traits investigated in this study, and this demographic characteristic had the most significant effect on calmness and dog sociability. Older dogs were calmer, less trainable, less social and less bold than younger dogs. This is in harmony with the findings of Bennett and Rohlf (2007) who showed, using questionnaires in a volunteer sample, that the age of the dog was positively associated with unfriendliness and negatively associated with anxious behaviours. In another questionnaire-based study Ley et al. (2009) found that extraversion negatively correlated with age. In contrast with these results, Seksel et al. (1999) did not find any associations with age in a behavioural test battery, while Strandberg et al. (2005) observed higher boldness in older dogs.

Age at acquisition is commonly believed to affect the adult behaviour of the dog, but scientific evidence is rare. Bennett and Rohlf (2007) even called this belief a misconception, as they did not find any associations between age at acquisition and different problematic behaviours. However, according to our results, this variable had a significant effect on calmness and boldness traits: dogs acquired before the age of 12 weeks were described as being calmer, and bolder than dogs acquired later, especially those acquired as adults. This finding could be explained from two different perspectives. On the one hand, owners who acquire a dog before the age of 12 weeks could be more caring and more likely to plan in advance by consulting relevant references on dog behaviour. On the other hand, since the work of Scott and Fuller (1965), the idea that a dog should be adopted before the age of 12 weeks has been widespread in the dog literature. As shown by the authors, dogs can be socialized much easier during the so-called sensitive period between 8 and 12 weeks of age, so that direct positive effects from relatively early interactions cannot be excluded. Importantly, Serpell and Jagoe (1995) reported a relationship between the age at acquisition and problem behaviours. These included increased fear of other dogs and of traffic and was interpreted as the result of the so-called “kennel syndrome” in which young dogs are not exposed early enough to a variety of social and non-social stimuli.

From both theoretical and practical points of view, the effect of sex in dogs on various personality traits could be of great importance. Females were more sociable than males (as expected from Notari and Goodwin, 2007) and males were more bold than females (in boldness, sex of the dog was the most important factor). Similar findings were reported with reference to “nerve stability” based on the behavioural test batteries (Goddard and Beilharz,

1983; Ruefenacht et al., 2002; Wilsson and Sundgren, 1997). Neutered dogs were found to be less calm. Bennett and Rohlf (2007) reported similar findings: neutered dogs were considered to be more nervous than sexually intact dogs. However, we have to emphasize again that the associations do not imply causal relationships. Neutering could well be the consequence of having experienced a behavioural problem, not the reason for showing a particular trait (see also Guy et al., 2001a, 2001b).

One-third of dogs in our sample did not receive any type of professional training courses, similarly to an Australian sample (Kobelt et al., 2003). Dogs without any professional training courses were less calm, and less trainable than trained dogs. In parallel, in a questionnaire survey, both Bennett and Rohlf (2007) and Kobelt et al. (2003) reported that trained dogs were more obedient and training level was found in association with a number of behaviour problems (e.g. Jagoe and Serpell; 1996; Voith et al., 1992). Maybe not surprisingly training level was the most significant predictor of trainability. On a similar vein, dogs kept only as a family member were less trainable than those dogs that had specific functions (e.g. work, guarding). These results could be interpreted in two ways: 1) dogs could become trainable and kept for a specific purpose as a result of participating in different training courses or 2) people may prefer to engage in training activity and use their dogs for specific purposes when the dog is more receptive to these trainings.

Owners who spend more time together with their dogs report to have more sociable individuals. Since more time together generally means that the dog is kept in the house or in a flat rather than in a garden or a kennel, the result suggests that housing conditions probably affect this trait (see Tami et al., 2008 for similar findings).

Despite the virtues of the study (large sample size and multiple personality trait–demographic variables associations), it has its own limitations. First, we have to emphasise again, that the association between the traits and variables reported here do not necessarily represent a causal relationship and even if they do so, the data were not enough to determine the direction of causality. Second, our respondents were interested in reading DOGS magazine and completing a personality questionnaire about their dog, which may biased the sample population. Third, our study was explorative in nature and should be viewed accordingly. The demographic variables may certainly be related to each other in several ways that were not uncovered here. However, we think that the results of our research could serve as hypotheses for future work, which then should be executed under more controlled conditions, including the careful selection of a representative sample and with more focus on direct behavioural measures.

STUDY II.

Personality matching in owner–dog dyads²

1. Introduction

For pet dogs the owner itself can be regarded as a special “environmental factor”. Many demographic characteristics of the owner, like gender, age, or previous experience with dogs were found to be associated with the personality of the dogs (e.g. Bennett and Rohlf, 2007; Ley et al., 2009; Masters and McGreevy, 2008). Moreover, the dog keeping practices (which could also influence the dogs’ behaviour) also depend on the owner. For example, for what purpose the owner keeps the dog, how much time the owner spends with the dog, how much training courses he/she is willing to attend with the dog, or whether the dog is allowed inside the house or not. Importantly, some of these management characteristics may be (partly) influenced by the owner’s personality. For example, active, outgoing owners may prefer more outside activities with the dog (e.g. walking, hiking), or more neurotic owners may be more protective of their dogs and fail to socialize them adequately (as suggested by Podberscek and Serpell, 1997b). As personality affects our interpersonal behaviour (how we interact with others), the owner’s personality may also influence how he/she behaves towards the dog. For example, Kis et al. (2012) found that more neurotic owners give more command to their dogs, while extraverted owners praise more often during a simple obedience task.

There is a growing research interest in the personality characteristics of the owners in the last few years. Studies can be grouped along four main topics: 1) personality differences between owners and non-owners (see Podberscek and Gosling, 2000 for review); 2) personality differences between owners of different breeds or different species (e.g. between ‘dog people’ and ‘cat people’, Gosling et al., 2010); 3) studying the association between the owners’ personality and some behaviour problems of the dogs (e.g. aggression of the dog, Podberscek and Serpell, 1997b); and 4) direct comparisons of the owner personality and dog behaviour (e.g. interpersonal behaviour, Zeigler–Hill and Highfill, 2010).

The fourth topic leads us to an interesting question: is there a personality matching between owners and dogs? With other words: is it true that “*dogs are like their owners*”?

² this chapter is based on: **Turcsán, B.**, Range, F., Virányi, Zs., Miklósi, Á., Kubinyi, E., 2012. Birds of a feather flock together? Perceived personality matching in owner–dog dyads. *Applied Animal Behaviour Science*, 140, 154–160.

Personality similarity and assortative mating have received wide interest in psychological studies. It is assumed that having a similar social partner helps to maintain the relationship by reducing the risk of conflicts and disagreements and validates our beliefs about the world and ourselves (Barelds and Barelds-Dijkstra, 2007; Byrne, 1971; Morry, 2005). A large number of studies on different levels of social relationships (e.g. married couples, friends, college roommates) provided evidences for the “*similarity–attraction hypothesis*” suggesting that the more similar two individuals are, the higher the attraction between them (e.g. Byrne, 1971; Byrne et al., 1967; Kurtz and Sherker, 2003). Evidence for the similarity–attraction hypothesis was found in many psychological aspects, for example personality traits (e.g. Luo and Klohnen, 2005), physical attractiveness (Feingold, 1988), or attitudes (Buunk and Bosman, 1986). Since owners usually regard their dogs as social partners (e.g. Dotson and Hyatt, 2008; McConnell et al., 2011), one could also expect a correspondence between owners’ and dogs’ personality traits. Accordingly, studies on dogs and owners suggest a link between the dogs’ and owners’ personality profile (e.g. O’Farrell, 1995; Podberscek and Serpell, 1997b; Zeigler–Hill and Highfill, 2010), calling for direct comparison between them. Such comparison requires a cross–species approach; overlapping personality traits should be compared between the two species. Gosling and John (1999) suggested that the human Five Factor Model could provide a common language for cross–species personality comparisons (even though the manifestation of these traits could be different in different species).

In this study, we tested for the association between the owners’ and their dogs’ perceived personality using the FFM framework. Unlike previous studies, we also investigated the possible sources of this correspondence. First, as an obvious source, owners may simply attribute similar personality traits to their dogs. To test this, we compared the owners’ personality provided by themselves to the dogs’ personality assessed by a peer person, and also investigated if others found the owner and dog similar (i.e. both partners were assessed by a peer person). Second, the time spent together could affect the similarity; studies on married couples and roommates found some convergence over time (e.g. Anderson et al., 2003). Other studies, however, found no effect of the length of the relationship on the perceived similarity between the partners (e.g. Caspi et al., 1992). We investigated the length of ownership, but, in light of the inconsistent literature in human relationships, we made no specific predictions about effects of it on similarity. Third, we also considered how multiple owner–dog relationships influence personality matching. Owners may share all personality traits with all of their dogs but there are also reasons to expect differences. Dogs may have different social roles in the family, or, in case of the second or third dog, owners may choose a

dog more consciously drawing on their increased experience. Fourth, another unique aspect of this study is repeating the same observation in two neighbouring countries (Austria and Hungary) in which dog keeping practices are somewhat different (Turcsán, unpublished results). Owners from different cultures may prefer different traits, paralleling the effect of culture on human relationships as it was shown in case of married couples (McCrae et al., 2008).

Hypothesis 1 – Based on the similarity–attraction hypothesis in humans, we expected higher similarity between the owners and their own dogs than in randomly paired dog–owner dyads.

Hypothesis 2 – In human studies, perceived similarity (when both partner’s personality is assessed by the same person) is usually higher than actual similarity (when the two assessments are made by different persons) (e.g. Barelds, 2005; Lee et al., 2009a). In line with this, we predicted weaker but significant similarity between the owners and dogs when a peer person assessed the dogs’ personality instead of the owner and when a peer person judged the personality profile of both the owner and the dog.

Hypothesis 3 – Although no previous research investigated similarity in multi–dog households, we expected differences between the perceived similarities of dogs living in the same household. In particular, we hypothesized that secondly acquired dogs would be perceived as more similar to the owner than the firstly acquired dogs because of owners optimizing their choice after gaining experience with their first dog.

Hypothesis 4 – We hypothesized that cultural effects influence the owners’ perceived personality matching between themselves and their dogs, resulting different similarity pattern in the two countries.

2. Method

2.1. Participants

Owners were recruited via email or personally from volunteers of the Clever Dog Lab database in Vienna, Austria and from the Family Dog Project database in Budapest, Hungary. Personality data about N = 670 owners and their N = 853 dogs were collected altogether (N = 205 owners and 271 dogs from Austria and N = 465 owners and N = 582 dogs from Hungary). From this sample we excluded 1) the incomplete questionnaires, 2) all cases when the owner was younger than 18 years old or the dog was younger than 1 year old, 3) all cases when the owner–dog relationship was shorter than 6 months (we judged that 6 months are

enough for the owner to reliably assess its behaviour), 4) all dogs which were the thirdly, fourthly, etc. acquired dog currently living in the household.

The final sample consisted of $N = 237$ dogs ($N = 178$ owners) from Austria and $N = 281$ dogs ($N = 211$ owners) from Hungary. The descriptive statistics of the samples in the two countries are presented in Table 2.1.

2.2. Questionnaires

In the first section of the questionnaire, each owner provided some demographic information about him/herself and their dogs (age, gender, and the dog's age at acquisition). In the second section, the owners filled out the personality questionnaire about their dogs, and in the third section, they assessed their own personality. The participants completed the questionnaires either on the internet or during a visit at one of the laboratories. The owners were told that the purpose of the study is to analyze the dog-owner relationship.

For measuring the human personality, we used the German or Hungarian version of the 44-item Big Five Inventory (BFI) developed by John and Srivastava (1999) (Appendix A). The German version of this questionnaire was created by Beatrice Rammstedt (Rammstedt and John, 2007) and its reliability was already tested (Lang et al., 2001). The Hungarian version was created by Enikő Kubinyi, and we tested its reliability in this study. The questionnaire includes 8 questions related to extraversion (e.g. *"Is full of energy"*); 9 questions for agreeableness (e.g. *"Can be cold and aloof"*); 9 questions for conscientiousness (e.g. *"Tends to be lazy"*); 8 questions for neuroticism (e.g. *"Is emotionally stable, not easily upset"*); and 10 questions for openness (e.g. *"Is curious about many different things"*). All personality traits contained reverse scored items.

The personality of the dog was measured by the 43-item C-BFI (Canine BFI, Appendix B). This questionnaire was developed by Gosling et al. (2003) based on the 44-item BFI, by little modifications in some questions (for the adaptation procedure, see Gosling et al., 2003). The German and Hungarian versions were created by Martin Tiefenthaler and Enikő Kubinyi, respectively, both cases following the adaptation procedure of Gosling et al. (2003).

In both questionnaire, the owners were asked to score themselves and their dogs using a 5-point scale (from disagree strongly to agree strongly). The trait structures and the coding methods were provided for us by Samuel Gosling, the trait scores were calculated by averaging the scores of the variables representing each trait.

2.3 Reliability of the questionnaires

Test–retest reliability of the Hungarian version of the BFI and Canine–BFI were assessed by asking the owners to fill out the questionnaires again. For the BFI, N = 69 owners provided assessment in two different times about themselves, for the Canine–BFI, N = 74 dogs were re–evaluated by the owner.

N = 53 peer ratings were collected assessing the personality of 43 owners; N = 77 peer ratings of the dog personality were provided for 61 dogs. All these peer ratings were analysed when assessing the inter–rater reliability of the questionnaires, but only one peer rating for each owner and for each dog were analysed when investigating the owner’s perception bias for similarity.

2.4 Statistical analyses

To test our *first hypothesis* (owners perceive their dogs similar to themselves), we computed Pearson correlations between the owners and dogs on the whole sample and compared them to the correlation between randomly assigned dog–owner pairs (similarly to the human “pseudo–couple analysis” Kenny et al., 2006) using Fisher’s exact test.

To test our *second hypothesis* (the similarity is not only the owners’ perception) we computed Pearson correlations between the peer–assessed dog personality dimensions and both the self–assessed owner dimensions and the peer–assessed owner dimensions.

For subsequent analyses, we assigned the dogs to three groups, based on the number of dogs in the household and the length of ownership. The length of ownership was computed from the dogs’ age at acquisition and the age at participation.

- 1) Single dogs: only one dog lives in the household
- 2) First dogs: in multi–dog households the dog with the longest relationship with the owner
- 3) Second dogs: in multi–dog households the dog with the second longest relationship with the owner.

The effects of the length of ownership, dog group and the country of residence on the owners’ perception of similarity (*Hypotheses 3 and 4*) were tested using general linear models (GLMs). We used the owner–assessed dog personality trait as dependent variable, the owner personality trait (the same as the dog trait) and the length of ownership as covariates, the dog group (single, first, second dogs) and country of residence (Austria, Hungary) as fixed factors. Interactions between the owner trait and length of ownership, owner trait and the dog group and owner trait and country were added to the model. These interactions aimed to assess whether length of ownership, dog group, or country has a significant effect on the owners’ perceived similarity on a given trait. According to the backward elimination procedure,

variables were removed from the model in the order of their decreasing significance until only significant variables were present (minimal adequate model). The argument in favour of the GLM method is that it tests the three hypotheses at once hereby reducing the *Type I* error. However, we also provided the more traditional zero-order (Pearson) correlations separately in the dog groups in each country, with Bonferroni correction to account for multiple comparisons.

To investigate the internal consistency of the traits derived from the questionnaires we calculated Cronbach's alpha coefficients for each trait.

The test-retest and inter-rater reliability were investigated using Intraclass correlation (one-way random measures). Statistical analyses were conducted with SPSS 17.0.

3. Results

3.1 Descriptive statistics

The descriptive statistics of the sample are presented in Table 2.1.

The mean age of the dog in the sample was 5.2 years (ranging from 1 year to 17 years); the mean length of the owner-dog relationship was 4.7 years. 47.3% of the dogs were males. The owners were mainly female (87.7%), their mean age was 35.4 years.

Table 2.1 Characteristics of the studied owner and dog populations in Austria and Hungary (N = 518)

Owners	Austria			Hungary		
	Total N	Women (%)	Mean age (SD)	Total N	Women (%)	Mean age (SD)
Owners with one dog	119	87.4%	39.6 (12.8)	141	83.7%	33.2 (10.1)
Owners with more dogs	59	89.8%	40.0 (12.9)	70	88.6%	34.2 (11.2)
Dogs	Mean length of			Mean length of		
	Total N	Female (%)	ownership (SD)	Total N	Female (%)	ownership (SD)
Single dogs	119	52.9%	4.1 (2.2)	141	49.6%	3.4 (2.2)
First dogs	59	54.2%	7.5 (3.1)	70	52.9%	7.2 (4.2)
Second dogs	59	57.6%	5.2 (2.9)	70	52.9%	3.2 (2.1)

3.2 Reliability

Reliability measures of the questionnaires are presented in Table 2.2.

The internal consistency of the human personality traits (Cronbach's alpha values) were high (~ 0.7 or above) for all five traits in both countries. The Cronbach's alpha values of the dog traits were also acceptable (~ 0.6 or above) for all but the openness trait of the Hungarian version (0.503).

The same pattern was found regarding the test–retest reliability in Hungary. The Intraclass correlations between the owners’ two assessment of themselves were high (above 0.7) for all five traits. The test–retest reliability of the dog traits were also acceptable (~ 0.6 or above) for all, but the openness trait (0.493).

The latter trait also had low inter–rater reliability; the correlation between the two raters’ judgement was not significant in case of the dog openness (0.185) but, interestingly, the same was found for the human openness trait (0.145). For the other human and dog traits, the inter–rater correlations were at least moderate (> 0.4) and significant.

Table 2.2 Cronbach’s alpha values, test–retest and inter–rater reliability measures (Intraclass correlations) of the questionnaire traits. ** $p < 0.01$, *** $p < 0.001$, n.s. not significant

	Human BFI				
	Extraversion	Agreeableness	Conscientiousness	Neuroticism	Openness
Cronbach’s alpha (Austria) (N = 205)	0.854	0.700	0.805	0.841	0.804
Cronbach’s alpha (Hungary) (N = 440)	0.832	0.790	0.796	0.853	0.797
Test–retest correlation (Hungary) (N = 69)	0.856***	0.845***	0.802***	0.858***	0.780***
Inter–rater correlation (Hungary) (N = 53)	0.475***	0.400**	0.523**	0.466***	0.145 n.s.
	Canine BFI				
	Extraversion	Agreeableness	Conscientiousness	Neuroticism	Openness
Cronbach’s alpha (Austria) (N = 271)	0.713	0.630	0.707	0.852	0.656
Cronbach’s alpha (Hungary) (N = 560)	0.636	0.752	0.703	0.813	0.503
Test–retest correlation (Hungary) (N = 74)	0.644***	0.767***	0.816***	0.711***	0.493***
Inter–rater correlation (Hungary) (N = 77)	0.466***	0.540***	0.470***	0.639***	0.185 n.s.

3.3 Perceived similarity between owners and dogs

Our *first hypothesis* suggested that owners would perceive their dogs as similar to themselves in all the five traits. We first tested similarity on the entire sampled population using Pearson correlation and found significant positive relationships between owners and dogs in all five traits, ranging from $r = 0.252$ (agreeableness) to $r = 0.458$ (neuroticism) (Table 2.3). However, this could be because any given dogs’ personality is similar to any given owners’ personality. To test this, we computed correlations between randomly assigned dog–owner pairs. The correlation between the random pairs were negligible, (ranging from $r = -0.051$

(conscientiousness) to $r = 0.041$ (agreeableness), Table 2.3). The correlations between real dog–owner pairs are significantly higher than those between random created dog–owner pairs in all five traits (Fisher’s exact test, $N = 389$, $z = 4.254 - 9.3475$, $p < 0.001$ for all).

Table 2.3 Pearson correlations of the Big Five dimensions between real owner–dog pairs, between peer–assessed dog personality and self–assessed owner/peer–assessed owner personality and between randomly assigned owner–dog pairs. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Personality dimension	Owner judgement of self and dog (N = 389)	Owner judgment of self, peer judgement of dog (N = 61)	Peer judgement of owner and dog (N = 43)	Random owner–dog pairs (N = 389)
Extraversion	0.312***	0.263*	0.318*	–0.014
Agreeableness	0.252***	0.263*	0.417**	0.041
Conscientiousness	0.282***	0.348**	0.632***	–0.051
Neuroticism	0.458***	0.330**	0.335*	0.019
Openness	0.288***	–0.134	0.175	0.023
Average	0.318	0.214	0.375	0.004

3.4 Personality similarity assessed by peer raters

We tested whether owners simply project their own characteristics on their dogs by comparing the owners’ scores about themselves to the dogs’ scores assessed by a family member. Our *second hypothesis* predicted weaker but significant similarity between the owners and dogs when a peer person assessed the dogs’ personality instead of the owner and when a peer person judged the owner–dog similarity.

In both analyses, the correlations between the dog and owner personality were significant in all, but the openness trait (Table 2.3), and all correlations differed from those between the random dog–owner pairs (Fisher’s exact test, $z = 3.022 - 15.6347$, $p < 0.01$ for all). The lack of association in openness traits could be due to the low reliability of this trait and suggests that the correlation found between the owners and dogs in this trait is only a perception. However, our results support, that the similarity in the remaining four traits may have objective cause.

