Applied Animal Behaviour Science xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

Heritability of behavioural traits in domestic dogs: A meta-analysis

Lenka Hradecká [a], Luděk Bartoš [a,b,*], Ivona Svobodová [a], James Sales [c]

[a] Department of Animal Science and Ethology, Czech University of Life Sciences Prague; Kamýcká 129, 135 11 Praha 6 - Suchdol, Czech Republic
[b] Department of Ethology, Institute of Animal Science, Přátelství 815,104 00 Praha-Uhříněves, Czech Republic
[c] Department of Animal Science and Food Processing, Faculty of Tropical AgriSciences, Czech University of Life Sciences, Kamýcká 129, 165 21 Praha 6-Suchdol, Czech Republic

ARTICLE INFO

Article history:
Received 13 February 2015
Accepted 15 June 2015
Available online xxx

Keywords:
Dog
Behavioural traits
Heritability
Meta-analysis
Canine

ABSTRACT

Reviews summarizing the literature on heritability of behavioural traits in dogs have been published repeatedly over the last four decades. The conclusions of these reviews vary to some extent. We applied meta-analysis and re-evaluated the literature available collecting 48 references dealing with heritability of behavioural traits in domestic dogs. For each study included, data was extracted for individual behavioural traits. Each of these traits was entered into the analysis as a separate unit of measure, giving a total of 1763 measures. We classified the traits measured in each study into five functional categories (Environment, Herding, Hunting, Play, and Psychical characteristic). The meta-analysis has shown low general heritability of the categorised behavioural traits analysed. Thus, the commonly used behaviour tests for many breeds, to determine the dog's eligibility for reproducing, traditionally required by many associations, is not supported by the present results of the meta-analysis.

Contents

1. Introduction

Behavioural differences between domestic dog breeds and between lines within breeds are known and have been also well documented (Mackenzie et al., 1986; Willis, 1995; Ostrander and Kruglyak, 2000; Houpt and Willis, 2001; Houpt, 2007; Hall and Wynne, 2012; Mehrkam and Wynne, 2014). In rare cases it has been reported that selective breeding for a few generations of dogs may result in apparently diverging behaviourally different strains or in eradicating or reducing the frequency of problematic behaviour (Murphree et al., 1974; Takeuchi and Houpt, 2003). Such reports have strengthened or re-enforced the traditional opinion of dog breeders on the importance of selection for the required behavioural activity used for working dogs despite the many decades of debate about heritability of such traits. Although reviews on heritability of behavioural traits in dogs have shown mostly low values as long ago as 40 years (Murphree et al., 1974), many associations or organizations for various breeds still formally require them to pass behavioural testing before the dog is allowed to reproduce. Nevertheless, the success of any breeding program incorporating behavioural traits in dogs

* Corresponding author at: Department of Ethology, Institute of Animal Science, Přátelství 815, 104 00 Praha Uhříněves, Czech Republic. Tel.: +420 731 650 801.
E-mail address: bartos@vuzv.cz (L. Bartoš).

http://dx.doi.org/10.1016/j.applanim.2015.06.006
0168-1591/

depends on an understanding of the genetics of such behavioural traits.

Both genotype and environment affect the development of behavioural traits in dogs (e.g., Scott and Fuller, 1965; but see Charney, 2012). The relationship between these two factors influences the potential success of any breeding and selection program (Mackenzie et al., 1986). There is a recent trend to locate putative genes affecting individual types of canine behaviour (Masuda et al., 2004; Ogata et al., 2006; Houpt, 2007; Lit et al., 2013; Kis et al., 2014). However, progress of this approach has not yet reached the stage of practical application for most behavioural traits. Therefore, estimating heritability of the behaviour still remains the essential tool for breeding programs in most cases.