3.5 The effect of the length of ownership, dog group and country on the perceived similarity

In order to investigate the effect of the length of ownership, dog group and the country of residence on the owners’ perception of similarity, we used the general linear models with the owner–assessed dog trait as dependent variable. The personality of the owners had a significant positive main effect in every GLMs (extraversion $F_{1,511} = 39.350$; agreeableness

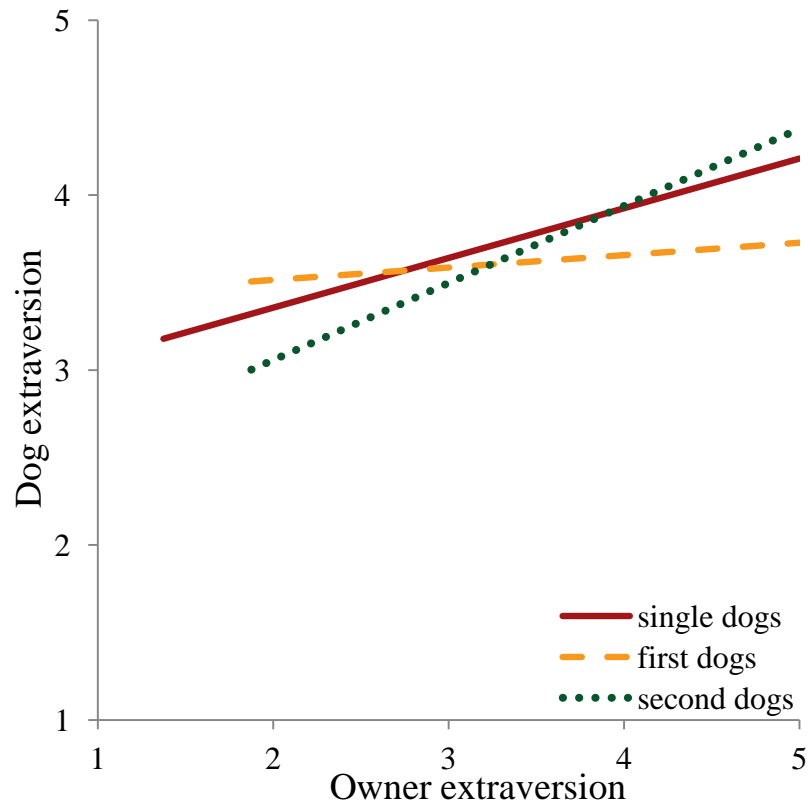
$F_{1,515} = 33.592$; conscientiousness $F_{1,514} = 40.450$; neuroticism $F_{1,512} = 76.262$; openness $F_{1,515} = 40.911$, $p < 0.001$ for all).

We made no predictions regarding the effect of the length of relationship on the similarity, because the human literature was inconsistent on this matter. We found no significant interaction between the length of ownership and owner personality, thus, the length of ownership did not affect (either positively or negatively) the owners' perceived similarity to their dogs. However, the GLM analyses revealed that the length of ownership had a negative main effect on the extraversion, agreeableness, and openness traits (extraversion $F_{1,511} = 20.245$; agreeableness $F_{1,515} = 20.697$; openness $F_{1,515} = 36.756$, $p < 0.001$ for all); the longer the relationship with the dog, the less extraverted, agreeable, and open the dog is, according to the owner. It might be due to the age effect, the length of ownership correlated strongly with the dog age (Pearson, $r = 0.938$, $p < 0.001$).

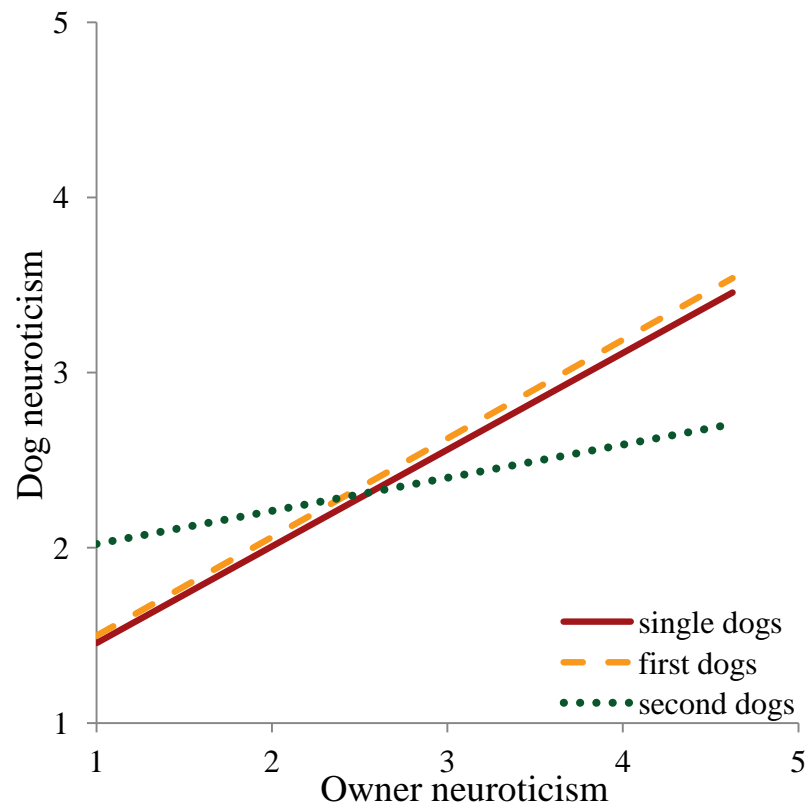
Our *third hypothesis* held that the dog group (single, first, second dog) will affect the similarity, secondly acquired dogs would be perceived as more similar to the owner than the firstly acquired dogs. We found significant interactions between the owner personality trait and dog group only in extraversion and neuroticism traits. There is a positive association between the dogs and owners extraversion in single and second dogs, but this association was missing in the first dogs (owner extraversion \times dog group, $F_{2,511} = 6.949$, $p = 0.001$, Figure 2.1a). In neuroticism, the positive association between the dog and owner traits was restricted to the single and first dogs and was absent in the second dogs group (owner neuroticism \times dog group, $F_{2,509} = 6.065$, $p = 0.002$, Figure 2.1b). Thus, as expected, the dog group (representing number of the dogs in the household and the dogs' acquisition order) affected the owners' perception of similarity, however, the second dogs were not always more similar than first dogs.

In our *fourth hypothesis*, we predicted different similarity pattern in the two countries (Austria and Hungary). However, only one significant interaction was found between the owner personality and the country of residence. In conscientiousness trait, the dog-owners association was present only in case of the Hungarian sample (owner conscientiousness \times country, $F_{1,514} = 4.362$, $p = 0.037$, Figure 2.1c).

a)



b)



c)

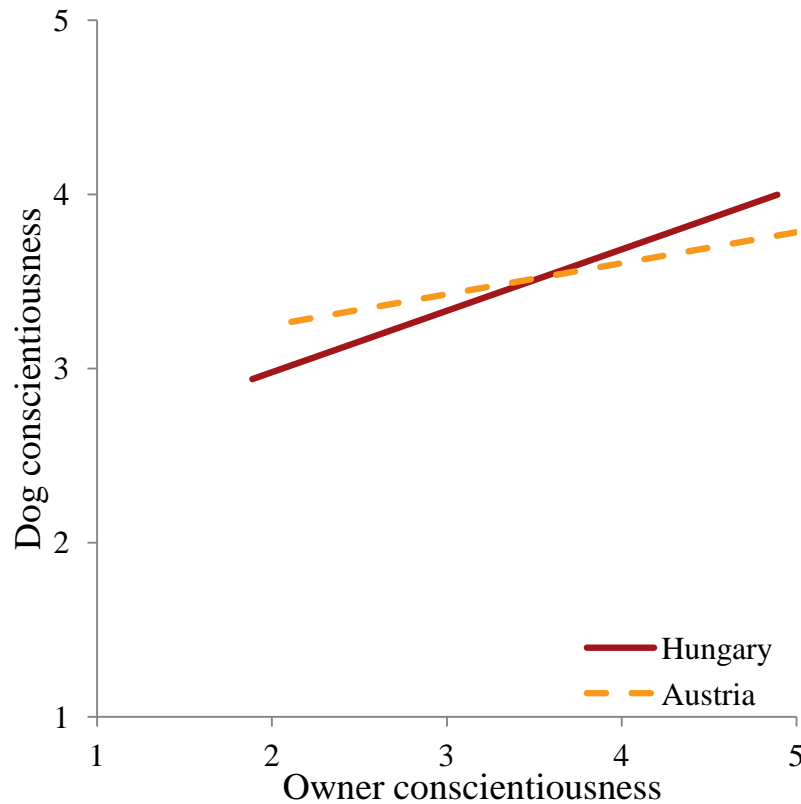


Fig. 2.1 The number of the dogs in the household and the country of residence modify the owner–dog personality associations. (a) In extraversion, the associations are positive in single and second dogs and absent in first dogs; (b) in neuroticism, the associations are positive in single and first dogs and absent in second dogs; and (c) in conscientiousness, the association is positive in Hungary and absent in Austria. For illustrative reasons, only the trend lines are presented, the lines were drawn on the basis of 518 data points

3.6 Correlation pattern separately in each country and dog group

Traditional zero–order (Pearson) correlations were computed for testing the strength of the correlations. Since both the country and dog groups had modifying effects on some of the associations, the correlations were computed separately in the dog groups in each country (Table 2.4).

We found the highest mean correlation in case of single dogs in both countries. In Hungary, second dogs were more similar to the owners than the first dogs, confirming (partly) our *Hypothesis 3* (however, no such pattern was found in the Austrian sample). The results of this correlation analysis revealed further interesting patterns. In the Hungarian sample the first and second dogs' similarity patterns complement each other and form the same similarity pattern as that of single dogs. This phenomenon is also present in the Austrian sample (except the correlation in agreeableness in the first dogs). In general, we found more and higher correlations between the owners and dogs in the Hungarian sample; particularly, no

significant correlations were found in conscientiousness and openness traits in the Austrian sample (confirming our *Hypothesis 4*).

Table 2.4 Bonferroni corrected Pearson correlations between owners and dogs in the Big Five personality dimensions. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Personality dimension	Austria			Hungary		
	single dogs (N = 119)	first dogs (N = 59)	second dogs (N = 59)	single dogs (N = 141)	first dogs (N = 70)	second dogs (N = 70)
Extraversion	0.427***	0.070	0.400**	0.238**	0.040	0.497***
Agreeableness	−0.014	0.324*	0.186	0.415***	0.210	0.293*
Conscientiousness	0.166	0.124	0.200	0.485***	0.267	0.393***
Neuroticism	0.532***	0.587***	−0.072	0.544***	0.294	0.323**
Openness	0.180	0.091	0.291	0.421***	0.224	0.418***
Average	0.258	0.239	0.201	0.421	0.207	0.385

4. Discussion

The present study examined whether dog owners perceive their dogs similar to themselves. Our results indicate that four of the five the personality traits measured in both countries and in both species are adequately reliable. However, the reliability of the openness trait (especially in dogs) is not satisfying suggesting caution when interpreting the results regarding this trait.

We found significant positive associations between owners' and dogs' personality traits, mirroring the personality similarity in human social relationships. While personality similarity have been found in various human–human partnership (reviewed in Montoya et al., 2008; Watson et al., 2004), to our knowledge, our study provides the first evidence of such a similarity in owner–dog relationship confirming that owners treat their dogs similarly to their human social partners.

The correlations between owners' and dogs' personality do not necessarily means a univocal causal relationship. For example, anxious, neurotic owners may make their dog more nervous, e.g. by behaving more inconsistently towards them (O'Farrell, 1995). On the other hand, the dog's different phobias tend to cause greater distress to a more anxious owner (O'Farrell, 1997).

This similarity may originate from several sources. In case of human social relationships, there are three, not mutually exclusive explanation about the origin of the similarity. First, humans may simply attribute similar personality traits to their social partners, either because

of a general tendency to project their self-views onto others, or because the relationship and attraction itself may lead to perceptions of higher similarity ('attraction-similarity hypothesis' e.g. Morry, 2005). This explanation cannot be ruled out completely in our study, however, we also found positive associations between peer and self ratings, and owners and dogs are assessed to be similar also by peer raters (in harmony with the results of Kwan et al., 2008) in four of the five traits. However it seems that the similarity found in openness trait is only a perception of the owners. Human studies also suggest a positive perception-bias in traits related to intelligence (e.g. Lee et al., 2009a), our findings in the openness trait may be analogues to it.

According to the second explanation, the characteristics of people sharing a relationship may become (more) similar over time due to convergent processes (e.g. Acitelli et al., 2001; Anderson et al., 2003). In a similar vein, the characteristics of owner and dog may become (more) similar with longer relationship. This hypothesis was not supported by our results. No interaction between the owner personality and the length of ownership proved to be significant, the association between the owner and dog personality did not change (either positively or negatively) with longer relationships. However, please note that we do not know what happen at the early state of the dog-owner relationship. It is possible that both dogs and owners do change adapting to the other partners' behaviour, however if so, these changes occur very early in the relationship when the dog is only a puppy and its personality is yet to develop. The length of ownership had a negative main effect on the dog extraversion, agreeableness, and openness traits, probably due to the strong correlation between the length of ownership and the dogs' age. These associations are in harmony with the results of previous studies: older dogs were found to be less active and extraverted, less sociable with others, and less trainable (e.g. Bennett and Rohlf, 2007; Kubinyi et al., 2009; Siwak et al., 2002).

The third explanation held, that people may actively seek similar others as social partners (similarity-attraction hypothesis, e.g. Byrne, 1971). Owners may have a tendency to select dogs that are similar to themselves, either at the individual or at the breed level. Although, we lack information about how owners choose a particular dog or why they select a given breed, some studies seem to confirm that the owner's personality characteristics affect their breed-choice. For example, Ragatz et al. (2009) found that the owners of "vicious breeds" scored themselves higher in sensation seeking and primary psychopathy, Egan and MacKenzie (2012) reported that persons with low agreeableness, high neuroticism and high conscientiousness preferred a dog breeds which they perceived as more aggressive. This

hypothesis is the most plausible explanation for our results, however, this hypothesis needs further investigations.

Having a second dog in the household affects the similarity pattern between the owner and dog in neuroticism and extraversion traits. The results of the post hoc correlation analysis revealed an interesting pattern: in multi-dog households, the two dogs' similarity patterns complement each other and form the same similarity pattern as that of single dogs. As far as we know, this is the first study reporting personality differences between dogs housed together. A possible explanation for the results is that owners may need to experience some degree of similarity with the dog. If they are not (or no longer) satisfied with the relationship of their first dog, they acquire a second. Owners may think over their need and choose their second dog more carefully than their first one, leading to differences in the first and second dogs' similarity pattern to the owner. Confirming this, we found the highest mean correlation in the case of single dogs in both countries, and also found that the second dogs were more similar to the owners than the first dogs, however, only in the Hungarian sample. It is possible that Austrian owners may in general choose their dogs more carefully, than Hungarian owners. The differences in the similarity pattern between first and second dogs in the Austrian sample may reflect different functions (e.g. companion, sport-mate), of these dogs in the household.

We also revealed cultural differences in the personality matching between owners and dogs in conscientiousness trait, which is consistent with cultural differences found in human studies about marital compatibility (McCrae et al., 2008). Owners found their dogs similar to themselves in this trait only on the Hungarian sample. Possible cultural differences in factors like dog keeping practices, dogs' general role in the household, shared activities, or factors affecting the dog choice may explain this difference. As another explanation, different people may find different traits attractive, self-dependent owners may value more the independence in a dog, while other owners regard their dogs as social support and desire a dog that shows more affiliative behaviour.

Taken together, personality similarity is an important factor in dog-owner relationship and the owner's need of similarity may play a role in the choice of breed and individual dog. Our study points out an interesting aspect of the human-dog relationship which was not previously explored. The results may also have some practical relevance (e.g. to help the owners to choose the appropriate dogs from the shelter or guide dogs, working dogs to get to suitable owners). Moreover, this similarity between the owner-dog and human-human relationship offers the possibility to use the dog-human relationship for modelling the development and

maintenance of social relationships among humans. However, we acknowledge that our subjects voluntarily participated in the study, and may be more interested in their dogs' behaviour than general dog owners are, therefore some caution might be needed when interpreting these results.

STUDY III.

Breed and breed–group differences in personality traits³

1. Introduction

In the recent years, purebred dogs have emerged as a model for understanding the genetic basis of behaviour regulation and several human diseases (Karlsson and Lindblad-Toh, 2008; Ostrander et al., 2000; Sutter and Ostrander, 2004). Compared to the traditional genetic model animals (e.g. rodents), dogs offer numerous advantages. They share slightly more genes with humans than mice and the shared genes show higher sequence similarity than in case of human and mouse genes (Wayne and Ostrander, 2004). Dogs also demonstrate a complex level of phenotypic similarity with humans, for example, in social cognitive behaviour (Miklósi et al., 2007) or diseases (e.g. narcolepsy, Lin et al., 1999, or obsessive–compulsive disorder, Moon–Fanelli and Dodman, 1998; reviewed in Sutter and Ostrander, 2004). Moreover, contrary to mice and rats, dogs are reared and studied in their natural environment (i.e. in human families), thus the variance in rearing history is mirroring the diversity of human environment.

Dogs also have a unique population structure which features makes them an excellent genetic model species: human artificial selection created a large number of genetically isolated breeds with reduced phenotypic and genetic heterogeneity and long extent of linkage disequilibrium (Parker and Ostrander, 2005; Sutter et al., 2004).

After the general adaptation to the anthropogenic environment), dogs have been selectively bred to perform a variety of practical tasks (e.g. herding sheep, hunting games, guarding livestock, pulling sled) which functions required different morphological and behavioural features. For example, for livestock guarding dogs with a certain body size (~ 40 kg) are required in order to scare off predators, however, any kind of predatory behaviour toward sheep or cows should be eliminated (Coppinger and Schneider, 1995). As a comparison, the optimal weight of sled dogs is 20–25 kg because larger dogs cannot dissipate heat quickly enough during running (Phillips et al., 1981), and the presence of certain predatory motor patterns (e.g. giving eye, stalking, chasing) is important for herding dogs (Coppinger and Schneider, 1995). This early selective breeding, therefore relied both on morphology, and also

³ this chapter is based on: **Turcsán, B.**, Kubinyi, E., Miklósi, Á., 2011. Trainability and boldness traits differ between dog breed clusters based on conventional breed categories and genetic relatedness. *Applied Animal Behaviour Science*, 132, 61–70.

on some sort of stable individual behaviour (including some personality traits), as the individuals should show the required behaviour traits in a reliable manner to be bred to future generations. As a result, certain ‘types of dogs’ emerged which were generally more suitable for a given function, due to their specific morphological and behavioural characteristics.

The modern definition of the term ‘breed’ emerged at the end of the 19th century with the formation of breed clubs and the establishment of the aims and regulations of the modern dog breeding. The set up of the breed–barrier rule (a dog may become a registered member of a breed only when both its dam and sire are registered members of the same breed) has given rise to more than 400 dog breeds recognized today (Clutton–Brock, 1995). These breeds display a great variation in morphology, physiology and behaviour making the dog phenotypically the most diverse mammal species. Most of these breeds are relatively young (100–200 years old; Parker et al., 2004) and were frequently created by cross–breeding members of different breeds. For example, aiming for specific morphological traits (e.g. small size, colour variation) usually involves crossings individuals across functional types of breeds, while crossing individuals from breeds of the same functional types could improve behavioural skills related to this function (e.g. herding) (vonHoldt et al., 2010). This period of time is relatively short on the evolutionary time–scale, even so, due to the small number of founders, the strong inbreeding (breed–barrier), and several bottleneck events in the breeds’ history (e.g. changing popularity, and ‘popular sire’ effect) (Sutter et al., 2008), the dog breeds became partly inbred, genetically isolated units (Saetre et al., 2006). Studies have shown that dogs can be correctly assigned to their respective breeds on the basis of genotype data (Parker et al., 2004; Sundqvist et al., 2006); according to Parker et al. (2004) the genetic variation among breeds accounts for more than 27% of total genetic variation which is higher than among human populations (Rosenberg et al., 2002).

While breeds do not have personality, the personality profile of several representatives grouped together can be used to characterize the typical behaviour of breeds. This approach assumes that individuals differ more between breeds than within a given breed. In the recent years, numerous studies reported differences between breeds, justifying this assumption in various behaviour (personality) traits (e.g. in aggressiveness – Duffy et al., 2008; trainability – Bradshaw and Goodwin, 1999; playfulness – Svartberg, 2006; or sociability – Seksel et al., 1999). These behavioural comparisons of dog breeds are diverse in their scopes: they may determine the suitability of breeds for a given work (Rooney and Bradshaw, 2004; Wilsson and Sundgren, 1997), rank breeds for various behavioural traits (Hart and Miller, 1985; Notari and Goodwin, 2007; Takeuchi and Mori, 2006) or compare various groups of dog breeds (Ley

et al., 2009; Starling et al., 2013; Svartberg, 2006). The breed-related differences found in these studies can be attributed both to environmental factors (e.g. systematic differences in the dog keeping practices) and to genetic differences. The genetic differences between breeds could be due to the selective breeding on morphology and function during the early formation of different functional types of dogs and/or due to the genetic constraints resulted from later cross-breeding events during the formation of the given breed.

Nevertheless, based on the high genetic homogeneity within breeds and the genetic background of some behaviour traits (see example later in *Study IV, 1.*) we can assume that some breed-typical behaviours are (at least partly) genetically determined. Analysing the behaviour differences among breeds could indirectly reflect the genetic background of the investigated behaviour traits. That is, traits with stronger genetic influence (higher heritability) should differ more between breeds than traits with stronger environmental influence. However, not all traits are necessary 'typical' for all breeds, some traits could be important only for some breeds, and not for others. As far as we know, no study yet investigated the within-breed individual variability directly.

Our aims in the current, basically explorative study were 1) to investigate breed-related differences and intra-breed variability in four personality traits, 2) to characterize breeds based on their typical behaviour and investigate their behavioural similarity/differences, and 3) to investigate the effect of two potential factors causing these differences, the earlier function and morphology of the breeds (reflecting to the early selective breeding) and the genetic relatedness between breeds (reflecting to the later cross-breeding events).

2. Method

2.1 Subject

The analyses of the present study are based on a subset of the database described earlier in *Study I (3.1)*. From this database of 14,004 individuals we first extracted all adult (> 1 year-old) purebred dogs, then all the breeds with at least 10 representatives. Altogether, 5733 dogs from 98 breeds were analysed. The dogs were on average 4.0 ± 3.0 years old, and 57.6% of them were males. Thirteen breeds were represented by at least 100 individuals, and the most frequent breed was the Labrador Retriever with 517 individuals.

2.2 Procedure

The questionnaire used in this study was also presented in *Study I (Table 1.1b)*. In short: it consisted of 24 items in which owners were asked to score their dogs using a 3–point scale. Principal component analysis revealed that 17 items belonged to four components, labelled as calmness, trainability, dog sociability and boldness. The calmness trait described the dogs' behaviour in stressful/ambiguous situations; a high score on this trait indicated calm and emotionally stable behaviour in these situations. Dogs that scored high regarding the trainability trait were described by their owners as inventive, intelligent and playful. Dog sociability referred to their behaviour toward conspecifics, with a high score indicating a low tendency for bullying or fighting with other dogs. Boldness was related to fearless behaviour with a high score corresponding to a low tendency to show fearfulness, aloofness. The stability of the PCA, the internal consistency of these traits as well as the test–retest and inter–rater reliability of the questionnaire were assessed earlier (*Study I, 3.3*).