Reviews summarizing the literature on heritability of behavioural traits in dogs have been published repeatedly over the last four decades (Mackenzie et al., 1985; Willis, 1995; Houpt and Willis, 2001; Takeuchi and Houpt, 2003; Houpt, 2007; Hall and Wynne, 2012). The conclusions of these reviews vary to some extent. Mackenzie et al. (1986) concluded that various scores such as those of German Schutzhund score show a low chance of heritability indicating that such performance scores are not an accurate reflection of the animal's genetic make-up. Willis (1995) pointed out that in many cases values did not differ significantly from zero, but some aspects of sensitivity were moderately heritable. Similar conclusion may be found in other reviews as for example by Houpt and Willis (2001) and Houpt (2007) who listed differences in heritability between categories of behavioural traits such as those used in guide dogs, hunting dogs, police and armed service work, herding and livestock protection dogs, etc. They also presented individual cases in which certain traits showed reasonable heritability. In their summary Takeuchi and Houpt (2003) with their emphasis on the development of molecular biology forecasted, optimistically, the development of new genetic treatment methods for problem behaviour and training programs suited to the individual. As stressed by Borenstein et al. (2009), the obvious limitation of "narrative reviews", such as those cited, is the subjectivity inherent in this approach. Different authors might use different criteria for deciding which studies have relevance and which do not. To overcome this, we applied meta-analysis and re-evaluated the literature available. Contrary to subjective qualitative narrative reviews, reviews by meta-analytic techniques account for variability among studies, and present a quantitative measure of effects and their precision.

Early studies have shown much higher values of heritability of traits such as hunting skills or components of behaviour required for in army or military working dogs are received from the dam rather than the sire (e.g., Geiger, 1973 cited in Mackenzie et al., 1986; Reuterwall and Ryman, 1973). Such a difference between the sexes in heritability of behavioural traits has usually disappeared when a more sophisticated statistical test was applied (e.g., Karjalainen et al., 1996; Liinamo et al., 1997, etc.). Multifactorial analysis revealed that values of heritability of behavioural traits were affected not only by biotic factors such as age and sex, suggesting importance of experience, training, and learning (e.g., Karjalainen et al., 1996; Meyer et al., 2012), but also by abiotic factors such as testing month, weather during the testing, place of testing, judges, etc. This questioned the methods of evaluating heritability. A remarkable increase in the heritability estimate was detected when the authors focused on the behavioural traits before the start of training or traits which are supposedly inborn or innate, needing no systematic training (e.g., Fält et al., 1982; Schmutz and Schmutz, 1998; Wilsson and Sundgren, 1998). Therefore, we analysed the heritability estimates not only according to dog breeds, but also according to sex of the parent, whether the analysis applied a multifactorial approach, and whether or not the tested trait needed to be learnt and/or trained.

2. Material and methods

2.1. Data

We have adopted an approach performing independent searches by two authors in the ISI Web of Knowledge database (www.isiknowledge.com) using the keywords "heritabil*", "dog*" and "behav*". We also performed searches among the references within those studies which had not been shown in the ISI Web of Knowledge database (e.g., Mackenzie et al., 1986; Houpt and Willis, 2001; Houpt, 2007) and in our own personal databases. Furthermore, we entered these keywords into Google (www.google.com), where we also used combinations of words "heritability" "dog" and "behavior" or "behaviour". Through this we obtained a contribution from a conference (Liinamo, 2004) and two theses (Hoffmann, 2000; Schiefelbein, 2012). For some studies we only found abstracts and therefore asked for the full versions from the authors of these studies. Last searches were done in March 2014.

For the meta-analysis we collected 47 references dealing with heritability of behavioural traits in domestic dogs (Table 1).