In the present study, we calculated the scores for each individual in each trait by averaging the scores from the variables representing that trait. The breed scores for the four traits were calculated by averaging the scores of the individuals belonging to that breed (e.g. Svartberg, 2006). We assessed the individual's deviation from the breed score by calculating the squared difference of each individual's trait score from its breed's mean. To assess the intra–breed variability we calculated the standard deviation in the four traits for each breed.

2.3 Breed groups

For our third aim (to investigate the effect of the earlier function/morphology and the genetic relatedness of breeds on the behaviour) we formed several breed–groups.

As reliable information about the history and practical usage of most of the breeds are scarce (if any), to investigate the effect of the earlier function we used the breed groups of the American Kennel Club (AKC, www.akc.org). Their seven groups were created based on morphological similarity and anecdotal information about the earlier function of the breeds (Table 3.2). Eight breeds which are not recognized by the AKC (Batavian Mountain Hound, German Bracke, German Hunting Terrier, Hovawart, Kromfohrlander, Landseer, Spanish Greyhound, White Swiss Shepherd Dog), were assigned to whichever AKC breed group most closely matched their classification by the Federation Cynologique Internationale (FCI, www.fci.be).

To analyse the effect of the breeds' genetic relatedness in the behaviour traits, we categorised the breeds into five genetic clusters according to Parker et al. (2007) (Table 3.3). Their clusters were created from 132 dog breeds based on similarity of 96 microsatellite markers in

the DNA sequence (Parker et al., 2007). Twenty-eight of our breeds were not investigated in Parker et al.'s study therefore omitted from this analysis.

2.4 Statistical analyses

1) Two Multivariate General Linear models (MANCOVA) were run, one to compare the trait scores and one to compare the intra-breed variability between the breeds. The effect sizes were estimated by calculating partial η^2 . Partial η^2 corresponds to the ratio of the variation accounted for by an individual independent variable (effect) to the sum of the variation accounted for by the independent variable and the variation unaccounted for by the whole model (effect + error).

2) To investigate the breeds' behavioural similarity, a cluster analysis was performed using the hierarchical agglomerative method. Hierarchical cluster analysis is an exploratory method aiming to identify relatively homogeneous groups of cases based on selected characteristics (in our case, groups of breeds based on the four behaviour traits). Distances between breeds were calculated from all four traits using the squared Euclidean distance method. The breeds were clustered based on the between-groups average linkage method; with this method, a given breed's behaviour has to be within a certain level of similarity to the cluster's average to be included in that cluster (Aldenderfer and Blashfield, 1984).

3) To compare the behaviour between the AKC breed groups and the genetic breed clusters, we used MANCOVA with Tukey post-hoc tests. SPSS 21.0 was used for the analyses.

3. Results

3.1 Breed differences in behavioural traits

There were significant differences between breeds in all four traits (MANCOVA, calmness: $F_{97,5653} = 4.806$; trainability: $F_{97,5653} = 7.254$; dog sociability: $F_{97,5653} = 7.644$; boldness: $F_{97,5653} = 4.774$, $p < 0.001$ for all). Based on the estimated effect sizes, the strongest breed differences were found in trainability and dog sociability (partial $\eta^2 = 0.111$ and 0.116 , respectively), the lowest in calmness and boldness (partial $\eta^2 = 0.075$ and 0.076 , respectively). To provide a general description about each breed's typical behaviour and within-breed individual variability, we ranked the breeds on the basis of these traits and on the basis of their standard deviation in each trait (Appendix C). As the number of individuals of a given breed could influence both the mean and the standard deviation of the traits, we replicated the ranking

procedure on a randomly chosen sample of 10 individuals/ breed. The ranks calculated on this random sample correlated well with those on the whole sample (Spearman correlation, $N = 98$, trait rank correlations ranging from $\rho = 0.786 - 0.866$; SD rank correlations ranging from $\rho = 0.619 - 0.769$, $p < 0.001$ for all) supporting that the different breed frequencies in this study only minimally influenced the results.

The mean intra-breed variability (SD) of each trait: calmness: 0.556; trainability: 0.392; dog sociability: 0.500; boldness: 0.527. It seems the highest intra-breed differences are in calmness, the lowest in trainability.

However, breeds also differed in the intra-breed variability of three of the traits (MANCOVA, trainability: $F_{97,5653} = 2.163$, partial $\eta^2 = 0.036$; dog sociability: $F_{97,5653} = 1.957$, partial $\eta^2 = 0.030$; boldness: $F_{97,5653} = 2.049$, partial $\eta^2 = 0.036$, $p < 0.001$ for all). No breed difference in the intra-breed variability was found in calmness ($p = 0.133$, partial $\eta^2 = 0.019$). It seems the highest breed differences in the intra-breed variability are in trainability and boldness, but the breeds are rather homogenous regarding calmness.

3.2 Behavioural breed clusters

Breeds were also clustered on the basis of their behaviour using hierarchical cluster analysis. Six breeds with extreme trait scores split off from the other breeds (see Appendix D). The first pair consisted of the Newfoundland and the Landseer, known to be strongly related (the Kennel Club in the UK classify them as coat colour varieties of a single breed). These breeds received extreme high scores in calmness, dog sociability and boldness. The next pair split off comprised of the Akita and the German Bracke, scored extremely low in dog sociability. Finally, the German Pincher and the Spanish Greyhound split off because of their extreme low calmness score.

The remaining 92 breeds were divided into six clusters according to the dendrogram, with 2–32 breeds in each cluster (Table 3.1). The clusters differed from each other in all the four traits (MANCOVA, calmness: $F_{5,86} = 17.097$, partial $\eta^2 = 0.498$; trainability: $F_{5,86} = 24.025$, partial $\eta^2 = 0.583$; dog sociability: $F_{5,86} = 18.222$, partial $\eta^2 = 0.514$; boldness: $F_{5,86} = 33.037$, partial $\eta^2 = 0.658$, $p < 0.001$ for all). These breed clusters were characterized as low, medium and high on each trait, based on the post-hoc differences between them. Groups which were significantly higher (or lower) on a trait than at least three other groups were categorized as high (or low) on that trait.

Table 3.1 Clusters of breeds created on the basis of hierarchical cluster analysis on calmness, trainability, dog sociability, and boldness traits. The numbers in front of the breeds represent the AKC breed groups and genetic clusters, respectively

Breed pairs split off because of extreme scores					
extreme high scores in calmness, dog sociability and boldness:					
3;_	Landseer	3;2	Newfoundland		
extremely low score in dog sociability:					
3;1	Akita	2;_	German Bracke		
extreme low score in calmness:					
3;_	German Pinscher	2;_	Spanish Greyhound		
Breed clusters					
Cluster 1 high calmness, medium trainability, high dog sociability, medium boldness					
4;2	Airedale Terrier	3;5	Greater Swiss Mountain Dog	3;5	Saint Bernard
1;4	American Cocker Spaniel	5;.	Havanese	7;3	Shetland Sheepdog
2;4	Beagle	1;4	Irish Setter	5;4	Shih Tzu
7;3	Bearded Collie	1;2	Labrador Retriever	3;1	Siberian Husky
3;5	Bernese Mountain Dog	3;5	Leonberger	1;.	Small Munsterlander
6;2	Bulldog	4;4	Miniature Schnauzer	4;2	Soft Coated Wheaten Terrier
5;4	Cavalier King Charles Spaniel	7;3	Old English Sheepdog	4;2	Staffordshire Bull Terrier
6;2	French Bulldog	5;4	Pekingese	2;3	Whippet
1;4	Golden Retriever	1;4	Pointer		
1;4	Gordon Setter	5;4	Pug		
Cluster 2 medium calmness, high trainability, low dog sociability, high boldness					
4;2	American Staffordshire Terrier	1;5	English Cocker Spaniel	4;.	Parson Russell Terrier
7;3	Australian Shepherd	7;.	Entlebucher Mountain Dog	6;5	Poodle
2;.	Batavian Mountain Hound	4;.	German Hunting Terrier	3;5	Rottweiler
7;3	Belgian Malinois	7;5	German Shepherd Dog	3;4	Standard Schnauzer
7;3	Border Collie	1;.	German Wirehaired Pointer	6;1	Tibetan Terrier
4;2	Border Terrier	3;4	Giant Schnauzer	1;4	Vizsla
3;2	Boxer	3;3	Great Dane	4;2	Welsh Terrier
4;4	Cairn Terrier	3;.	Hovawart	4;4	West Highland White Terrier
2;4	Dachshund	4;2	Irish Terrier	2;.	Wirehaired Dachshund
6;4	Dalmatian	4;4	Jack Russell Terrier	6;4	Wolfspitz
3;4	Doberman Pinscher	5;5	Miniature Pinscher		
Cluster 3 medium calmness, high trainability, high dog sociability, high boldness					
1;4	Flat-Coated Retriever	1;4	German Shorthaired Pointer		
Cluster 4 low calmness, medium trainability, medium dog sociability, low boldness					
7;.	Appenzeller Sennenhund	5;.	Kromfohrlander	2;5	Rhodesian Ridgeback
7;.	Beauceron	2;.	Miniature Dachshund	6;1	Shiba Inu
7;.	Briard	5;4	Miniature Poodle	1;4	Weimaraner
7;3	Collie	7;.	Polish Lowland Sheepdog	7;.	White Swiss Shepherd Dog
2;4	Ibizan Hound	7;.	Pyrenean Shepherd		
Cluster 5 low calmness, low trainability, low dog sociability, medium boldness					
1;4	Brittany	6;.	German Spitz	5;.	Yorkshire Terrier
4;.	Bull Terrier	5;5	Maltese		
5;4	Chihuahua	3;2	Perro de Presa Canario		
Cluster 6 high calmness, low trainability, medium dog sociability, low boldness					
3;1	Alaskan Malamute	6;.	Coton de Tulear	6;.	Eurasier
3;.	Anatolian Shepherd Dog	3;.	Dogue de Bordeaux	2;3	Irish Wolfhound
6;1	Chinese Shar-Pei	1;4	English Setter	6;1	Lhasa Apso

3.3 Differences among the AKC breed groups

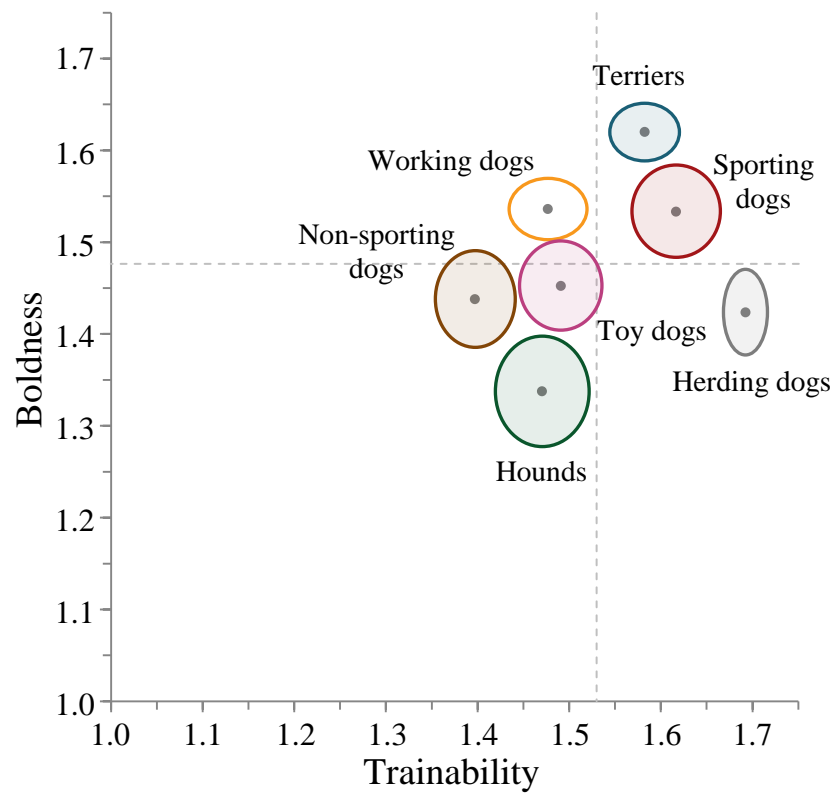
The 98 breeds present in this study were classified into seven AKC groups (Table 3.2). Following the description of the groups provided by the AKC (www.akc.org), the *Sporting dogs* group used mostly for cooperative hunting, includes pointers, retrievers, setters and spaniels. Breeds from the *Hounds* group were used for independent hunting, includes scenthounds, greyhounds and dachshunds. The breeds in the *Working dogs* group were bred to perform such jobs as guarding livestock or pulling sleds. *Terriers* are middle or small sized breeds, used for independent hunting. *Toy dogs* group includes small sized breeds with the main function: companionship. Breeds in *Herding dogs* group are middle or large sized and were used for control the movement of other animals. The *Non-sporting dogs* (or Other) is a diverse group in terms of size and utility, as this group also includes the breeds with undetermined earlier function.

Table 3.2 Breed distribution in the studied sample according to the AKC categorization

AKC group name	N of breeds	N of individuals
Sporting dogs	15	1197
Hounds	11	528
Working dogs	20	1025
Terriers	14	808
Toy dogs	11	561
Herding dogs	15	1122
Non-sporting dogs	12	492
All groups	98	5733

Significant differences in the trainability and boldness scores were found between these groups (MANCOVA, trainability: $F_{6,91} = 5.767$, partial $\eta^2 = 0.275$, $p < 0.001$; boldness: $F_{6,91} = 3.975$, partial $\eta^2 = 0.208$, $p = 0.001$) (Figure 3.1a). The differences between the groups regarding calmness and dog sociability traits were not significant (calmness: $F_{6,91} = 1.850$, partial $\eta^2 = 0.109$, $p = 0.098$; dog sociability: $F_{6,91} = 1.900$, partial $\eta^2 = 0.111$, $p = 0.089$) (Figure 3.1b). According to the post-hoc tests, Herding dogs were reported by their owner to be more trainable than Hounds ($p < 0.05$), Working dogs ($p < 0.01$), Toy dogs ($p < 0.05$) and Non-sporting dogs ($p < 0.001$). Sporting dogs were also more trainable than Non-sporting dogs ($p < 0.01$). Terriers scored higher on boldness than Hounds ($p < 0.01$) and Herding dogs ($p < 0.05$); Working dogs were also bolder than Hounds ($p < 0.05$).

a)



b)

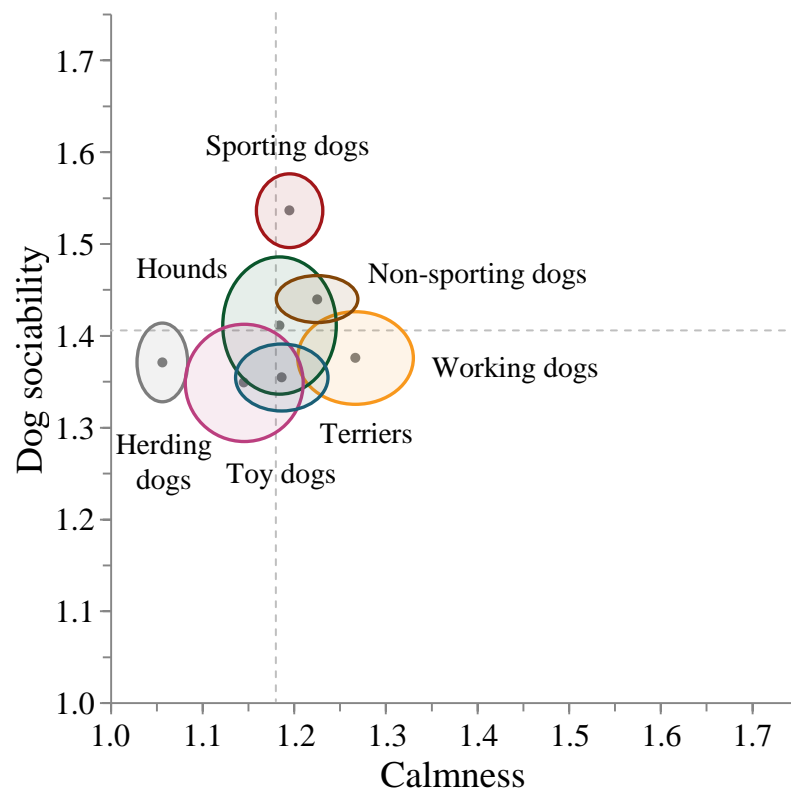


Fig. 3.1 Behaviour profiles of the AKC breed groups in a) trainability and boldness and b) calmness and dog sociability traits. Data points are group averages, the diameters of the ellipses represent the SE of trainability/calmness, the heights the SE of boldness/dog sociability. Dashed lines represent the population means

3.4 Differences among the genetic breed clusters

70 breeds from the 98 present in this study were classified into five genetic breed clusters according to the study of Parker et al. (2007) (Table 3.3). A subset of breeds with the closest genetic relationship to the wolf (used as outgroup) has split off first from the rest of the breeds with modern European origins. This cluster (labelled as ‘Ancient breeds’) contained breeds with ancient Asian or African origin, mainly primitive type dogs. The modern European breeds were later divided into four clusters.

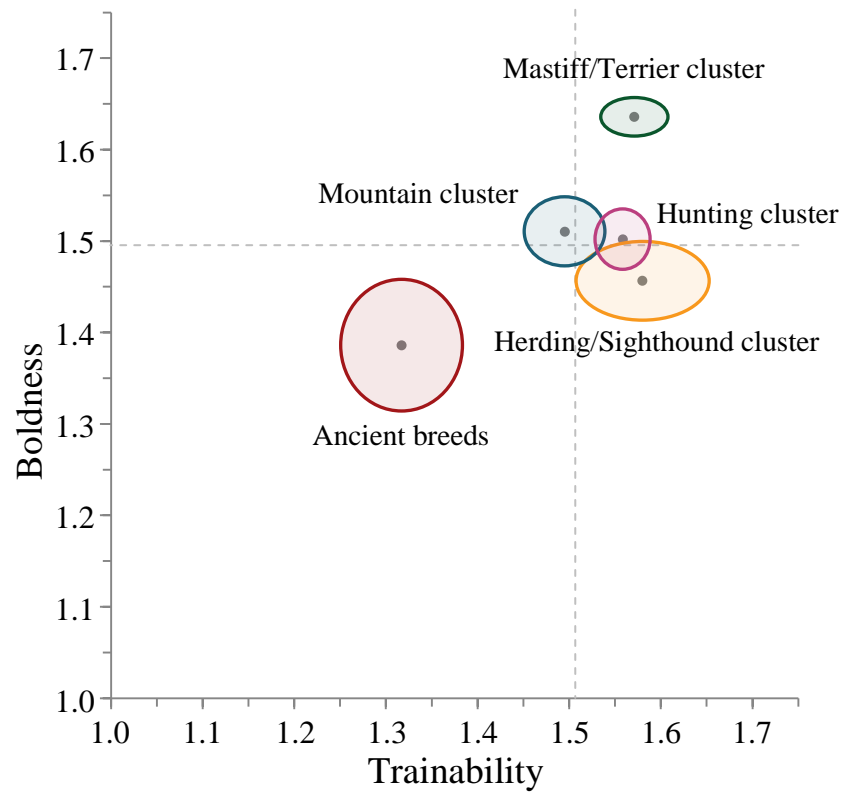
Table 3.3 Breed distribution in the studied sample according to the genetic relatedness (Parker et al., 2007)

Genetic cluster name	N of breeds	N of individuals
Ancient breeds	7	192
Mastiff/Terrier cluster	13	1019
Herding/Sighthound cluster	10	674
Mountain cluster	11	958
Hunting cluster	29	1974
All groups	98	5733

These five clusters differed also in trainability and boldness (MANCOVA, trainability: $F_{4,65} = 3.703$, partial $\eta^2 = 0.186$, $p = 0.009$; boldness: $F_{4,65} = 3.831$, partial $\eta^2 = 0.191$, $p = 0.007$) (Figure 3.2a). No significant differences in calmness and dog sociability traits were found (calmness: $F_{4,65} = 2.113$, partial $\eta^2 = 0.115$, $p = 0.089$; dog sociability: $F_{4,65} = 1.048$, partial $\eta^2 = 0.061$, $p = 0.390$) (Figure 3.2b).

According to the post-hoc tests, the cluster of Ancient breeds was less trainable than the Mastiff/Terrier cluster ($p < 0.05$), the Herding/Sighthound cluster ($p < 0.05$), and the Hunting cluster ($p < 0.01$). The Mastiff/Terrier cluster was bolder than the Herding/Sighthound cluster, the Ancient breeds, and the Hunting cluster ($p < 0.05$ for all).

a)



b)

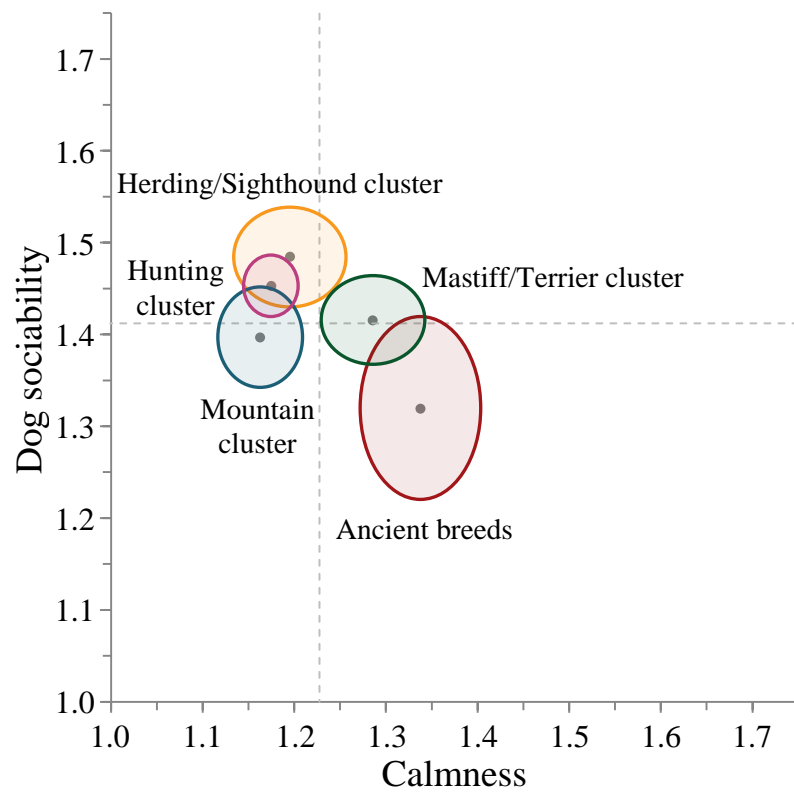


Fig. 3.2 Behaviour profiles of the genetic breed clusters in a) trainability and boldness and b) calmness and dog sociability traits. Data points are group averages, the diameters of the ellipses represent the SE of trainability/calmness, the heights the SE of boldness/dog sociability. Dashed lines represent the population means

4. Discussion

The main focus of this study was directed to the typical behaviour and behavioural differences among dog breeds. Our first aim was to investigate breed-related differences and intra-breed variability in four personality traits (calmness, trainability, dog sociability and boldness).