We included correlation coefficients of behavioural traits of interest and sample sizes in order to calculate combined effect sizes and their precision (95% confidence intervals). No restrictions were placed on criteria such as year in which publish or language of publications. In theory, heritability and genetic correlation must be positive and within the range 0 to 1. It happened, however, that various authors presented values that were negative or in excess of 1. This may be due to relatively small data sets with the variability of the estimators being quite large, increasing the probability of a negative estimate when the true heritability is close to zero (Bartlett, 1976). Heritability values in excess of 1 may result from insufficient numbers or high standard errors attached to them (Willis, 1995). Therefore, for this study we have only used heritability estimates within the range 0 to 1 and removed traits with negative heritability estimates (Reuterwall and Ryman, 1973; Bartlett, 1976; Goddard and Beilharz, 1982; Kreiner et al., 1992; Wilsson and Sundgren, 1998) and estimates greater than 1 (Fält et al., 1982; Wilsson and Sundgren, 1998; Liinamo et al., 2007). For each study included, data was extracted for the individual behavioural trait. The range was from one trait per study (Mackenzie et al., 1985) up to 16 traits per study (Goddard and Beilharz, 1985). Each of the traits entered the analysis as a separate measure, giving a total of 1761 measures. The problem with data like these is that the authors usually used their own terms for the traits, particularly those papers written in a language other than English. As shown by Saetre et al. (2006), a pattern of co-inheritance was found to be similar for 16 behavioural traits examined in German shepherd and Rottweiler dogs. Hence, we decided to unify the behavioural traits into summarising categories. Such an approach is always subjective and it could happen that each reader would make his or her own classification. Nevertheless, we classified these measures from each study into one of the five functional categories (Environment, Herding, Hunting, Play, and Psychical characteristic) based on the focus of the study and indices which it contained. This classification was first discussed with local dog experts and the result is shown in Table 2. For the category Environment, 119 measures of the behavioural trait were used from 18 studies (Table 2). An additional three studies could not be used due to missing data (Scott and Bielfelt, 1976; Fält et al., 1982; Houpt and Willis, 2001). For the category Herding, 153 measures were taken from six studies of the Border Collie (Table 2). For Hunting 247 measures from 34 studies were available. For the category Play, we only obtained two measures from two studies. The largest set of measures was collected from the category Psychical characteristics, from which we analysed 1232 measures originating from 36 studies (Table 2). An additional two studies

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006

Table 1
Summary of studies used to evaluate the heritability of the dog behavioural traits.

Study	Country	Breed	Branch	Traits	Before training	Trainability	Sex	Heritability	Number of progeny (male/female)	From sires	From dams
Geiger (1973) cited in Mackenzie et al. (1986)	Germany	Dachshund		Hare tracking, nose, seek, obedience	NA	NA, Yes	M, F	0–0.46	1463	21	
Reuterwall and Ryman (1973)	Sweden	German Shepherd Dog		Affability, disposition for self-defence, disposition for self-defence and defence of handler, disposition for fighting in a playful manner, courage, ability to meet with sudden strong auditory disturbance, disposition for forgetting unpleasant incidents, addictiveness to different situations and environments	NA	NA, No	M, F	−0.11–0.26	958	29	
Bartlett (1976)	USA	Unknown	Guide dog	Body sensitivity, ear sensitivity, protective instinct, fighting instinct, confidence, self-right, energy, willingness, intelligence, nose	NA	NA, No, Yes	M, F, both	−0.21–0.49	601/1001		
Scott and Bielfelt (1976)	USA	Unknown	Guide dog	Sit, come, fetch, trained response, willing in training, body sensitivity, ear sensitivity, new experience response, willing new experience, traffic, footing crossing, closeness, heel	NA	NA, No, Yes	Both	0–0.24			
Pfleiderer-Högner (1979)	Germany	German Shepherd Dog		Tracking, obedience, man work, character	NA	NA, No, Yes	M, F	0.01–0.2	1291	37	
Fält et al. (1982)	Sweden	German Shepherd Dog	Puppies	Yelp, shriek, contact 1, fetch, retrieve, reaction, social competition, activity, contact 2, exploratory behaviour	Yes	NA, No, Yes	M, F	0.05–1.11			
Goddard and Beilharz (1982)	Australia	Labrador Retriever	Guide dog	Success, fear, dog distraction, excitability	Yes	NA, No	M, F	−0.04–0.67	394		
Goddard and Beilharz (1983)	Australia	Labrador Retriever	Guide dog	Nervousness, suspicion, concentration, willingness, distraction, dog distraction, nose distraction, sound shy, hearing sensitivity, body sensitivity, fearfulness	Yes	NA, No	Both	0–0.58	249		
Goddard and Beilharz (1985)	Australia	Diallel cross Labrador Retriever German Shepherd Dog Boxer Kelpie	Guide dog fearfulness	Avoidance of objects, startle response, excessively alert, party whistle, person jumping behind the dog, small toy horse, starting pistol, beach ball thrown away from the dog, toy car traveling in circles, model guide dog, aluminium bowl dropped on the ground, metal door banged, jumping at the dog, opening umbrella in front of the dog, holding the dog and speaking loudly, plastic rubbish bag	Yes	NA, No	Both	0.05–0.88	102		
Mackenzie et al. (1985)	USA	German Shepherd Dog	Working dog	Temperament	Yes	No	Both	0.51	575	18	71
Vangen and Klemetsdal (1988)	Finland	Finnish Spitz	Hunting	Findings birds, holding birds	No	Yes	Both	0.11–0.18	4864		
Vangen and Klemetsdal (1988)	Finland	English Setter, Finnish Spitz	Hunting	Hunting eagerness, style, speed, independence, seeking width, ability to work in the field, cooperation, bird-finder index	No	NA, No	M, both	0.09–0.22	224		
Vangen and Klemetsdal (1988)	Finland	Finnish Spitz	Hunting	Search ability, mark, bark, follow the bird	No	NA	Both	0.02–0.1	4864		