In the present study, more than 5500 owners of 98 dog breeds have reported considerable differences between breeds in these traits. The strongest inter-breed differences were observed in dog sociability and trainability. We derived the breeds' 'typical' behaviour by averaging the scores of individual dogs within a given breed based on the assumption that these behavioural traits might distinguish not only among individual dogs, but could be also typical for larger population of dogs representing breeds. However, not all traits were characteristic for all breeds; there were large differences between the traits in their intra-breed variance. The highest mean intra-breed variance was found in calmness, the lowest in trainability. Moreover, the intra-breed variability also differed between breeds, that is, breeds differed regarding which traits can be considered as 'typical' for them; the lowest differences between breeds was found in calmness and the highest in trainability. We characterized our four traits relative to each other based on these results.

In calmness we found the lowest inter-breed difference and relatively high intra-breed variability. Breeds were rather homogenous regarding the intra-breed variability. Therefore, this trait seems to be the less likely breed-typical, relative to the other three traits; individual dogs' calm behaviour may more likely to be affected by environmental factors. It was also supported by the results of the breed-group comparisons, no difference in calmness was found between the AKC groups or genetic clusters.

In trainability we found relatively high inter-breed difference and the lowest intra-breed variability. Breeds also differed regarding their intra-breed variability. Together, trainability was the most breed-typical from our traits. AKC breed groups and genetic breed clusters also differed in this trait. However, the review of Ruefenacht et al. (2002) suggests that traits related to working performance or trainability showed a rather low heritability (0.01–0.16). Breed-specific differences in the environmental factors might cause such breed-differences. For example, owners of certain breeds may be more likely to attend professional training courses.

In dog sociability, we found the highest inter-breed differences and medium intra-breed variance. Breeds differed in the intra-breed variability, but also on medium level (compared to the other traits). This trait seems to be breed-typical, however no differences between breed groups were found in this trait. Therefore it seems, that aside from the breeds' general tendency to be sociable towards their conspecifics, environmental factors like the early socialization with other dogs, neutering, or keeping more dogs in the household could affect the individuals' behaviour.

In boldness, we found the lowest inter-breed differences, and relatively high intra-breed variability which suggest that this trait is rather not typical for breeds (compared to trainability or dog sociability). However, we also found the highest breed difference in the intra-breed variability in boldness, suggesting that a small number of breeds are homogenous in this trait. This is in harmony with the results regarding the breed group comparisons, where the differences in this trait were only due to one group, the terriers high score in boldness.

Our second aim was to characterize the breeds based on their typical behaviour and investigate their behavioural similarity/differences. Breeds were ranked on the bases of these four traits to describe their behavioural profiles. If breed-typical behaviour is merely an artificial concept and individuals are more different within breeds than between, than some would expect that popular breeds could have representatives from both ends of the ranks resulting an average trait value. However, two of the five most popular breeds, the Beagle and Labrador Retriever scored higher than the mean \pm SD on dog sociability, while another two (the German Shepherd Dog and Jack Russell Terrier) obtained lower-than-mean scores. Jack Russell Terriers and Labrador Retrievers also scored higher than the population average on boldness. The behavioural profiles of the breeds also showed some correspondence with other studies. For example, the breeds' profile regarding dog sociability obtained in our study was similar to those in dog-directed aggression described in Duffy et al. (2008).

To investigate the breeds' behavioural relationship we also provided a behavioural clustering. Although we divided the breeds into six clusters on the basis of the dendrogram, we should note that our clustering was only to characterize the main parts of the dendrogram. These six clusters could be also divided on the basis of a higher level of similarity. These behavioural clusters correspond neither to the breed groups of the kennel clubs, nor to the genetic breed clusters of Parker et al. (2007). However, some of the breed-pairs clustered together corresponded well to their genetic and functional similarity. For example, pairs like the Border Collie and the Australian Shepherd, the Newfoundland and the Landseer, or the Shorthaired and Wirehaired Dachshund had a highly similar behavioural profile and clustered

together. In contrast, some breed-pairs which are genetically closely related and share similar earlier function, like the Shetland Sheepdog and the Collie (Neff et al., 2004), the English and American Cocker Spaniel or the Alaskan Malamute and the Siberian Husky clustered far from each other in their behavioural profiles.

We found some correspondence with the behavioural breed clusters of other studies. For example nine breeds were present in our sample from the Cluster 1 of Svartberg (2006) and eight of them also clustered together in our sample. However, most of these correspondences are usually breed-pairs clustered together in several studies, like the German Shepherd Dog and the Dobermann (Bradshaw and Goodwin, 1999; Notari and Goodwin, 2007; Takeuchi and Mori, 2006). Differences between the studies are most likely due to the different behavioural traits used for the clustering the breeds.

Our third aim was to investigate the possible effects of the dogs' earlier function/morphology and their genetic relatedness on these traits. To our knowledge the present analysis was the first to investigate the effect of genetically supported grouping on the behavioural traits of dogs. Our results suggest that two of our traits, the trainability and the boldness differ both among the AKC groups and among genetic breed clusters.

Trainability: Herding dogs and Sporting dogs were the most trainable, Non-sporting dogs were the least trainable group according to the AKC categorization. Regarding the genetic clusters, the Herding/Sighthound cluster and Hunting cluster were the most trainable, while the Ancient breeds cluster was the least. These results point in the same direction, especially because the Non-sporting dogs AKC group is dominated by breeds with ancient Asian origin (corresponding partly to the Ancient breeds genetic cluster). Similar behaviour differences were previously shown in several surveys. Both Seksel et al. (1999) and Ley et al. (2009) have found that the group of Pointing dogs (here classified as Sporting dogs) and Herding dogs are highly trainable. Accordingly, Serpell and Hsu (2005) constructed a rank order among different breeds, and found that the most trainable breeds are either the representatives of Herding or Pointing dogs. The authors explained their results on the basis of the cooperative or independent type of the work the breeds were originally bred for. Both the Herding and Sporting dogs groups contain breeds originally used for cooperative tasks, with continuous visual contact of their human partner. These breeds may have a higher tendency to follow the communicative gestures of their owner, even when they are not kept for their original purpose anymore. For example, Gácsi et al. (2009) found that breeds working under close human guidance utilise better the human pointing than breeds working independently, out of humans' view.

Boldness: Terriers scored the highest and Hounds and Herding dogs the lowest on boldness, according to the AKC categorization. Similarly, the Mastiff/Terrier genetic cluster was bolder than the Herding/Sighthound cluster, the cluster of Ancient breeds, and the Hunting cluster according to the genetic categorization. This is in harmony with the previous findings that terriers are described as typically energetic, excitable and reactive dogs (Hart, 1995; Ley et al., 2009; Scott and Fuller, 1965). Although terriers are predominantly small in size, their earlier function of hunting alone both over and under the ground (for preys like rats, fox or even badger) may have required some measure of boldness, which trait seems to be still characteristic for them.

The differences found between the AKC groups and genetic clusters often parallel each other. It is not surprising since the genetic relatedness is often associated with morphological and functional similarity and shared geographic origin (Parker et al., 2004; vonHoldt et al., 2010). However, the genetic relationship between the breeds resulted sometimes surprising joint clusters regarding the function of the breeds. For example, the high trainability of the Herding/Sighthound genetic cluster could be only due to the Herding “part” of this cluster. While Herding dogs were the most trainable AKC group, Hounds scores rather low on this trait. On the other hand, the Mastiff/Terrier genetic cluster was the boldest, which corresponds well to the AKC comparison where Terriers were the boldest and Working dogs (representing the Mastiff–part) the second boldest group.

Taken together we found large differences among dog breeds in four behavioural traits. Our results showed that trainability could be in general considered typical for a large number of breeds, while calmness is more likely to differ between individuals rather than between breeds. However, the description of the typical behaviour of the 98 most frequent breeds may help prospective owners to choose between dogs. Breed–grouping based on genetic relatedness or used by the American Kennel Club does not provide behaviourally homogeneous groups. However, it is important to note that environmental factors like early socialization, dog keeping practices, and the behaviour of the owner can modify the behaviour of individual dogs from the core characteristics typical of their breeds.

STUDY IV.

Gene polymorphisms in association with dog personality traits⁴

1. Introduction

As mentioned in the previous chapter, the breed's typical characteristics do not determine 100% of the behaviour of all individuals belonging to that breed. There are also large intra-breed differences observed in certain behavioural characteristics which could be attributed to environmental influences, and, of course, to the interaction of thousands of polymorph genes. The amount of the genetic influence of the personality traits varies. However, studies analysing the heritability (how much of the individual variance could be attributed to genetic factors) found that some has a considerable genetic background, similar to some of the human traits (reviewed in Ruefenacht et al., 2002). For example, the heritability of activity was estimated as being 0.53 (Wilsson and Sundgren, 1998), the heritability of aggression ranges between 0.2 – 0.8 (Liinamo et al., 2007), the heritability of fearfulness was found to be 0.46 (Goddard and Beilharz, 1982). Breed comparisons (see in the previous chapter) also offer some insight about the genetic background of behaviour traits. Such comparisons are based on the assumption that, as breed-typical behaviours are at least partly genetically determined, traits with stronger genetic influence should differ more between breeds than traits with stronger environmental influence. However these types of quantitative studies could only provide estimates of the number of underlying genes, but they cannot single out the effect of particular genes.

Due to the complex, multilevel interaction between individual genes, identifying possible target genes in association with a certain trait is not easy. Genome-wide association studies (GWAS) investigate thousands of single-nucleotide-polymorphisms (SNPs) (using microarrays or chips) that can capture most of the genetic variation in the studied population. This explorative method assesses the entire genome aiming to identify genetic variants (risk factors) that are associated with a target trait (e.g. using case-control design) (e.g. Bush and

⁴ this chapter is based on: Kubinyi, E., Vas, J., Héjjas, K., Ronai, Zs., Brúder, I., **Turcsán, B.**, Sasvári-Székely, M., Miklósi, Á., 2012. Polymorphism in the tyrosine hydroxylase (TH) gene is associated with activity-impulsivity in German Shepherd dogs. *PLoS ONE*, 7: e30271. and

Kis, A., Bence, M., Lakatos, G., Pergel, E., **Turcsán, B.**, Pluijmakers, J., Vas, J., Elek, Zs., Brúder, I., Földi, L., Sasvári-Székely, M., Miklósi, Á., Ronai, Zs., Kubinyi, E., 2014. Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (*Canis familiaris*). *PLoS ONE*, 9: e83993.

Moore, 2012; Ng and Kirkness, 2010). This approach could point out candidate SNPs for further experimental studies, however, this technique is highly expensive to be conducted on large number of individuals.

The candidate gene approach assumes that the phenotypic trait is determined to some extent by smaller number of genes that have a detectable effect. Candidate genes investigated in association with a given trait are primarily selected based on the literature (e.g. on GWAS results, or associations in other species), or on an a priori knowledge of the biochemical pathway underlying the trait in question. As a hypothesis-driven approach, this method investigates only a small number of genes (or gene variants) which usually relate to the neurotransmitter and hormonal systems.

In dogs, the usual strategy is to find allele variation in certain genes for which some effect can be hypothesized based on human studies. In the recent years several such polymorphisms were found (e.g. in serotonin or dopamine pathways, van den Berg et al. 2004, 2005; Héjjas et al., 2007a), however, the exact genetic nature of the polymorphism in dogs is usually different from that of humans. For example, the variability could affect different exons, the length or the number of repeated regions could be different, and single-nucleotide-polymorphisms are usually found in different positions in the DNA sequence and they very likely cause different changes in the amino-acid chain (Héjjas et al., 2007a). Therefore, direct comparison between species is usually not possible (i.e. longer gene variants in one species may mean higher risk to show a certain phenotype in one species, and lower risk in the other). Nevertheless, candidate gene studies in animals could contribute to the understanding of human gene \times behaviour relationships.

Morphological traits are frequent targets of dog genetic studies due to their uniformity within breeds, high heritabilities (Carrier et al., 2005), and relatively accurate analytical methods (Sutter et al., 2008). Because of the established (usually strict) morphological breed standards of the breed clubs, the assessment of the morphological phenotypes of breeds does not require an individual-based measurement (Sutter et al., 2008). Recent genetic studies revealed that a small numbers of genes with large phenotypic effect are responsible for the size, coat and skeletal variation among breeds (for a review see Shearin and Ostrander, 2010).

The identification of the behavioural phenotype is more difficult. Some studies adapted a similar method as in morphological studies (i.e. breed ratings provided by some experts), as they aimed to analyse behaviour traits which were assumed to show high across-breed variability and low within-breed variability (e.g. pointing behaviour, Chase et al., 2009; Jones et al., 2008). However, relying solely on breed stereotypes could bias the results, since the

behavioural traits may be more affected by demographic variables, dog keeping practices (e.g. Kubinyi et al., 2009) and cultural differences (Wan et al., 2009) than morphological traits. In order to reveal a valid association between genetic factors and complex behavioural traits, an individual-based analysis is more preferable. Such analyses, however, require a large sample as they need to be carried out within a single breed. Individuals from different genetically isolated populations (such as breeds) are more likely to show behavioural differences due to their population-specific background and not due to the presence of a single gene (Hamer and Sirota, 2000).

Our aim in the current study was to develop a reliable, individual-based phenotyping tool for behavioural-genetic analyses and to investigate the associations between certain candidate gene polymorphisms and personality traits in dogs. In this chapter I will summarize two of our studies on this field.

A widely investigated system in candidate gene studies is the dopamine neurotransmitter system. Dopamine is involved in the brain's reward system, and has many other functions in cognition, movement control, and attention (Nieoullon, 2002). In human studies, genetic polymorphisms in the dopamine system were related to a number of psychiatric diseases (see Wong et al., 2000 for review), novelty seeking and ADHD (Benjamin et al., 1996; Ebstein et al., 1996; Gizer et al., 2009; Paterson et al., 1999). As activity and novelty seeking traits are also relevant in a number of other species (e.g. Fidler et al., 2007; Lit et al., 2010a; Vas et al., 2007), these human associations have generated a wide interest in animal behaviour-genetic studies (e.g. reviewed in Viggiano et al., 2003, 2004). Regarding dogs, Héjjas et al. (2007b) found an association between a variable number of tandem repeat (VNTR) polymorphism in the dopamine D4 receptor gene (DRD4) and the level of activity-impulsivity among police German Shepherd Dogs. Another possible target gene in the dopaminergic system is the tyrosine hydroxylase (TH) which is a rate-limiting enzyme catalyzing the conversion of the precursor of dopamine (dihydroxyphenylalanine, DOPA). Takeuchi et al. (2005) found that there is a high sequence homology between the dog and human TH gene; they also reported four SNPs in this gene in dogs, and significant variations in the allelic frequencies among five dog breeds (Takeuchi et al., 2005).

In our first study, we investigated whether the polymorphisms in the TH gene (similarly to the DRD4 polymorphism) are also associated with the activity-impulsivity phenotype of dogs.

The target of our second study was the oxytocin neurohormonal system. The oxytocin is considered to have a key function among the regulators of social behaviour (for reviews see Ebstein et al., 2012; Lee et al., 2009b), for example relating to autism (Hollander et al., 2007),

mother–infant attachment and maternal behaviour (Campbell, 2008) or mediating the psychosocial effects of human–animal interactions (Beetz et al., 2012). Oxytocin receptor gene (OXTR) is the most frequently investigated candidate gene in this neurohormonal system. In humans, variants in OXTR have been found in association with differences in social behaviour phenotypes such as social recognition (Skuse et al., 2013), prosocial behaviour (Tost et al., 2010) or empathy (Wu et al., 2012). Since the oxytocin system is evolutionarily conserved in terms of structure and function, studies on non–human animals found similar effect of oxytocin on behaviour. For example administration of oxytocin reduces anxiety–like behaviours in rodent species (e.g. Yoshida et al., 2009; Ayers et al., 2011), and increased proximity to conspecifics in newborn macaques (Simpson et al., 2014). As dogs also show social behaviours analogous to humans (Topál et al., 2009b) and humans share their social environment with dogs, human–kept dogs could provide a more relevant (and more natural) model of the human social behaviour than monkeys kept in captivity or of rodents kept in laboratory settings. Moreover, Marx et al. (2011) recently showed a high sequence similarity between the human and the dog OXTR gene.

In our second study, we investigated the associations between polymorphisms in the OXTR gene and the social behaviour of dogs.

Taken together, we aimed at developing a valid and reliable behaviour test for measuring activity–impulsivity and social behaviour traits in dogs and to identify some of the underlying genetic factors of these complex traits.

Hypothesis 1 – Based on the role the TH gene plays in the dopaminergic system we hypothesised that polymorphisms in this gene will be associated with activity–impulsivity behaviour of dogs.

Hypothesis 2 – Based on human findings, the polymorphisms in the OXTR gene were expected to associate with social behaviours of dogs towards humans.

2. Method

2.1 Subjects

To reduce the possibility of false positive results due to breed differences, both of our analyses were carried out within a single breed, the German Shepherd Dog. This breed displays a large individual diversity in behaviour which manifests also in its popularity as pet and also its frequent use in different practical purposes (e.g. as guide dog for the blinds, police

dog, drug detection dog). We collected our subjects from owners attending dog training schools and volunteers from the Family Dog Project database (Budapest, Hungary). Altogether, N = 104 German Shepherds were involved in both studies, no more than two dogs from the same household and none of them were siblings or in parent–offspring relationship. The descriptive statistic of our sample as presented in Table 4.2.

2.2 Procedure

To investigate both the activity–impulsivity and the social behaviour, the dogs participated in a behaviour test series conducted outdoors, on a remote area. The experimenter assessed the behaviour *in situ*, by filling in a score–sheet (Appendix E), however, all experiments were recorded on video, as well. Different situations and variables were used to measure the two behaviours.

2.2.1 Activity–impulsivity phenotype

The situations we evaluated when assessing the activity–impulsivity were:

1. Spontaneous activity (Figure 4.1a)

The owner stands still without paying special attention to the dog, while holding the dog on a leash (1.5–2 m). The dog is allowed to move freely within the range of the stretched leash and is not corrected or rewarded for any behaviour. This test lasts for 1 minute. Experimenter stays at a distance of at least 3 m from the dog without paying any attention to the dog.

2. Separation from the owner (Figure 4.1b)

The dog is tethered to a tree on a 3 m leash, while the owner is hiding behind an object (e.g. a tree) 5–6 m from the dog, which blocks the dog from seeing the owner (1. separation phase). After 1 minute has elapsed the experimenter approaches the dog, greets it and initiates play with a tug for 30 sec. At the end she steps back to the camera and the dog is alone again (2. separation phase). After another 1 minute, the owner comes back, greets the dog and initiates play with the tug.

3. Lying on the side (Figure 4.1c)

The owner commands the dog to lie down. Then he/she crouches down next to the dog, turns the dog on its side. The owner tries to keep the dog in this position for 30 seconds. If the dog gets up before the 30 seconds elapses, the test restarts. Petting and talking to the dog is

allowed. The test is terminated if the dog refuses to lie on the side for 60 seconds, or gets up again during the second try.

4. Separation II (“Hiding”) test (Figure 4.1d)

The experimenter holds the dog on leash, and the owner is asked to hide behind an object (e.g. a tree) 15–20 m away from the dog. After 30 seconds, the experimenter releases the dog and says “Go!”. If the dog does not start to move at once she gently touches the rear end. If the dog still refuses to approach the owner for 5 seconds, the experimenter asks the owner to call the dog.

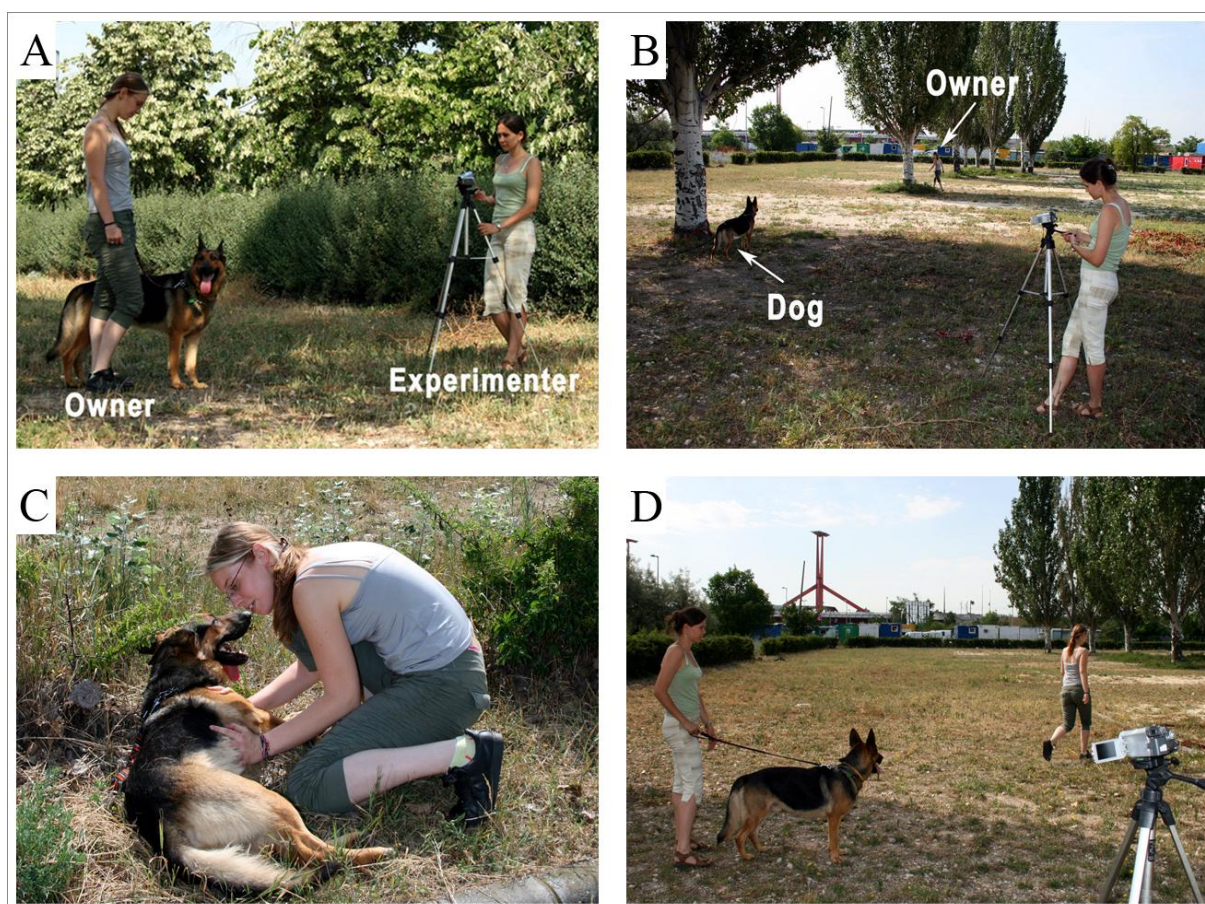


Fig. 4.1 Illustrations for the subtests used for assessing activity–impulsivity of the dogs. a) Spontaneous activity; b) Separation from the owner; c) Lying on the side; d) Separation II (“Hiding”) test

Coded variables (0–3 scale, see Appendix E): 1) the duration of moving the legs during the Spontaneous activity subtest, 2–3) the duration of moving the legs during in the Separation subtest (1. and 2. separation phases), 4) the latency of lying down in the Lying on the side

subtest, 5) the duration of vocalization in the Separation II subtest, and 6) the latency to approach the owner in the Separation II subtest.

We also used a questionnaire, the Dog–ADHD Rating Scale (Dog–ADHD RS) to analyse the activity–impulsivity behaviour of the dogs. This questionnaire was developed in Hungary by adapting a human ADHD questionnaire for dogs (Vas et al., 2007) and was used in previous studies to assess this phenotype (Héjjas et al., 2007b; Wan et al., 2013). It consists of two subscales: seven items compose the activity–impulsivity scale and six items make up the inattention scale (Table 4.1). The owners were asked before they participated in the test series to complete this questionnaire, rating how frequently they observe the listed behaviours on a 4–point scale (from 0: never to 3: very often). The scale scores were calculated for each dog by taking the mean of the scores of the items belonging to each scale. Both scales of the Dog–ADHD RS already showed satisfactory internal consistency, test–retest reliability, inter–observer reliability, and external validity (Vas et al., 2007).

Table 4.1 The Dog–ADHD Rating Scale questionnaires applied in the study (Vas et al., 2007)

Activity–impulsivity scale
Your dog leaves from its place when it should stay
Your dog cannot be quiet; it cannot be easily calmed
Your dog fidgets all the time
Your dog is excessively difficult to control; if it lunges, it is hard to hold it back
Your dog always wants to play and run
Your dog is likely to react hastily, and that is why it is failing tasks
Your dog cannot wait; it has no self–control
Inattention scale
Your dog has a difficult time learning, because it is careless, or other things can easily attract its attention
It is easy to attract your dog’s attention, but loses its interest soon
It is difficult for your dog to concentrate on a task or play
It seems that your dog does not listen even if it knows that someone is speaking to it
Your dog solves simple tasks easily, but it often has difficulties with complicated tasks, even if it knows them and has practiced them often
Your dog’s attention can be easily distracted

2.2.2 Social behaviour

The situations we evaluated when assessing the dogs’ social behaviour were:

1. Greeting by the experimenter (see also in Héjjas et al., 2009) (Figure 4.2a)

The owner holds the dog by the leash. The experimenter approaches the dog in a friendly way (says “*Hello*” to the owner and the dog, and smiles). She stops out of reach of the leash and waits for 3 seconds. If the dog is not aggressive, she steps next to the dog then pets the dog’s head and back. After petting, the experimenter steps 1 m away from the dog. She waits for 3 seconds for the dog to follow, then pets the dog again (if it is possible). The owner stands still during the test, but he/she is allowed to talk if it is necessary.

2. Separation from the owner (Figure 4.1b)

See above.

3. Problem solving test (Figure 4.2b)

The experimenter puts a piece of sausage into a cage that can be retrieved by pulling out a string. The owner stands 1 m from the cage, holds the leash of the dog and is not allowed to interfere (speak or gesticulate). The dog has 1 minute to manipulate the cage/string and get the food. Trial ends when the dog gets the food, or after the 1 minute elapsed (in which case the experimenter gives the food to the dog). This trial is repeated once more.

4. Threatening approach (see also in Vas et al., 2005) (Figure 4.2c,d)

The owner stands motionless next to the dog and holds the leash. The experimenter steps away from the dog (~ 10 m), then approaches the dog slowly, by leaning forward her upper body and staring at the eyes of the dog (Figure 4.2c). The experimenter stops approaching if the dog shows signs of aggression (e.g. snapping), severe fear (e.g. hiding behind the owner), or when she reached the dog (or when the dog approached the experimenter in friendly manner). After it, the experimenter steps back again (~ 5 m from the dog), crouches down, and calls the dog in a friendly way (Figure 4.2d). The owner then lets the dog approach the experimenter.

5. Separation II (“Hiding”) test (Figure 4.1d)

See above.



Fig. 4.2 Illustrations for the subtests used for assessing social behaviour of the dogs. a) Greeting by the experimenter; b) Problem solving test; c) Threatening approach and d) Calling the dog after threatening

Coded variables (0–3 scale, see Appendix E): 1–3) latency to approach the experimenter in the Greeting, Separation and at the end of the Threatening approach subtests, 4–5) the latency to approach the owner during the Separation and Separation II subtests, 6–7) the latency to follow the experimenter when she steps away from the dog during the Greeting, and Separation subtests, 8) the latency to follow the owner during the Separation subtest, 9–11) the duration of orientation to the owner in the Separation (1. and 2. phase) and Separation II subtests, 12) the walking style the dog used when approaching the owner after the Separation II subtest, 13–16) the number of orientation to the owner and to the experimenter during the two trials of the Problem solving subtest, and 17) the final reaction in the Threatening approach subtest.

2.3 Reliability, validity

The test–retest reliability of the test was measured by retesting 14 dogs and comparing their two performances. In order to check inter–rater reliability 28 test videos were coded by two

independent raters (the experimenter *in situ* and an independent coder from the video recordings). To investigate the construct validity of our activity–impulsivity behaviour scale we correlated the dogs’ behaviour test scores to their Dog–ADHD RS questionnaire scores.

2.4 DNA sampling and genotyping

Buccal smears from the inner surface of the cheek were collected from all dogs participating in the study in a non–invasive way (using cotton swabs) (see Héjjas et al., 2007a).

The DNA was isolated, sequenced and genotyped by our collaborative partners, in the laboratory led by Dr. Mária Sasvári–Székely and Dr. Zsolt Rónai at the Department of Medical Chemistry, Molecular Biology and Pathobiochemistry at the Semmelweis University, Budapest, Hungary. For the detailed procedure of the genotyping, see Héjjas et al. (2007a, 2007b, 2009) and Wan et al. (2013).

2.5 Statistical analyses

The six behavioural variables measured for activity–impulsivity were grouped together in a behaviour scale based on the results of Brúder et al. (unpublished).

On the variables indented to assess the dogs’ social behaviour towards humans, we carried out a Principal Component Analysis with the same setup and procedure as described in *Study I* (2.4). The scores of all scales were calculated for each dog as the mean of the variable scores related to each scale. The internal consistency of the derived scales was characterized by Cronbach’s alpha, the test–retest reliability and inter–rater reliability were assessed using Intraclass correlation (one–way random measures). The relationship between the activity–impulsivity behaviour scale and two scales of the Dog–ADHD RS was analysed by Pearson correlation, the difference between the two correlations was assessed by Steiger’s Z test.

For each gene polymorphism we investigated frequencies and the Hardy–Weinberg equilibrium of the genotypes. Rare homozygote genotypes (< 10%) were grouped together with heterozygotes. To investigate the associations between the TH and OXTR genotypes of the dog and its activity–impulsivity and social behaviour, we used One–Way ANOVA with Tukey post–hoc test.

SPSS 21.0 was used for all the analyses, except Steiger’s Z test which was calculated using the following web site: <http://www.quantitativeskills.com/sisa/statistics>.

3. Results

3.1 Descriptive statistics

Approximately half of our subjects were males, the dogs' mean age was ~ 4 years. The number of male owners were much higher (42%) than in the other studies included in this thesis, the owners' mean age was ~ 33 years (Table 4.2).

Table 4.2 Descriptive statistics of the owners and dogs in the present study (N = 104)

Dog's characteristics		Owner's characteristics	
Age	mean \pm SD = 3.9 \pm 2.7	Age	mean \pm SD = 32.7 \pm 11.8
Sex	male: 53.8%	Gender	man: 41.7%
	female: 46.2%		woman: 58.3%
Neutered status	intact: 17.0%		
	neutered: 83.0%		
Training	nothing: 16.3%		
	basic obedience: 13.5%		
	one special: 52.9%		
	2 or more special: 17.3%		

3.2 Principal component analysis

According to the PCA, the 17 behaviour variables assessing the social behavioural of dogs comprised three components that accounted for 50% of the common variance (Table 4.3). Based on the variables loading higher than 0.4 we labelled the components as Proximity seeking (6 variables); Reaction to separation from owner (7 variables); and Looking at humans (4 variables). However, this latter scale was composed of variables from a single subtest (Problem solving), therefore it does not fit to the personality trait criteria (consistency across situations).

3.3 Reliability

Two out of the four Cronbach's alpha values were above 0.7, the value for the Activity–impulsivity behaviour scale (0.677) and Looking at humans (0.663) were lower, however, still adequately high (e.g. Hsu and Serpell, 2003).

The test–retest reliabilities of the test scales were also satisfactory for three out of four scales; the Intraclass correlations between the first and second test were: Activity–impulsivity behaviour scale: 0.637; Proximity seeking: 0.738; Reaction to separation from owner: 0.628,

$p < 0.01$ for all). The test–retest reliability of the Looking at Humans scale was not significant (ICC correlation: 0.350, $p = 0.094$).

The inter–rater reliabilities (Intraclass correlations between two independent coders) were: Activity–impulsivity behaviour scale: 0.774; Proximity seeking: 0.818; Reaction to separation from owner 0.818; Looking at humans 0.412, $p < 0.05$ for all.

Table 4.3 Component structure, explained variance, Cronbach’s alpha values and Eigenvalues of components. Loadings > 0.4 are in bold

Variables	Proximity seeking	Reaction to separation from owner	Looking at humans
Latency to approach the E in Separation	0.825	0.075	−0.042
Latency to follow the E in Separation	0.793	0.142	−0.145
Latency to follow the E in the Greeting	0.782	−0.086	−0.104
Latency to approach the E in the Greeting	0.735	−0.010	−0.072
Final reaction in the Threatening approach	0.585	−0.199	0.146
Latency to approach the E after Threatening	0.453	0.207	0.171
Latency to approach the O in Separation II	0.112	0.695	0.232
Latency to approach the O in Separation	0.214	0.663	0.076
Duration of orientation to the O in Separation II	−0.080	0.617	0.005
Motion type towards the O in Separation II	0.098	0.612	0.102
Latency to follow the O in Separation	0.246	0.600	−0.145
Duration of orientation to the O in Separation 1	−0.228	0.600	0.051
Duration of orientation to the O in Separation 2	−0.173	0.592	−0.084
N of orientation to the E in Problem solving 2	0.129	−0.127	0.821
N of orientation to the E in Problem solving 1	0.071	−0.087	0.729
N of orientation to the O in Problem solving 2	−0.202	0.190	0.674
N of orientation to the O in Problem solving 1	−0.117	0.317	0.556
Explained variance	19.692%	18.217%	12.003%
Cronbach’s alpha	0.800	0.749	0.663
Eigenvalue	3.348	3.097	2.040

According to the Cronbach’s alpha values, test–retest and inter–rater reliabilities, three of the derived behaviour scales are consistent across situations and over time, therefore can be considered as personality traits. The Looking at humans scale seems to be less consistent across time, which also confirms that this scale cannot be considered as personality trait.

Both scales of the Dog–ADHD RS correlated with the Activity–impulsivity behaviour scale (Pearson, activity–impulsivity: $r = 0.534$, $p < 0.001$; inattention: $r = 0.231$, $p = 0.018$); the

correlation between the behaviour scale and the activity–impulsivity questionnaire scale was significantly higher (Steiger’s Z test, $z = 3.118$, $p < 0.001$).

3.4 Gene polymorphisms

In the TH gene, a repeat polymorphism in the intron 4 was found (as reported previously in Héjjas et al., 2007a) with two alleles present in the German Shepherd Dogs. In the short allele (allele 1) a 36 basis–pairs long sequence is present as a single copy. In the long allele (allele 2) the sequence is in a duplicated form. The genotype frequency did not deviate from the Hardy–Weinberg equilibrium ($p = 0.29$) (Table 4.4). Two dogs (1.9%) were homozygotes for the short allele (1/1 genotype), 35 (33.7%) dogs were heterozygotes (1/2 genotype) and 67 dogs (64.4%) possessed the longer alleles exclusively (2/2 genotype). As the short allele was rare in the population, homozygotes (1/1) and heterozygotes (1/2) were combined for statistical analysis.

Table 4.4 Allele frequencies for the studied German Shepherd population. Statistical tests for Hardy–Weinberg Equilibrium (HWE) are also provided

Gene	Genotype	Frequency	Hardy–Weinberg Equilibrium
TH intron 4	1/1	1.9%	$p = 0.291$
	1/2	33.7%	
	2/2	64.4%	
OXTR –213AG	AA	12.1%	$p = 0.876$
	AG	48.5%	
	GG	39.4%	
OXTR rs8679684	AA	37.5%	$p = 1.000$
	AT	47.1%	
	TT	15.4%	
OXTR 19131AG	AA	36.5%	$p = 0.749$
	AG	49.0%	
	GG	14.4%	

In the dog OXTR gene, one known (rs8679684) and two novel (–213AG, 19131AG) single nucleotide polymorphisms (SNP) were found. The –213AG⁵ SNP is located in the 5’ flanking region, whereas rs8679684 and 19131AG SNPs can be found in the 3’ untranslated region of the gene. Linkage analysis revealed that the rs8679684 and 19131AG SNPs are in strong linkage disequilibrium ($D' = 0.98$, $R^2 = 0.96$). The genotype frequencies were in Hardy–

⁵ referred to as –212AG in Kis et al., 2014

Weinberg equilibrium for all three polymorphisms ($p > 0.749$ for all) (Table 4.4) and in all three polymorphisms, the rarest homozygote was $> 10\%$ in the population.

3.5 Gene \times behaviour associations

The TH polymorphism was associated with both the Activity–impulsivity behaviour scale ($F_{1,102} = 5.765$, $p = 0.018$, Figure 4.3a), and the Dog–ADHD activity–impulsivity scale ($F_{1,102} = 8.922$, $p = 0.004$, Figure 4.3b).

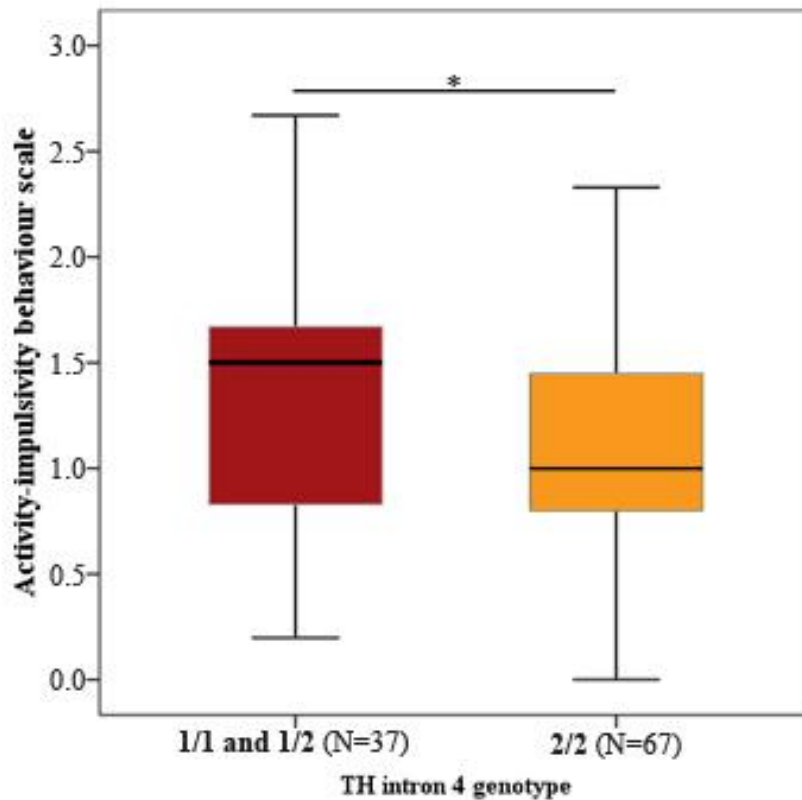
Dogs possessing at least one short allele were reported to be more active–impulsive by the owners and reached higher scores on the behavioural scale than homozygotes possessing the longer alleles exclusively. Omitting the rare 1/1 genotype (two dogs) did not affect the results significantly.

In the OXTR gene, the rs8679684 polymorphism was associated with Proximity seeking ($F_{2,90} = 4.298$, $p = 0.016$, Figure 4.4a) and Reaction to separation from the owner ($F_{2,91} = 5.010$, $p = 0.009$, Figure 4.4b) traits. Dogs carrying the T allele (opposed to the AA genotype) showed lower proximity seeking towards the experimenter and higher reaction to separation from the owner.

The 19131AG polymorphism, similarly to the rs8679684, was associated with both Proximity seeking ($F_{2,91} = 5.647$, $p = 0.005$, Figure 4.5a) and Reaction to separation from the owner ($F_{2,92} = 4.996$, $p = 0.009$ Figure 4.5b), likely as a result of the linkage disequilibrium between these SNP–s. The presence of the G allele (opposed to the AA genotype) was associated with lower proximity seeking towards the experimenter and higher reaction to separation from the owner.

We found no significant associations with the –213AG polymorphism and also no association with the Looking at humans trait.

a)



b)

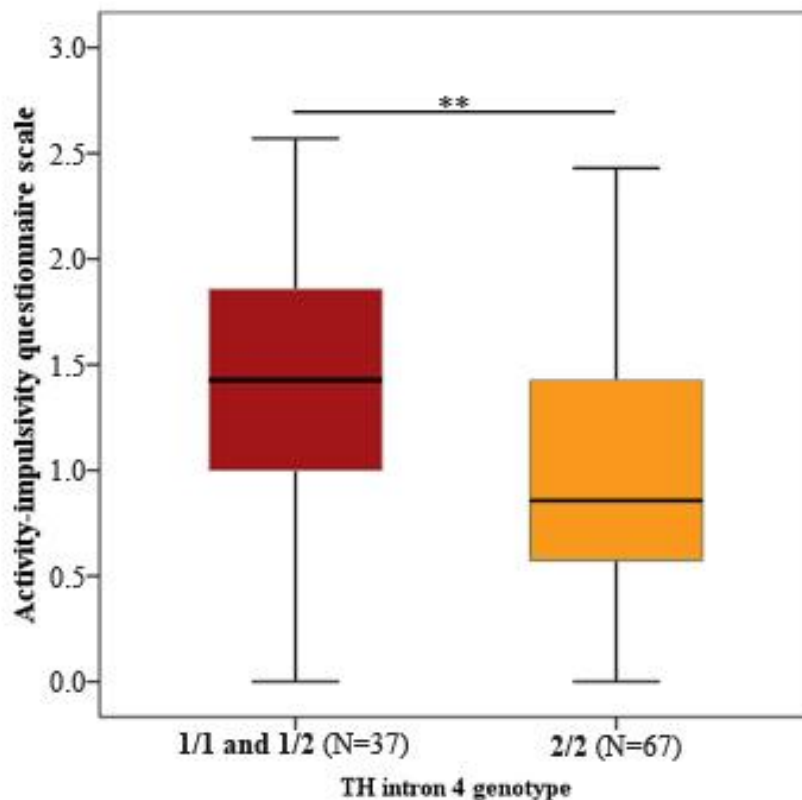
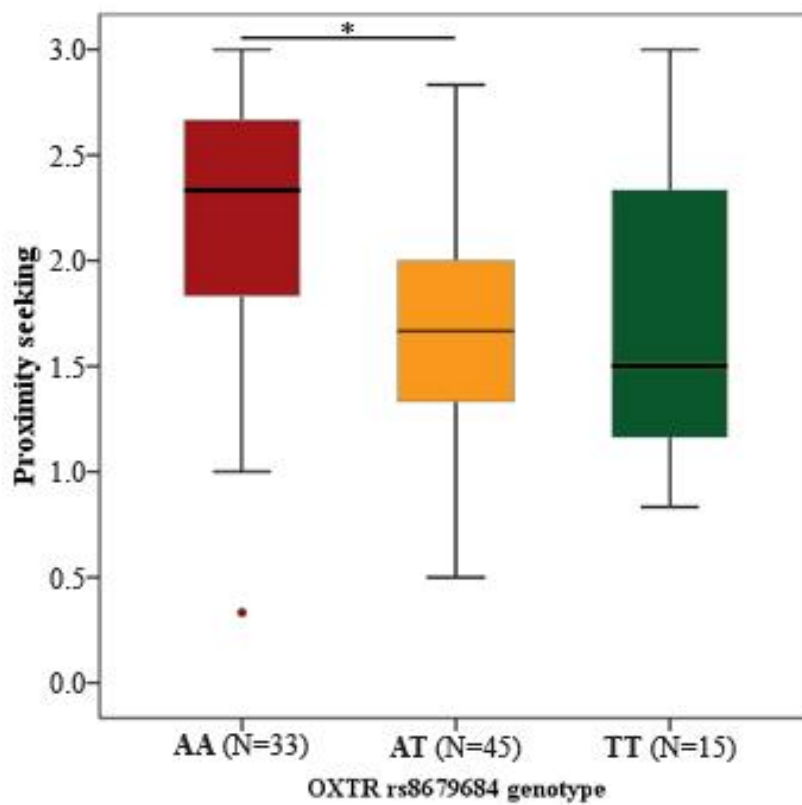