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006

Table 1 (*Continued*)

Study	Country	Breed	Branch	Traits	Before training	Trainability	Sex	Heritability	Number of progeny (male/female)	From sires	From dams
Vangen (1990)	Finland	German Short Haired Pointer, German Wire Haired Pointer	Hunting	Hunting eagerness, style, speed, ability to work in the field, cooperation with the handler	NA	NA, No	Both	0.14–0.35			
Kreiner et al. (1992)	Austria	Dachsbracke, Tyrolean Bracke, Brandlbracke, Styrian Coarse Haired Mountain Bracke	Hunting	Positive value, leash, postpone, shoot, obedience, behaviour on dead deer, dead point, welding work, sharp, scent, search	No	NA, No, Yes	Both	−0.006–0.91	3385		
Karjalainen et al. (1996)	Finland	Finnish Spitz	Hunting	Frequency of barking, searching scores, barking scores, following scores, total impression scores, total merit scores	No	NA	Both	0.055–0.16	1683		
Liinamo et al. (1997)	Finland	Finnish Hound	Hunting	Search, pursuit, tongue, ghost, check work, character, combined traits	No	NA, No, Yes	Both	0.01–0.15	5666		
Wilsson and Sundgren (1997)	Sweden	German Shepherd Dog, Labrador Retriever	Behavioural test for service dog	Courage, sharpness, defence drive, prey drive, nerve stability, hardness, temperament, affability, ability to cooperate	Yes	No	Both	0.05–0.37	2107		
Schmutz and Schmutz (1998)	USA	German Short Haired Pointer, German Wire Haired Pointer, Griffon, Large Munsterlander, Pudel Pointer	Hunting	Nose, search, waterworks, pointing, tracking, desire, cooperation, weighted total score	No	NA, No	Both	0.05–0.8	484		
Wilsson and Sundgren (1998)	Sweden	German Shepherd Dog	Puppy test for service dog work	Yelp, shriek, contact 1, fetch, retrieve, large ball, tug of war, activity, contact 2, objects visited	Yes	No	M, F, Both	−0.6–1.67	277/277	84	109
Hoffmann (2000)	Germany	Border Collie	Herding behaviour	Outrun, lift, fetch, drive, fangen, pen, shed	No	NA	Both	0.002–0.205			
Houpt and Willis (2001)	USA	German Shepherd Dog	Police service dog	Self-defence, courage, dispositional forget unpleasant incidents, adaptability to different situations	NA	NA, No	Both	0.02–0.14			
Houpt and Willis (2001)	USA	English Setter, German Wire Haired Pointer, German Short Haired Pointer, German Shepherd Dog, Labrador Retriever	Hunting	Hunting eagerness, water retrieving, tracking, temperament, nervousness	NA	NA, No	Both	0.22–0.58			
Brenøe et al. (2002)	Norway	German Short Haired Pointer, German Wire Haired Pointer, Brittany Spaniel Breton	Hunting	Hunting eagerness, speed, style, independence, seeking width, ability to work in the field, cooperation, bird finder index	No	NA, No	M, F	0–0.28	1505		
Hoffmann et al. (2002)	Germany	Border Collie	Herding behaviour	Outrun, lift, fetch, drive, fangen, pen, shed	No	NA	Both	0.002–0.129	337		
Ruefenacht et al. (2002)	Switzerland	German Shepherd Dog	Standardized behaviour test	Self-confidence, nerve stability, reaction to gunfire, temperament, hardness, defence drive, sharpness	No	NA, No	M, F, both	0.09–0.42	3497		