Fig. 4.3 Association between tyrosine hydroxylase (TH) intron 4 genotypes and a) activity–impulsivity behaviour scale, and b) Dog–ADHD RS activity–impulsivity scale. 1/1, 1/2 genotype represents the group of individuals possessing at least one short allele. Subjects in the 2/2 genotype possess two long alleles. * $p < 0.05$, ** $p < 0.01$

a)



b)

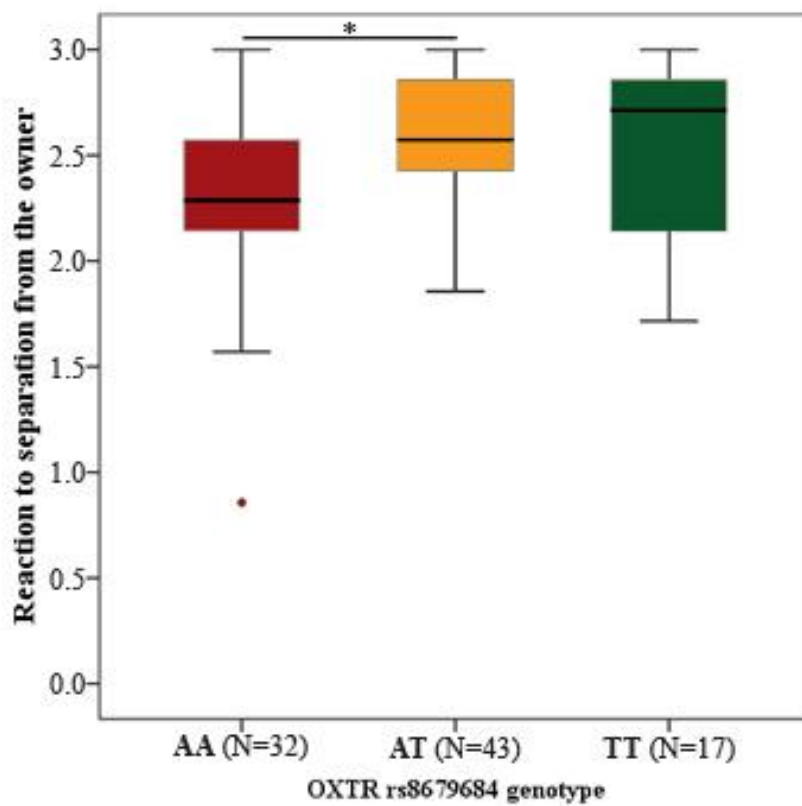
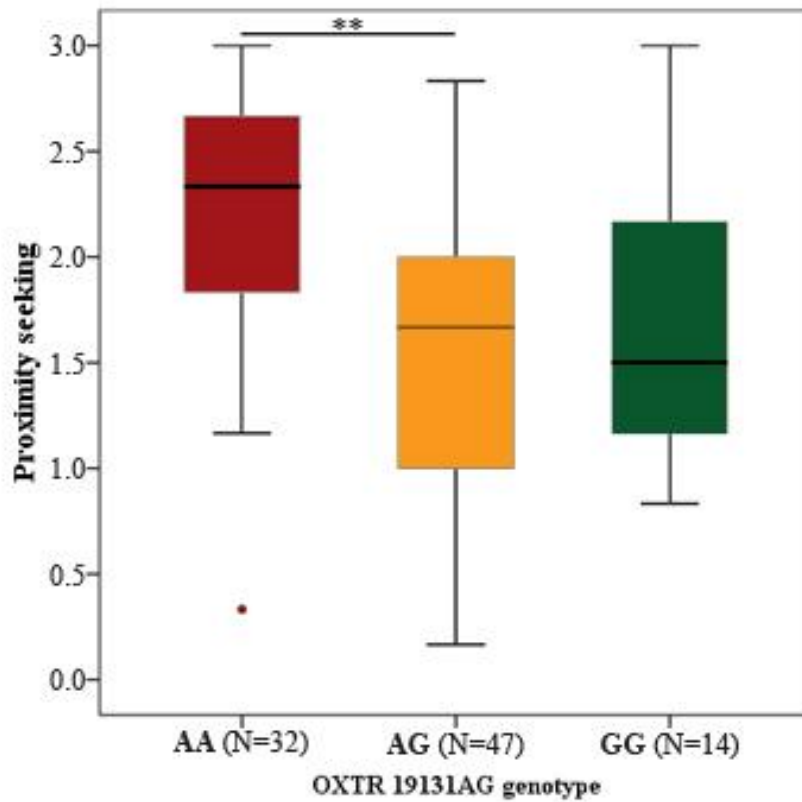


Fig. 4.4 Association between oxytocin receptor (OXTR) rs8679684 genotypes and a) Proximity seeking and b) Reaction to separation from the owner traits. * $p < 0.05$

a)



b)

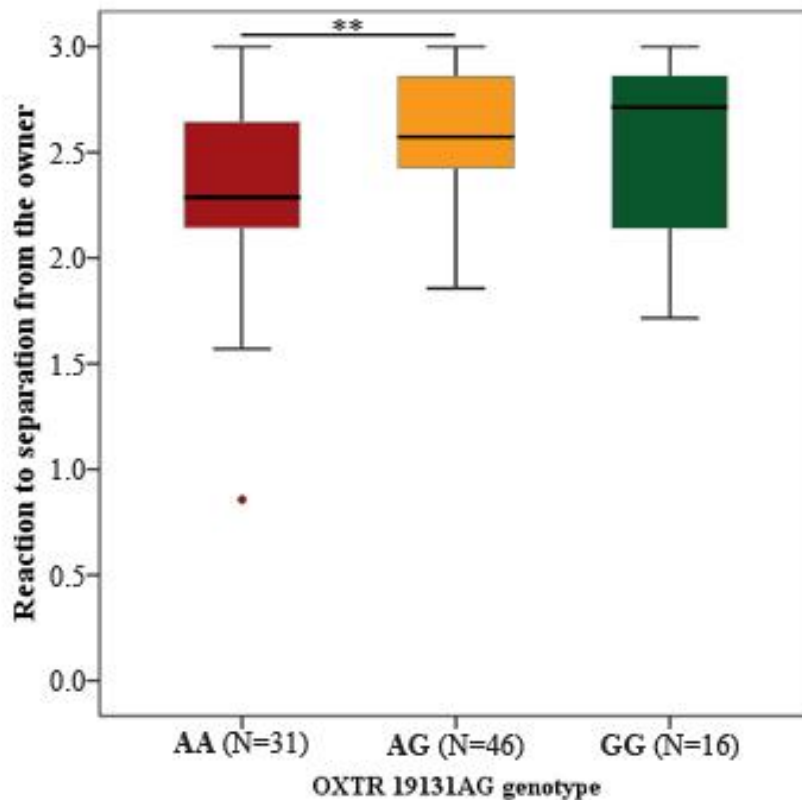


Fig. 4.5 Association between oxytocin receptor (OXTR) 19131AG genotypes and a) Proximity seeking and b) Reaction to separation from the owner traits. * $p < 0.05$, ** $p < 0.01$

4. Discussion

The aim of this study was twofold: 1) we aimed to develop a valid and reliable behaviour test for measuring activity–impulsivity and social behaviour in dogs and 2) identify gene \times behaviour association between these traits and genes of the dopamine and oxytocin systems.

In our first study, we investigated the polymorphisms in the tyrosine hydroxylase (TH) gene in association with the activity–impulsivity of the dogs. A new behaviour scale was developed to assess this behavioural trait based on six behaviour variables in four situations. A high score on this trait indicates high motor activity, high latency of lying to the side, more vocalization during separation from the owner, and faster approach of the hiding owner. Previous studies described similar traits, for example Hennessy et al. (2001) assessed locomotor activity by measuring how many times the dog crosses the lines on the floor. This trait also fits into the framework of Jones and Gosling (2005), corresponding to the activity trait. We demonstrated the internal consistency, inter–rater reliability and test–retest reliability of this Activity–impulsivity behavioural scale. Moreover, we also found a good correspondence between this behaviour scale and the owner’s assessment of the dogs’ active–impulsive behaviour (demonstrating the convergent validity of this trait).

In the TH gene, a repeat polymorphism was found in the intron 4. This polymorphism strongly affects the size of the intron, thus the biological function of this repeat variation is supposed to be the modulation of the splicing (Héjjas et al., 2007a).

This polymorphism was associated with activity–impulsivity trait measured by both by the owner’s report (the Dog–ADHD RS) and by the behaviour test. Dogs possessing at least one short allele were reported and found to be more active–impulsive, compared to animals possessing only the long allele. This association was independent of the age, sex and the training status of the dogs (Kubinyi et al., 2012). Other genetic polymorphisms in the dopamine system have already been found in association with this phenotype (in DRD4 gene, Héjjas et al., 2007b; Wan et al., 2013), however, this is the first report of a similar association with the TH gene in dogs.

The human TH gene also contains a repeat polymorphism in the intron A, which may function as a transcriptional enhancer (Persson et al., 2000). This polymorphism was associated with neuroticism and extraversion (Tochigi et al., 2006), and both of these personality traits (but especially extraversion) are linked with facets of activity and impulsivity in humans (Whiteside and Lynam, 2001). Thus, our results on dogs seem be in accordance with human

studies. However, further study is needed to reveal mechanism and function of the TH gene variants on molecular/cellular level, and also the neuronal and hormonal regulation of the activity–impulsivity behaviour in dogs.

In our second study, we investigated the associations between polymorphisms in the oxytocin receptor gene (OXTR) and the social behaviour of dogs. Using principal component analysis we derived three behaviour traits from 17 variables observed in 5 test situations. Proximity seeking relates to how willingly the dog approaches and interacts with a stranger; high score indicates faster approach and more time spend close to the experimenter. Reaction to separation from owner relates to how intensely the dog shows owner–directed behaviours when left alone and how intensively greets the owner after separation; high score on this trait means more time looking at the owners’ direction and faster approach / more intense greeting of the owner after separation. Finally, the Looking at humans trait relates to the number of times the dog looks at the passive owner and stranger while facing a problem box; dogs with a high score looked more at humans. Proximity seeking and Reaction to separation from the owner traits showed convincing internal consistency, test–retest reliability and inter–rater reliability, and can be considered as personality traits. The Looking at humans trait was not repeatable over time and was composed only of variables from the Problem solving subtest. The dogs might have remembered how they had solved the problem in the first occasion, therefore looked less at the owner or experimenter for help.

In the OXTR gene we determined three SNPs, two of which were previously unknown. One of these SNPs, the –213AG is located on CpG area which are the main targets of epigenetic modifications (e.g. by methylation). The biological function of this SNP may be to alter the methylation pattern of the promoter region thereby changing the gene function (i.e. the mRNA expression level). The other two SNPs (rs8679684, 19131AG) are located in the 3’ UTR region, thus they might also influence the amount of the protein expressed by altering microRNA (miRNA) binding.

Two of these polymorphisms were found to be associated with the social behaviour of dogs. The rs8679684 and 19131AG SNPs were associated with Proximity seeking and Reaction to separation from the owner traits. This study provides the first evidence that polymorphisms in the OXTR gene are related to human directed social behaviour in dogs, and the associations we observed are in line with previous findings in humans. Although direct parallels are hard to draw between the dog and human social behaviours, our association in Proximity seeking of the dogs might correspond to human results in prosocial behaviours (e.g. Tost et al., 2010; Yamasue et al., 2012). Human findings also indicate that oxytocin relates to the mother–infant

attachment (e.g. Campbell, 2008; Chen et al., 2011), our results in Reaction to separation from the owner (often regarded as an indicator of their attachment to the owner, Gácsi et al., 2001; Topál et al., 1998) might be in accordance with these findings. On the other hand, it has also been shown in human studies that oxytocin increases looking at the eye-region of faces (Guastella et al., 2008). However, we found no association between the OXTR polymorphisms and the dogs' tendency to look at humans in problem solving situations. In human studies, this phenotype is usually tested by presenting the subjects pictures of human faces on a monitor (e.g. Lischke et al., 2012). As a possible explanation, looking at humans in a problem solving situation might have a different function (e.g. asking for help), therefore different behaviour regulation, than looking at human faces in a neutral situations.

Again, we have to emphasise, that at this point, we do not have any information about the cellular and molecular mechanisms involved in the regulation of the social behaviours in dogs, nor about the explicit functions of the SNP polymorphisms we found in the OXTR gene, therefore further molecular studies are needed.

Nevertheless, both of our candidate gene studies further extend the role of the dog as a model species in behaviour genetic research.

GENERAL DISCUSSION

1.1 General aims of the studies

Researchers long recognized that some individuals behave more similar to each other than to others. It was observed in many species that individuals behave consistently across similar situations, and over time. These consistent individual characteristics (personality) became the focus of a large number of studies in the last decades and have been examined in a broad range of nonhuman species including great apes, ferrets, hyenas, rodents, hedgehogs, zebra finches, snakes, guppies, and even octopuses (see Gosling, 2001 for a full review). My overarching goal in this thesis was to investigate the personality (that is, consistent individual behaviour) in dogs. Personality, as any phenotypic trait, is the result of an interaction between genes and environment. The aims of the studies described in this thesis were to develop reliable methods to evaluate certain personality traits in dogs, and to investigate the effect of environmental and genetic factors in association with these traits.

1.2 Methods

Both methods of personality assessment (behaviour test, questionnaire) were applied in our studies. Previous studies (e.g. Gosling and Vazire, 2002), as well as our research found that both methods are suitable for assessing personality in dogs.

A strength of the questionnaire method is that it allowed us to investigate a large and diverse sample of dogs (especially when using web-based questionnaires). Such sample size was necessary to address questions like the effects of interaction between environmental factors on personality (*Study I*) or breed-typical behaviour (*Study III*). Large sample size is advantageous not only for reasons of statistical power, but also because hereby we were able to investigate rare characteristics of dogs (i.e. less popular breeds, or the effect of being born at the owner) which might not be possible on a smaller sample. Although it can be argued that each owner brings his or her own subjective biases into play when rating the dog, the inter-rater reliability for all our questionnaires (*Study I–III*) were high, confirming that other persons have similar impressions about the dog's behaviour.

Behaviour test used in *Study IV* has the advantage to evaluate real-life behaviour of the dogs. Although we used a scoring method to assess the behaviour, the psychometric properties

evaluated showed adequate reliability, different people agreed when they scored a dog's behaviour. In the case of the activity–impulsivity trait, the scoring of the experimenter and the rating of the owner also correlated with each other, even though they were based on different situations observed at different times.

1.2.1 Reliability, validity

The accuracy of the evaluation of the dog personality depends on the reliability and validity of the measurement. The procedure used in a study must be replicable since the behaviour of the subject must be consistent across the replication in order to call it personality.

In our studies three aspects of reliability were addressed: internal consistency, inter–rater reliability, and test–retest reliability. Internal consistency is the reliability across questionnaire items or behaviour variables within a trait. That is, it investigates whether variables or items that are purported to measure a single construct yield consistent scores. The inter–rater reliability refers to the agreement among observers regarding the behaviours in questions, while the test–retest reliability assesses the subjects' behavioural consistency across time. Our results indicated that the internal consistency levels of all the traits addressed in the four studies, as well as the inter–rater and test–retest reliabilities were acceptable and comparable to those found in other studies of dog personality.

1.2.2 Methodological limitations

Although, our methods meet the majority of the reliability criteria, they had their limitations. One weakness of our studies is the dog and owner demographics. Although we argued previously that questionnaires (and online data collection) contribute to the diversity of the sample collected, our participants were still a self–selected sample of dog owners. This self–selection bias and the question of online sampling have also been a target of concern in human psychological research. For example, McCabe et al. (2006) and McGraw et al. (2000) found that data collected through the Internet were not different from those collected through traditional means, and Walsh et al. (1992) found that a self–selected sample and a randomly selected sample did not differ significantly in demographic information. However, we cannot exclude that our owners (both those who filled out our questionnaires and those who participated in the behaviour test with their dogs) might be more interested in the participation because they might be more interested in their dogs' behaviour in general. On the other hand, the majority of the dog behaviour studies in the literature are also conducted on a similarly specialized group of owners who are interested enough in dog behaviour to participate in

behaviour tests or complete lengthy questionnaires, so our results are comparable to the results of other studies.

Finally, the ultimate criterion in determining whether a personality assessment tool is useful is whether it predicts behaviour (validity). The main weakness of our questionnaire studies is that so far we failed to address the issues of construct validity, which should be the goal of further studies.

1.2.3 The personality traits found in our studies

In all four studies we investigated only a part of the dogs' whole personality.

In the largest and most comprehensive review of dog personality literature (Jones and Gosling, 2005) categorized the personality in seven trait categories (dimensions): Reactivity, Fearfulness, Sociability, Responsiveness to Training, Aggression, Activity, and Dominance. It was suggested that Reactivity and Fearfulness might represent different facets of a larger Fearfulness or Neuroticism factor. We found that the traits we created using principal component analyses (*Study I* and *Study IV*) fit well into this framework (except Looking at humans), covering all except the Dominance dimension. Calmness, trainability, dog sociability and boldness traits found in *Study I* correspond to the Reactivity, Responsiveness to training, Aggression (partly) and Fearfulness dimensions, respectively. The Activity–impulsivity trait created in *Study IV* is parallel to the Activity dimension, Proximity seeking, Reaction to separation from owner traits represent different facets of Jones and Gosling's (2005) Sociability dimension.

In *Study II* we applied another approach, trying to conceptualize the dog personality in terms of traits paralleling the human five-factor model (Extraversion, Agreeableness, Conscientiousness, Neuroticism, Openness) using an already established questionnaire. Interestingly, the developer of this questionnaire (Gosling et al., 2003) found that Conscientiousness does not appear as a separate personality dimension in non-human species, and Gosling and John (1999) also suggested that dog personality may include a factor that can be conceptualized as a combination of openness and conscientiousness. Contrary to these suggestions, we found that owners (both from Austria and Hungary) were able to apply the questions related to conscientiousness onto their dogs, however, openness trait was not found to be reliable in dogs in our samples.

Nevertheless, our studies provided further evidence that personality axes related to reactivity–fearfulness–neuroticism, sociability–aggression–agreeableness, and activity–extraversion

exist in dogs. Trainability, conscientiousness and some aspects of openness may relate to each other (Jones, 2008) composing another, more dog-specific (less human-like) personality axis.

1.3 Summary of the main results, and their possible applications

As mentioned in the *General introduction*, there is a wide scientific and practical interest in dog personality.

From a scientific perspective, animal models have the potential to help investigating many fundamental questions about personality that are difficult or impossible to address based on human studies alone. The shorter lifespan of the individuals, the greater experimental control, and the greater ability to measure physiological parameters provide unique opportunities to examine the development, the environmental and biological bases of personality. Dogs have already been shown to be adequate models of human social behaviour (Topál et al., 2009b) and genetics (Overall, 2000). As dogs are exposed to similar environmental and social influences as humans, they can be more natural models in many aspects than standard laboratory animal species. Importantly, some personality traits are homologous in vertebrates and in humans (Gosling and John, 1999), therefore dogs can be proposed as a model for studying human personality. (However, we should note that the behavioural manifestation of the homologues traits could be different across species).

From an applied perspective, many groups, such as shelters and working-dog programs, are interested in predicting the dogs' future behaviour in different situations (e.g. the dogs' behaviour after re-homed, or the individuals' suitability for different works). Therefore reliable methods in assessing dogs' personalities could also have large practical values. Moreover, in the development of complex traits (such as personality), both genetic and environmental factors play a crucial role in shaping the individual's sensitivity to develop certain traits possibly through interactions (Wermter et al., 2010). Uncovering such genetic and environmental risks of certain behaviours or behaviour problems and understanding the genetics affecting working behaviour may enable dog trainers to predict the behavioural tendencies of a chosen dog even at early puppyhood.

Last, but not least, from the perspective of the owners, dog personality studies could help in selecting a suitable dog for the family. Dogs hold a special place in many people's lives, in Western countries, choosing a dog generally means choosing a family member, a best friend or a lifelong companion. Careful selection at individual and breed level could reduce the

future conflicts between dogs and people (e.g. problematic behaviours), avoiding possible health consequences of such conflicts (dog biting), and enhancing the well-being of both the owner and the dog. On the other hand, dogs not fitting well into the family may need costly and excessive trainings to correct their behaviour, or they may be abandoned or relinquished to animal shelters. Reliable puppy temperament tests or individual-based descriptions of breed-typical behaviour provided by researchers could be useful for prospective owners when considering obtaining a new puppy in the family.

Taken together, developing reliable tools for characterizing the dogs' consistent behaviour and studying the genetic and environmental factors affecting the personality enable researchers to use the dog as a model for human personality research, dog trainers and owners to work more efficiently and choose more appropriate individual for the given household or for a given work.

The four studies that compose this thesis can be grouped along two main lines of research: in *Study I* and *II* we investigated the effect of the environmental and dog keeping factors on the dog personality; *Study III* and *IV* were designed to address the genetic background on some dog personality traits. The main goals and results of the studies, the most important novelty they present in the literature, as well as their possible scientific and practical applications are summarized below.

Study I Demographic and environmental factors in association with dog personality traits

Environmental factors, such as dog and owner demographics (e.g. age, gender), and dog keeping practices (e.g. training, purpose of the dog in the family) can shape dogs' personalities. The effect of these factors may be part of why temperament assessments of puppies have not been very accurate in predicting adult dogs' behaviour (e.g. Goddard and Beilharz, 1986; Hennessy et al., 2001; Wilsson and Sundgren, 1998).

The aim of this exploratory study was to analyze the effects of multiple environmental factors and their interaction on four dog personality traits (calmness, trainability, dog sociability and boldness).

We identified the most relevant variables that may act as environmental factors in influencing each trait. The most important factors affecting the personality traits were the age of the dog, the sex and neutering status, the training level and the dog's age at acquisition. Older dogs were calmer, less trainable, less social and less bold than younger dogs. Females were more sociable toward other dogs than males, males were bolder than females, and neutered dogs were found to be less calm than intact dogs. Dogs without any professional training courses

were less calm, and less trainable than dog which received at least one type of professional training. Dogs acquired before the age of 12 weeks were calmer and bolder than dogs acquired in older age.

Some of these are in agreement with previous studies, while others have not previously been reported in the literature. These factors did not act independently from each other; instead we found complex interactions between them in association with each personality trait.

The main virtue of our study was the large sample size (> 10,000 individuals) which allowed us to investigate a diverse group of dogs and owners and study environmental characteristics which effects rarely or never studied before.

The main limitation of this study is the self-selection bias mentioned above and the fact that the number of potential environmental factors is vast; our study investigated only 14 of them.

The main novelty of this study was the statistical method applied in order to investigate the multi-level interactions of the environmental factors. Regression tree method was not used in personality research before, despite its virtues in analyzing large data sets, handling large number of variables and uncovering non-linear relationships between them.

We think that the value of our study lies in providing hypotheses for future (experimental) work. There are several questions which our work has raised, for example: what is the direction of causality between the environmental factors and behaviour? How much and how far can the keeping environment shape personality? And how long-lasting are these effects? Further studies are needed to answer these questions.

Study II Personality matching in owner–dog dyads

The personality of the owner can also act as a special environmental factor in shaping the dog's personality. Previous researches pointed out that the owner's personality and his/her behaviour towards the dog can indeed affect the dog's behaviour (e.g. Kis et al., 2012; Podberscek and Serpell, 1997b; Zeigler-Hill and Highfill, 2010).

The main goal of this study was to investigate the relationship between the owners' and dogs' personality profile.

We demonstrated moderate correlations between the owners' and dogs' personality in extraversion, agreeableness, conscientiousness and neuroticism traits, which correlations were significantly higher than those between randomly assigned dog-owner pairs, mirroring the personality similarity found in various human-human social relationships.

The main virtue of this study was that we took into account the number of dogs in the household, expecting (and founding) differences between the dog types (single, first, second

dogs) in the similarity pattern. In case of multi-dog households, second dogs were assessed as more similar to the owner; moreover, the first and second dogs' similarity pattern complemented each other. We also replicated this study in a neighbouring country, pointing out cultural differences in the similarity pattern between Hungary and Austria (more and higher similarity was found in Hungarian owner-dog pairs).

As a limitation, we would like to mention that although we investigated whether other persons also find the owner and dog similar to each other (and they do), we cannot exclude the possibility that a part of the similarity we found originates from the owners projecting their own personalities onto the dogs. However, Kwan et al. (2008) suggests that owners project their own personality onto the dogs less than they project it onto other people. The other limitation is, again, the self-selection bias: our subjects were owners who voluntarily participate in the study and may be more interested in their dogs' behaviour than general dog owners are. It is possible that in case of dogs not kept as a family member (e.g. living in rural areas), we won't find any similarity between owners and dogs.

The main novelty of this study is that we found, that owners choose dogs as they choose human social partners. Despite that personality matching in human relationships is a popular topic in human psychology, according to our knowledge, no studies before addressed the personality similarity between owners and dogs. Moreover, if the firstly chosen dogs do not satisfy the owners' expectation of similarity, they acquire a second dog.

However, there are still questions left open by our study. First, the cultural differences we found in the similarity pattern suggest that dog keeping characteristics and the general role of the dog in the family affect which traits are relevant to the dog-owner similarity. Future research conducted in other countries where the dog keeping characteristics are somewhat different could explore these relationships. Second, we concluded in the discussion that the owner's choice for a similar dog is the most plausible explanation regarding our results. However, we know very little yet about how and why the owners choose a puppy or a particular breed, presenting a hypothesis for further studies.

Third, our results suggest that dog-human relationship could be used as a model for the development and maintenance of social relationships among humans. Aside from the traditional evolutionary causes explaining people's preference for similarity, like sexual imprinting or genetic similarity (e.g. Rushton and Bons, 2005), the person's choice of a social partner is also affected by cognitive, psychological, and cultural factors. These same factors could also affect the person's choice of an animal partner; studying them may reveal important insights about humans. Finally, these results could also be valuable for people

working for shelters or working dog organizations. Finding a dog who matches the prospective owner's personality could help to reduce the conflicts between the owner and dog and the risk of returning the adopted dog to the shelter.

Study III Breed and breed-group differences in personality traits

Evidence from genetic studies (e.g. Ruefenacht et al., 2002; Saetre et al., 2006) indicates that personality traits have genetic components. Based on the reduced genetic heterogeneity between dog breeds, comparing breeds on the basis of their typical behaviour could indirectly reflect the genetic background of the traits (i.e. traits with higher heritability should differ more between breeds than traits with stronger environmental influence).

Our aims in the third study were to investigate the breed-related differences and similarities in four personality traits (calmness, trainability, dog sociability and boldness), and to analyse the effect of two factors, the earlier function of the breed and the genetic relatedness between breeds on the traits.

Although all of our four traits differed between breeds, trainability was found to be the most typical on breed level, while calmness was the least breed-typical of our traits. We provided a descriptive analysis of 98 breeds in terms of their mean values and within-breed variability in these traits; moreover, to investigate their behavioural similarity and divergence we also grouped them based on their typical behaviour. Investigating the effect of earlier function and genetic relatedness, we found that both of these factors had a marked effect on trainability and boldness traits. For example, herding dogs and cooperative hunting dogs (pointers, retrievers) were found to be highly trainable, and terriers were found to be bolder than almost all other groups, in harmony with previous studies.

The main virtue of this study, again, arises from the large sample size, allowing us to investigate and characterize more breeds than any other study on this topic.

This study, of course, also has limitations. First, we did not investigate the typical keeping characteristics of the breeds. It is highly possible that some characteristics are more typical for some types of breeds (e.g. larger dogs were more likely to attend formal obedience training than small dogs, Kobelt et al., 2003). Second, as we worked with questionnaires, the owners' assessment of their dog could be biased by stereotypical beliefs of its breed. However, the diversity and the large number of dogs/breeds investigated may help to minimize these biases. The novelties of our investigation were the analysis of within-breed individual differences of the traits (no study explicitly addressed this topic before), and the analysis of the genetic relatedness.

Our descriptions of the breeds' typical behaviour were, in some cases, in contrast with their breed standards provided by the kennel clubs. For example, according to its breed standard, the Spanish Greyhound should not be overly shy (one of the eliminating faults, www.fci.be), however, this breed was found to be the least bold of all the breeds with an extreme low value. Therefore, owners should not rely on the breed standards when choosing a breed as even the vague behavioural characteristics provided there do not always reflect reality. Descriptions which are based on observation of individuals (like ours) could provide a more reliable characterization of the typical behaviour of real dog breed populations, which might help owners to choose the appropriate breed as a pet. Such descriptive analyses could also be useful when investigating cultural differences in the breeds' behaviour (e.g. different popular breeds), comparing geographic regions (e.g. different inbreeding level) or, when updated regularly, to follow possible trends and changes in the breeding population.

Study IV Gene polymorphisms in association with dog personality traits

Our fourth study was focusing on direct gene \times phenotype associations using the candidate gene approach. It was based on the assumption that some neurobiological and neuroendocrine systems (the main targets of the candidate gene studies), are highly conservative in evolutionary terms, therefore they may also retain some of their functions across species (i.e. affecting similar behaviour).

This study focused on the dopamine and oxytocin systems. Based on previous human and dog studies, we aimed to find associations between polymorphism in the tyrosine hydroxylase gene (TH, a candidate gene of the dopamine system) and activity–impulsivity phenotype in dogs. Human studies also reported associations between the oxytocin and several aspects of interpersonal and social behaviour; our second aim was to find associations between the oxytocin receptor gene (OXTR) polymorphisms and social behaviour in dogs, paralleling the human findings.

According to our results, in German Shepherds, the repeat polymorphism in the TH gene was related to activity–impulsivity assessed by both a behavioural test battery and a questionnaire. Two of the three SNPs found in the OXTR gene were related to Proximity seeking and Reaction to separation from the owner traits of the dogs.

Previous studies with similar aims mostly use questionnaires, or breed rating method when assessing the behavioural phenotype. The main virtue of this study was that we used a behavioural test battery on the individual level.

The main limitation of this study is the statistics. Behavioural traits, as any complex phenotype are determined by the interaction of numerous genes, thus the effect of a single gene is relatively small (i.e. specific alleles explain only a small part of the phenotypic variation). Due to the pioneer nature of our study, the statistical tests were not corrected for multiple comparisons. Moreover, although there are advantages of using only one breed in the analysis, it makes the results hard to generalize. Some breeds may lack these alleles or have others instead, and due to the very complex, cascading interaction between genes, even the same allele might function differently on different genetic background (i.e. in different breeds).

The main novelty in this study was that it provided the first evidence that polymorphisms in the OXTR gene are related to human-directed social behaviour in dogs. The involvement of oxytocin in determining social behaviour was previously studied mainly on rodents (e.g. Ayers et al., 2011) or on apes (e.g. Simpson et al., 2014), however dogs can be more easily studied in their natural social environment (human family).

Both gene \times behaviour associations we described in this study support the external validity of human findings, and offer the dog as a model for studying underlying genetic factors of ADHD or certain social disorders. However, by all means, our results also raised questions providing topics for further studies. First, as mentioned, our results might be specific to the (Hungarian) German Shepherd population, therefore further studies should replicate our findings on other dog populations and on other breeds. Second, further studies are also needed to reveal the molecular function of the different alleles, and their possible contribution to the gene function. Third, the effect of an allele could be environment-dependent. That is, epigenetic modifications due to environmental conditions could enhance or reduce the effect of an allele. Accordingly, some genetic effects may be found in specific environment, while other environmental influences may mask the same genetic effect. One SNP we found in the OXTR gene is located in a CpG island (a target place for epigenetic modifications), so this gene could be a perfect candidate for studying such gene \times environment interactions in OXTR gene in dogs.

1.4 Future directions in dog personality research

The most fundamental questions in dog personality research remain:

- 1) What to assess when measuring personality in dogs?

2) How best to assess personality in dogs?

Regarding the first question, what dog personality research needs the most are a standard taxonomy (i.e. nomenclature and descriptions) of the personality traits and a descriptive model of the personality structure. A standard taxonomy would facilitate the communication of different groups interested in assessing dog personality, enabling the researchers to reliably compare their results. A generally accepted structure of personality would permit researchers to study specified domains of personality characteristics, rather than examining traits partly overlapping across studies.

Regarding the second question, the lack of standard criteria in the methodology in dog personality research has been mentioned many times in this thesis, and also noted by a number of authors (e.g. Diederich and Giffroy, 2006; Taylor and Mills, 2006). What makes matters worse is that sometimes, important decisions about the future of individual dogs are made on the basis of unreliable test results (i.e. euthanizing shelter dogs). The absence of reports of reliability needs to be remedied in order to facilitate the development of a consensus regarding the structure and taxonomy of dog personality. Besides, reliable methods could also reduce the unnecessary replications of the study aims, design and evaluation.

As currently we are very far from reaching any consensus regarding the general structure of personality in dogs, a possible solution could be to move toward measuring specific personality traits (which are, more or less, accepted as existing in dogs, like fearfulness), instead of developing a global personality inventory trying to capture all the traits. The standardisation of specific trait measure would offer a greater comparability of research across dog studies and even across species, and could still leave space for further studies constructing more general tools based on these individual trait measures.

Topics for future studies are also proposed by some of the limitations of our studies, and by the questions our results gave rise to.

First, we know very little about where personality comes from. Although, we investigated both the environmental and genetic factors in associations with dog personality, we still do not know how much does the genetic background determine personality, how much of the adult personality is the result of interaction with the environment, and how the genetic and environmental factors interact in shaping the behaviour. Future studies about the biological basis of dog behaviour and personality (e.g. neural and endocrine mechanisms, epigenetic effects) are clearly needed to elucidate these issues.

Another future direction for dog personality is the evaluation of a more diverse sample of dogs and owners, including dogs not living as members of the family. Most of the dog personality studies (including our studies) target only a small and self-selected sample of dog owners. Analysing the consistent individual behaviour of dogs living in rural areas, or dog that are kept solely and strictly for a given practical function (e.g. like police dogs), could very well lead to different personality structure and different genetic and environmental associations.

Related to this, people's culture and experiences might shape how they regard their dogs and how they conceptualize their dogs' general behaviour. For example, people living in a country where dogs are used as a food source or where dogs present an epidemiological risk, may not find features, like intelligent, affectionate, or warm to be meaningful when characterizing a dog. Moreover, human social conditions, lifestyle, socioeconomics, public attitudes towards pets, laws and regulations of pet keeping, or conventions and possibilities to solve problems related to pets' behaviour in each country could shape dog management factors (e.g. popular breeds, neutering practices, socialisation methods, the prevalence of dog training, behaviour therapy, etc.). As keeping practices of dogs cannot be considered separately from the social and cultural contexts in which they live (Houpt et al., 2007), cross-country or cross-continent differences in the above mentioned factors could lead to different personality \times environment associations (e.g. Wan et al., 2009), different level of inbreeding and typical characteristics of certain breeds of dogs, etc. Nevertheless, cross-cultural comparisons and differences present an undeveloped field in dog personality literature.

Taken together, dog personality is a young, but dynamically developing field of ethological studies. Dog personality attracts great scientific interest, is a matter of public concern, and has a wide range of practical applications, including significant influence on the dog-human bond. However, many aspects of dog personality are rarely investigated or still an open question. Our work contributes to the understanding of dog personality in general, and could facilitate further research by providing background, raising questions, and hypotheses for future studies. We hope that sooner or later our results also reach the general public (e.g. owners, shelters, working dog programs) where they could be also beneficial in applied settings.

ACKNOWLEDGEMENTS

And so it has come. I'm writing the very last words in my doctoral thesis.

I don't think the one page space I dedicated to the acknowledgement is enough to mention the names and deeds of all the people who contributed to my studies, but I will give it a try.

First of all: **Family and friends**. If I were to try to describe all the ways in which you have helped me, it would go on forever, so I won't try. I promise if I ever win the Nobel Prize (which is not a sheer impossibility just terribly unlikely), I will prepare a better speech. Until then, just thank you for everything.

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Third, I would also like to "thank" my **pets** for providing the necessary (and sometimes unnecessary) distraction during the writing process. Writing a doctoral thesis and trying to meet the deadline is one thing, but writing a doctoral thesis and trying to meet the deadline while a cat purrs peacefully in your lap and a dog snores unabashedly in your bed is something completely different.

Fourth – as it is the only part of the thesis which is completely personal – I decided to include an unconventional group of people and express my gratitude to some of my favourite **composers** who, albeit indirectly, contributed in writing this thesis (without claim of completeness): Wolfgang Amadeus Mozart, John Williams, Charles Gounod, Felix Mendelssohn, Antonín Dvořák, Modest Petrovich Mussorgsky, Pyotr Ilyich Tchaikovsky, and Yann Tiersen.

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And last, but not least, I thank **You** for your attention!

APPENDICES

Appendix A. (Study II) The human personality questionnaire (44–BFI) and its scoring key

Personality Questionnaire

Here are a number of characteristics that may or may not apply to you. Please write a number next to each statement to indicate the extent to which you agree or disagree with that statement.

1 **2** **3** **4** **5**
 disagree strongly disagree a little neither agree nor disagree agree a little agree strongly

I see myself as someone who . . .

1	Is talkative	23	Tends to be lazy
2	Tends to find fault with others	24	Is emotionally stable, not easily upset
3	Does a thorough job	25	Is inventive
4	Is depressed, blue	26	Has an assertive personality
5	Is original, comes up with new ideas	27	Can be cold and aloof
6	Is reserved	28	Perseveres until the task is finished
7	Is helpful and unselfish with others	29	Can be moody
8	Can be somewhat careless	30	Values artistic, aesthetic experiences
9	Is relaxed, handles stress well	31	Is sometimes shy, inhibited
10	Is curious about many different things	32	Is considerate and kind to almost everyone
11	Is full of energy	33	Does things efficiently
12	Starts quarrels with others	34	Remains calm in tense situations
13	Is a reliable worker	35	Prefers work that is routine
14	Can be tense	36	Is outgoing, sociable
15	Is ingenious, a deep thinker	37	Is sometimes rude to others
16	Generates a lot of enthusiasm	38	Makes plans and follows through with them
17	Has a forgiving nature	39	Gets nervous easily
18	Tends to be disorganized	40	Likes to reflect, play with ideas
19	Worries a lot	41	Has few artistic interests
20	Has an active imagination	42	Likes to cooperate with others
21	Tends to be quiet	43	Is easily distracted
22	Is generally trusting	44	Is sophisticated in art, music, or literature

Scoring key:

Extraversion items: 1, 6R, 11, 16, 21R, 26, 31R, 36

Agreeableness items: 2R, 7, 12R, 17, 22, 27R, 32, 37R, 42

Conscientiousness items: 3, 8R, 13, 18R, 23R, 28, 33, 38, 43R.

Neuroticism items: 4, 9R, 14, 19, 24R, 29, 34R, 39

Openness items: 5, 10, 15, 20, 25, 30, 35R, 40, 41R, 44

Note: An R after an item indicates that the item is reverse coded.

Appendix B. (Study II) The dog personality questionnaire (Canine BFI) and its scoring key

Dog Personality Questionnaire

Here are a number of characteristics that may or may not apply to your dog. Please write a number next to each statement to indicate the extent to which you agree or disagree with that statement.

1 **2** **3** **4** **5**
 disagree strongly disagree a little neither agree nor disagree agree a little agree strongly

I see my dog as an individual who . . .

1	Is talkative, vocal	23	Tends to be lazy
2	Is disagreeable, difficult to please	24	Is emotionally stable, not easily upset
3	Does things thoroughly	25	Is inventive, finds new ways to get his/her way
4	Is down, depressed, blue	26	Has an assertive personality
5	Is original, comes up with new ways of doing things	27	Can be cold and aloof
6	Is reserved	28	Perseveres until the task is finished
7	Is helpful and unselfish	29	Can be moody
8	Can be somewhat careless	30	Appreciates sensory experiences
9	Is relaxed, handles stress well	31	Is sometimes shy, inhibited
10	Is curious about many different things	32	Is considerate and kind
11	Is full of energy	33	Does things efficiently
12	Starts quarrels with others	34	Remains calm in tense situations
13	Is a reliable dog	35	Enjoys learning and doing new things
14	Can be tense	36	Is outgoing, sociable
15	Appears contemplative, thoughtful	37	Is sensitive to the needs and feelings of others
16	Shows a lot of enthusiasm	38	Is playful, determined
17	Has a forgiving nature	39	Gets nervous easily
18	Tends to be disorganized	40	Appears to “reflect,” mull things over
19	Worries a lot	41	Is cooperative
20	Is unimaginative, dull	42	Is easily distracted
21	Tends to be quiet	43	Is sophisticated
22	Is generally trusting		

Scoring key:

Extraversion/Energy: 1, 6R, 11, 16, 21R, 26, 31R, 36

Agreeableness/Affection: 2R, 7, 12R, 17, 22, 27R, 32, 37, 41

Conscientiousness: 3, 8R, 13, 18R, 23R, 28, 33, 38, 42R

Neuroticism: 4, 9R, 14, 19, 24R, 29, 34R, 39

Openness/Intelligence: 5, 10, 15, 20R, 25, 30, 35, 40, 43

Note: An R after an item indicates that the item is reverse coded.

Appendix C. (Study III) Trait scores, within–breed variance (SD), and rankings of breeds on calmness, trainability, dog sociability and boldness. High trait rank means high mean score on that trait; high SD rank means low within–breed variance

Breed	N	AKC group	Genetic cluster	Calmness				Trainability				Dog sociability				Boldness			
				Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank
Airedale Terrier	24	4	2	1.425	7	0.512	25	1.567	53	0.394	51	1.552	25	0.404	13	1.597	32	0.491	36
Akita	20	3	1	1.300	32	0.560	50	1.460	69	0.441	69	0.738	98	0.469	33	1.433	61	0.612	78
Alaskan Malamute	11	3	1	1.655	2	0.411	5	1.127	96	0.561	96	1.341	62	0.551	72	1.394	68	0.467	27
American Cocker Spaniel	15	1	4	1.347	21	0.389	4	1.307	84	0.353	30	1.250	78	0.661	95	1.622	26	0.354	5
American Staffordshire Terrier	76	4	2	1.379	11	0.581	64	1.597	44	0.370	40	1.299	76	0.523	60	1.610	28	0.473	30
Anatolian Shepherd Dog	13	3		1.354	17	0.578	63	1.215	93	0.506	87	1.212	84	0.742	98	1.180	94	0.617	79
Appenzeller Sennenhund	27	7		0.844	96	0.575	60	1.652	26	0.286	13	1.352	59	0.434	24	1.333	74	0.547	57
Australian Shepherd	167	7	3	1.072	65	0.585	67	1.817	3	0.285	12	1.448	44	0.491	38	1.501	51	0.550	58
Batavian Mountain Hound	12	2		1.167	52	0.643	88	1.583	46	0.313	19	1.333	64	0.597	89	1.528	46	0.483	34
Beagle	200	2	4	1.202	46	0.550	41	1.568	52	0.426	62	1.609	14	0.403	12	1.544	42	0.533	51
Bearded Collie	46	7	3	1.222	43	0.535	32	1.604	38	0.356	33	1.685	6	0.410	15	1.515	49	0.402	11
Beauceron	10	7		1.000	80	0.558	48	1.740	13	0.212	3	1.475	38	0.571	82	1.167	96	0.572	64
Belgian Malinois	66	7	3	0.912	89	0.537	34	1.736	14	0.385	47	1.152	91	0.570	81	1.606	31	0.526	44
Bernese Mountain Dog	94	3	5	1.372	14	0.552	45	1.434	71	0.451	71	1.673	7	0.397	11	1.525	47	0.555	59
Border Collie	193	7	3	1.072	67	0.523	27	1.805	4	0.259	9	1.325	68	0.512	48	1.468	60	0.532	50
Border Terrier	11	4	2	1.255	38	0.566	54	1.636	28	0.408	56	1.318	69	0.501	45	1.697	12	0.433	18
Boxer	135	3	2	1.185	50	0.543	38	1.628	29	0.340	24	1.348	61	0.575	82	1.664	18	0.474	31
Briard	33	7		1.012	79	0.663	89	1.600	39	0.409	57	1.227	83	0.543	67	1.263	85	0.577	67
Brittany	10	1	4	0.980	85	0.476	13	1.260	91	0.267	11	1.475	38	0.506	46	1.333	74	0.667	89
Bull Terrier	23	4		1.052	71	0.604	78	1.313	83	0.404	55	1.304	74	0.603	90	1.725	6	0.385	8
Bulldog	92	6	2	1.363	16	0.576	61	1.430	73	0.429	66	1.486	35	0.514	52	1.609	29	0.500	38
Cairn Terrier	27	4	4	1.244	40	0.591	70	1.393	78	0.488	84	1.389	56	0.581	87	1.494	53	0.580	72
Cavalier King Charles Spaniel	20	5	4	1.320	27	0.461	9	1.600	39	0.477	83	1.713	3	0.284	2	1.317	79	0.663	88
Chihuahua	73	5	4	0.901	90	0.550	41	1.493	64	0.440	68	1.072	95	0.520	57	1.356	70	0.610	77
Collie	56	7	3	1.121	63	0.636	86	1.568	51	0.369	39	1.496	33	0.497	42	1.280	82	0.672	90
Coton de Tulear	16	6		1.238	41	0.735	97	1.363	80	0.352	29	1.578	20	0.498	43	1.333	74	0.558	60

Appendix C. (Continued)

Breed	N	AKC group	Genetic cluster	Calmness				Trainability				Dog sociability				Boldness			
				Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank
Dachshund	74	2	4	1.138	58	0.624	84	1.530	61	0.474	80	1.311	71	0.533	65	1.496	52	0.574	65
Dalmatian	123	6	4	1.033	76	0.597	75	1.472	67	0.457	73	1.435	47	0.512	48	1.594	35	0.561	61
Doberman Pinscher	124	3	4	0.929	88	0.592	71	1.613	34	0.368	37	1.311	72	0.552	73	1.503	50	0.513	41
Dogue de Bordeaux	14	3		1.400	9	0.538	35	1.229	92	0.421	61	1.482	37	0.465	31	1.429	63	0.591	74
English Cocker Spaniel	20	1	5	1.040	74	0.600	76	1.610	35	0.375	43	1.400	55	0.522	58	1.517	48	0.398	10
English Setter	11	1	4	1.164	54	0.731	96	1.291	88	0.459	74	1.500	29	0.500	44	1.212	88	0.719	97
Entlebucher Mountain Dog	17	7		1.071	68	0.600	76	1.800	5	0.224	4	1.235	81	0.555	76	1.667	17	0.408	12
Eurasier	21	6		1.343	24	0.465	11	1.295	85	0.459	74	1.560	24	0.512	48	1.270	84	0.621	81
Flat-Coated Retriever	18	1	4	1.378	12	0.586	68	1.789	7	0.242	5	1.694	4	0.450	28	1.833	1	0.287	2
French Bulldog	60	6	2	1.387	10	0.570	58	1.403	76	0.466	77	1.488	34	0.522	58	1.661	19	0.508	40
German Bracke	11	2		1.127	62	0.492	17	1.509	63	0.575	98	0.841	97	0.718	97	1.212	88	0.582	73
German Hunting Terrier	12	4		0.817	97	0.674	91	1.533	60	0.535	95	1.188	86	0.667	96	1.778	4	0.518	42
German Pinscher	12	3		0.667	98	0.500	20	1.683	21	0.376	44	1.583	18	0.359	7	1.389	69	0.618	80
German Shepherd Dog	413	7	5	1.103	64	0.565	53	1.613	33	0.373	42	1.139	92	0.562	80	1.637	22	0.482	33
German Shorthaired Pointer	20	1	4	1.260	35	0.555	47	1.800	5	0.304	15	1.563	23	0.512	48	1.833	1	0.333	3
German Spitz	12	6		0.883	93	0.618	81	1.283	90	0.471	79	1.354	58	0.548	69	1.583	36	0.571	63
German Wirehaired Pointer	31	1		1.368	15	0.493	18	1.768	10	0.354	31	1.250	78	0.585	88	1.677	13	0.468	28
Giant Schnauzer	63	3	4	1.302	31	0.542	37	1.733	15	0.305	16	1.337	63	0.537	66	1.757	5	0.370	7
Golden Retriever	364	1	4	1.257	36	0.566	54	1.563	55	0.388	49	1.573	21	0.459	29	1.579	38	0.483	34
Gordon Setter	11	1	4	1.236	42	0.463	10	1.655	25	0.311	18	1.727	2	0.425	19	1.424	64	0.598	75
Great Dane	76	3	3	1.208	45	0.623	83	1.437	70	0.428	65	1.372	57	0.555	76	1.469	59	0.561	61
Greater Swiss Mountain Dog	72	3	5	1.131	61	0.577	62	1.608	36	0.412	58	1.535	26	0.518	55	1.403	66	0.579	67
Havanese	75	5		1.352	18	0.541	36	1.568	50	0.376	44	1.513	27	0.525	61	1.409	65	0.609	76
Hovawart	96	3		1.246	39	0.530	28	1.690	19	0.341	25	1.297	77	0.516	53	1.649	20	0.450	23
Ibizan Hound	30	2	4	0.893	92	0.621	82	1.487	65	0.469	78	1.450	43	0.519	56	1.200	92	0.699	95
Irish Setter	30	1	4	1.287	33	0.562	52	1.700	17	0.301	14	1.767	1	0.347	3	1.322	78	0.622	82
Soft Coated Wheaten Terrier	19	4	2	1.137	59	0.570	58	1.600	39	0.389	50	1.566	22	0.478	37	1.544	43	0.435	20
Irish Terrier	15	4	2	1.320	27	0.627	85	1.573	49	0.328	21	1.167	90	0.532	64	1.711	10	0.395	9

Appendix C. (Continued)

Breed	N	AKC group	Genetic cluster	Calmness				Trainability				Dog sociability				Boldness			
				Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank
Irish Wolfhound	13	2	3	1.631	4	0.446	6	1.031	98	0.453	72	1.692	5	0.356	6	1.282	81	0.542	54
Jack Russell Terrier	327	4	4	0.998	82	0.550	41	1.643	27	0.368	37	1.191	85	0.546	68	1.672	16	0.431	17
Kromfohrlander	54	5		1.000	80	0.559	49	1.774	9	0.246	6	1.116	93	0.511	47	1.241	88	0.544	56
Labrador Retriever	517	1	2	1.323	26	0.535	32	1.667	24	0.354	31	1.642	10	0.433	23	1.712	9	0.434	19
Landseer	12	3		1.850	1	0.243	1	1.600	39	0.362	36	1.604	16	0.470	34	1.806	3	0.265	1
Leonberger	16	3	5	1.163	55	0.690	94	1.400	77	0.511	90	1.609	13	0.353	4	1.583	36	0.638	86
Lhasa Apso	16	6	1	1.350	19	0.376	3	1.125	97	0.526	93	1.438	46	0.423	17	1.354	71	0.412	13
Vizsla	44	1	4	1.018	77	0.549	40	1.777	8	0.306	17	1.580	19	0.395	10	1.485	55	0.637	85
Maltese	49	5	5	0.988	83	0.610	79	1.314	82	0.526	93	1.112	94	0.631	94	1.347	73	0.691	93
Miniature Dachshund	18	2		1.167	52	0.510	23	1.556	57	0.420	59	1.403	52	0.447	27	1.241	88	0.694	94
Miniature Pinscher	25	5	5	0.896	91	0.507	22	1.576	48	0.426	62	1.330	66	0.615	93	1.640	21	0.419	15
Miniature Poodle	26	5	4	1.069	69	0.669	90	1.546	58	0.465	76	1.231	82	0.424	18	1.295	80	0.676	91
Miniature Schnauzer	15	4	4	1.333	25	0.458	8	1.613	32	0.396	52	1.500	29	0.559	79	1.333	74	0.579	67
Newfoundland	31	3	2	1.632	3	0.487	16	1.426	74	0.511	90	1.621	11	0.432	22	1.677	13	0.339	4
Old English Sheepdog	10	7	3	1.200	47	0.471	12	1.560	56	0.350	28	1.475	38	0.275	1	1.700	11	0.368	6
Parson Russell Terrier	86	4		1.037	75	0.534	31	1.763	11	0.343	26	1.236	80	0.554	75	1.674	15	0.460	26
Pekingese	16	5	4	1.350	19	0.554	46	1.288	89	0.450	70	1.328	67	0.604	91	1.542	44	0.530	48
Perro de Presa Canario	12	3	2	0.850	95	0.610	79	1.433	72	0.328	21	1.063	96	0.575	82	1.472	58	0.540	53
Pointer	10	1	4	1.140	57	0.582	66	1.680	22	0.253	8	1.650	8	0.474	35	1.633	24	0.457	25
Polish Lowland Sheepdog	20	7		0.940	87	0.592	71	1.830	2	0.262	10	1.188	86	0.443	26	1.433	61	0.531	49
Poodle	47	6	5	1.192	49	0.486	15	1.617	31	0.397	53	1.303	75	0.552	73	1.475	57	0.577	67
Pug	82	5	4	1.402	8	0.482	14	1.520	62	0.432	67	1.613	12	0.407	14	1.724	7	0.422	16
Pyrenean Shepherd	23	7		1.052	71	0.561	51	1.687	20	0.386	48	1.413	49	0.549	70	1.188	93	0.479	32
Rhodesian Ridgeback	64	2	5	1.256	37	0.567	56	1.472	66	0.371	41	1.453	42	0.556	78	1.276	83	0.622	82
Rottweiler	137	3	5	1.346	23	0.595	74	1.604	37	0.399	54	1.310	73	0.491	38	1.577	39	0.501	39
Saint Bernard	21	3	5	1.305	30	0.680	93	1.200	95	0.562	97	1.500	29	0.474	35	1.635	23	0.446	22
Chinese Shar-Pei	13	6	1	1.200	47	0.739	98	1.215	93	0.360	34	1.500	29	0.550	71	1.128	97	0.687	92
Shetland Sheepdog	21	7	3	1.171	51	0.511	24	1.695	18	0.383	46	1.607	15	0.376	8	1.349	72	0.703	96

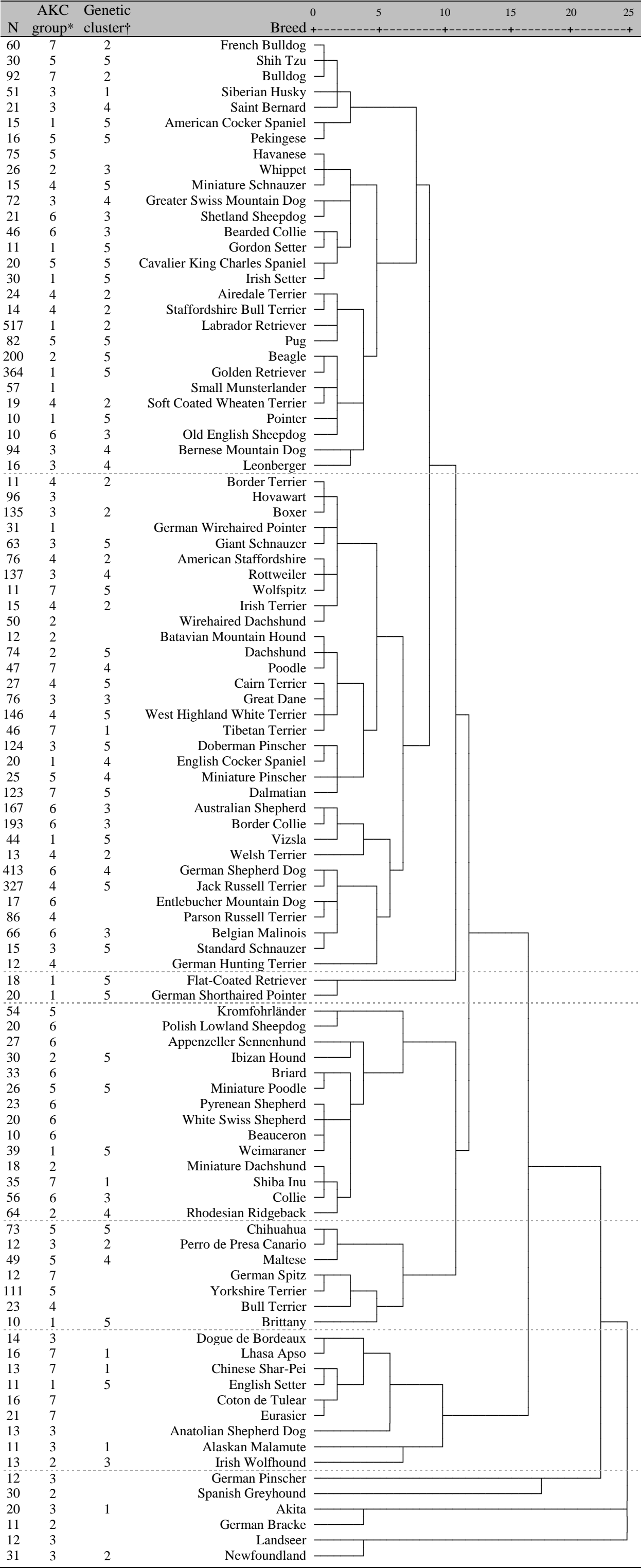
Appendix C. (Continued)

Breed	N	AKC group	Genetic cluster	Calmness				Trainability				Dog sociability				Boldness			
				Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank	Trait score	Trait rank	SD	SD rank
Shiba Inu	35	6	1	1.131	60	0.640	87	1.577	47	0.475	81	1.414	48	0.437	25	1.171	95	0.579	67
Shih Tzu	30	5	4	1.373	13	0.530	28	1.380	79	0.510	89	1.483	36	0.580	86	1.622	26	0.523	43
Siberian Husky	51	3	1	1.455	5	0.498	19	1.294	86	0.505	86	1.402	54	0.525	61	1.628	25	0.456	24
Small Munsterlander	57	1		1.053	70	0.568	57	1.625	30	0.334	23	1.504	28	0.464	30	1.561	40	0.472	29
Spanish Greyhound	30	2		0.880	94	0.704	95	1.293	87	0.517	92	1.650	8	0.392	9	0.933	98	0.750	98
Staffordshire Bull Terrier	14	4	2	1.443	6	0.676	92	1.586	45	0.426	62	1.446	45	0.614	92	1.595	33	0.526	44
Standard Schnauzer	15	3	4	0.987	84	0.548	39	1.720	16	0.211	2	1.183	89	0.427	20	1.556	41	0.412	13
Tibetan Terrier	46	6	1	1.274	34	0.520	26	1.422	75	0.503	85	1.402	53	0.493	41	1.594	34	0.535	52
Weimaraner	39	1	4	1.072	66	0.594	73	1.759	12	0.248	7	1.474	41	0.428	21	1.256	86	0.543	55
Welsh Terrier	13	4	2	1.015	78	0.451	7	1.877	1	0.192	1	1.404	51	0.526	63	1.718	8	0.636	84
West Highland White Terrier	146	4	4	1.153	56	0.550	41	1.460	68	0.476	82	1.408	50	0.492	40	1.537	45	0.526	44
Whippet	26	2	3	1.346	22	0.501	21	1.546	58	0.360	34	1.596	17	0.354	5	1.397	67	0.499	37
White Swiss Shepherd Dog	20	7		1.050	73	0.587	69	1.680	22	0.321	20	1.350	60	0.516	53	1.250	87	0.529	47
Wirehaired Dachshund	50	2		1.216	44	0.581	64	1.600	39	0.420	59	1.185	88	0.465	31	1.607	30	0.445	21
Wolfspitz	11	6	4	1.309	29	0.339	2	1.564	54	0.344	27	1.318	69	0.420	16	1.485	55	0.639	87
Yorkshire Terrier	111	5		0.942	86	0.533	30	1.342	81	0.506	87	1.331	65	0.571	82	1.487	54	0.576	66

AKC groups: 1 Sporting dogs; 2 Hounds; 3 Working dogs; 4 Terriers; 5 Toy dogs; 6 Herding dogs; 7 Non-sporting dogs

Genetic clusters: 1 Ancient breeds; 2 Mastiff/Terrier cluster; 3 Herding/Sighthound cluster; 4 Mountain cluster; 5 Hunting cluster

Appendix D. (*Study III*) Dendrogram illustrating the relationship between breeds based on four personality trait: calmness, trainability, dog sociability, and boldness. The length of the connecting lines represents the squared Euclidean distance between breeds. The six behavioural clusters are separated by dashed lines



*AKC groups: 1 Sporting dogs; 2 Hounds; 3 Working dogs; 4 Terriers; 5 Toy dogs; 6 Herding dogs; 7 Non-sporting dogs

†Genetic clusters: 1 Ancient breeds; 2 Mastiff/Terrier cluster; 3 Herding/Sighthound cluster; 4 Mountain cluster; 5 Hunting cluster

Appendix E. (*Study IV*) Behavioural variables coded in each subtest (E: experimenter, O: owner)

Subtest	Variable description	Score			
		0	1	2	3
Spontaneous activity	Duration of moving the legs	no moving	1–50 %	51–99 %	100 %
Greeting	Latency of approaching the E	no approach	5–15 s	1–5 s	immediately
	Latency of following the E after petting the dog	no follow	5–15 s	1–5 s	immediately
Separation	Duration of moving the legs in the 1. separation phase	no moving	1–50 %	51–99 %	100 %
	Duration of orientation to the O in the 1. separation phase	no orientation	1–50 %	51–99 %	100 %
	Latency of approaching the E	no approach	5–15 s	1–5 s	0 s
	Latency of following the E after petting the dog	no follow	5–15 s	1–5 s	0 s
	Duration of moving the legs in the 2. separation phase	no moving	1–50 %	51–99 %	100 %
	Duration of orientation to the O in the 2. separation phase	no orientation	1–50 %	51–99 %	100 %
	Latency of approaching the O	no approach	5–15 s	1–5 s	0 s
	Latency of following the O after petting the dog	no follow	5–15 s	1–5 s	0 s
Lying on the side	Latency of lying to the side	immediately	1–14 s	15–30 s	not lying down
Threatening approach	Final reaction	avoid	neutral	2	friendly
	Latency of approaching the E after threatening	no approach	10–30 s	1–9 s	immediately
Problem solving	Number of looking at the O in the 1. trial	0 time	1 time	2 times	3 times
	Number of looking at the E in the 1. trial	0 time	1 time	2 times	3 times
	Number of looking at the O in the 2. trial	0 time	1 time	2 times	3 times
	Number of looking at the E in the 2. trial	0 time	1 time	2 times	3 times
Separation II (hiding)	Duration of orientation to the O	no orientation	1–50 %	51–99 %	100 %
	Duration of vocalization	no vocalization	1–50 %	51–99 %	100 %
	Latency of approaching the O	no approach	5–15 s	1–5 s	immediately
	Motion type towards the O	no approach	walking	trotting	galloping

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SUMMARY

The general aims of the studies described in this thesis are to develop reliable ethological methods for measuring personality traits in dogs and to identify both environmental and genetic factors in association with these traits. As several human personality traits have analogues in this species, dogs could be an adequate model for studying many questions about personality that are difficult to address based on human studies alone. Moreover, many groups (owners, shelters, dog trainers), are interested in predicting the dogs' future behaviour in different situations, therefore developing reliable tools for characterizing the dogs' personality and studying the genetic and environmental factors affecting it could also have large practical values.

In *Study I*, assessing the questionnaire data of > 10,000 dogs we aimed to analyze the effects of multiple environmental factors and their interaction on four personality traits. We identified the most relevant variables in association with each trait, and also uncovered complex interactions between.

In *Study II*, we focused on the personality of the owner as a special environmental factor affecting the dogs' personality. We found positive correlations between the owners' and dogs' personality profile. This similarity is not (only) the owner's projection, does not change with the length of relationship, but the number of dogs in the household and the country of residence affect it.

In *Study III*, we investigated the discriminative potential of four personality trait among dog breeds, and investigated the effect of earlier function and genetic relatedness between breeds on the behaviour. Trainability was found to be the most typical on breed level, while calmness was the least breed-typical of our traits; trainability and boldness traits were also affected by the earlier function and the genetic relatedness between breeds.

In *Study IV*, we investigated two candidate genes, the tyrosine-hydroxylase (TH) and the oxytocin receptor gene (OXTR) in association with activity-impulsivity and social behaviour of the dogs. According to our results, the allelic variations in the TH gene was related to activity-impulsivity trait, allelic variations in the OXTR gene were related to Proximity seeking and Reaction to separation from the owner traits of the dogs.

ÖSSZEFOGLALÓ

E disszertációban bemutatott kutatásaink általános célja, hogy etológiai módszerekkel felmérjük a kutyák esetében megfigyelhető személyiségvonásokat, valamint megvizsgáljuk az e vonásokat befolyásoló egyes genetikai és környezeti hatásokat. Minthogy egyes humán személyiségjegyek analógja vizsgálható ennél a fajnál, így a kutya alkalmas modell lehet az emberi személyiségvizsgálatokhoz. Gyakorlati szempontból nézve a kutya személyiségének megbízható felmérése, és a személyiséget befolyásoló környezeti / genetikai faktorok vizsgálata számos csoport (kiképzők, menhelyek, és nem utolsó sorban gazdák) számára szintén fontos lehet.

Első vizsgálatunkban a személyiségvonásokat befolyásoló demográfiai, valamint kutyatartással kapcsolatos jellemzőket vizsgáltuk egy több, mint 10.000 kutyát tartalmazó kérdőíves adatsort elemezve. Kutatásunkban azonosítottuk az egyes vonásokat legerősebben befolyásoló tényezőket, valamint elemeztük a környezeti hatások közötti komplex interakciókat is.

Második vizsgálatunkban a gazda személyiségét, mint speciális környezeti tényezőt vizsgáltuk a kutya személyiségével összefüggésben. Pozitív korrelációt találtunk a kutya és gazdája személyisége között, mely hasonlóság nem tudható be kizárólag a gazda szubjektív értékelésének, illetve nem változik a kapcsolat hosszával. A korreláció mintázata azonban eltér az egyedül, illetve másik kutyával élő kutyák között, valamint a két vizsgált ország, Magyarország és Ausztria között.

Harmadik vizsgálatunkban az vizsgáltunk, az egyedek személyiségét mennyiben befolyásolja a fajta, illetve fajtacsoport, amibe tartoznak. Kimutattuk, hogy az általunk vizsgált vonások közül leginkább a képezhetőség, legkevésbé pedig a nyugodtság függ a fajtától, valamint, hogy a képezhetőség és merészség vonásokat mind a fajták (feltételezhető) korábbi funkciója, mind pedig a fajták közötti genetikai hasonlóság mértéke befolyásolja.

Negyedik vizsgálatunkban két kandidáns gén, a tirozin–hidroxiláz (TH) és az oxitocin receptor gén (OXTR) allélpolimorfizmusai valamint a kutyák aktivitása–impulzivitása és szociális viselkedése között kerestünk kapcsolatot. Eredményeink szerint a kutyák aktivitása és impulzivitása a TH gén allélváltozataival, a kutyák közelségkeresése és szeparációs viselkedése pedig az OXTR allélváltozataival mutatott összefüggést.