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006

Table 1 (*Continued*)

Study	Country	Breed	Branch	Traits	Before training	Trainability	Sex	Heritability	Number of progeny (male/female)	From sires	From dams
Hoffmann et al. (2003a)	Germany	Border Collie	Herding behaviour	Outrun, lift, fetch, drive, pen, shed, without the effect of the dog handler	No	NA	Both	0.0009–0.101	337	147	201
Hoffmann et al. (2003b)	Germany	Border Collie	Herding behaviour	Disqualification, retired, bite sheep, get lost from sheep without the effect of the dog handler	No	NA	Both	0.0009–0.107	337	147	201
Liinamo (2004)	Finland	Finnish Hound	Hunting	Search, pursuit, tongue, ghost	No	NA	Both	0.07–0.16	13,641		
Lindberg et al. (2004)	Sweden	Flatcoated Retriever	Hunting	Reaction to shot, single marking test, reaction when throwing the game, interest in search, retrieving, delivery, grip, interest in water retrieving, cooperation, waiting passively in a group	No	NA, Yes	Both	0.12–0.74	1159		
Boenigk et al. (2005)	Germany	Hovawart	Puppy behavioural test	Contact, acoustic and optical influences, prey drive, appearance assessment, temperament	Yes	NA, No	Both	0.02–0.13	5608	298	460
Courreau and Langlois (2005)	France	Belgian Shepherd Dog	Defence capacity traits	Jumping, following, fetching, attacking, guarding, obedience, biting, global success	No	NA, Yes	M, F	0.07–0.18	2427	298	866
Mäki et al. (2005)	Finland	Rottweiler	Working trials	Behaviour traits, appearance at shows	No	NA	Both	0.2–0.4	258/134		
Strandberg et al. (2005)	Sweden	German Shepherd Dog	Behavioural test DMA on working dogs	Playfulness, chase proneness, curiosity/fearlessness, aggressiveness	NA	No	Both	0.094–0.315	5959		1697
Boenigk et al. (2006a)	Germany	Hovawart	Juvenile evaluation, performance test	Appearance assessment, play instinct, hunting affinity, group of people, acoustical influences, shoot, strange person, optical influences, temperament	No	NA, No	Both	0.01–0.14	2811	493	735
Boenigk et al. (2006b)	Germany	Hovawart	Behaviour test	Appearance assessment, hunting affinity, group of people, acoustical influences, optical influences, temperament	NA	NA, No	Both	0.03–0.11	4113	283	431
Pérez-Guisado et al. (2006)	Spain	English Cocker Spaniel	Aggressive behaviour	Dominant aggressive behaviour	Yes	No	M, F	0.2–0.46	28/23		
Saetre et al. (2006)	Sweden	German Shepherd Dog, Rottweiler	Behavioural test DMA on working dogs	Social contact, play, chase, sudden appearance, metallic noise, ghost	No	NA, No	Both	0.04–0.19	10,553	1252	2482
van den Berg et al. (2006a)	Nedherlands	Golden Retriever	Aggression	Aggression toward strangers	NA	No	Both	0.9			
Liinamo et al. (2007)	Netherlands	Golden Retriever	Aggression	Many types of aggression	NA	No	Both	0–0.9999	325	108	125

Table 1 (*Continued*)

Study	Country	Breed	Branch	Traits	Before training	Trainability	Sex	Heritability	Number of progeny (male/female)	From sires	From dams
van der Waaij et al. (2008)	Sweden	German Shepherd Dog, Labrador Retriever	Working dog	Courage, sharpness, defence drive, prey drive, nerve stability, hardness, temperament, cooperation, affability, gun shyness	NA	NA, No	M, F, both	0.03–0.7	4570	303	405
Arvelius et al. (2009)	Sweden	Border Collie	Herding behaviour	17 Traits	NA	NA	Both	0.3	2700		
Buse et al. (2009)	Germany	Hovawart	Behavioural traits	Behaviour toward strangers and kids, response to external influences, response to dominance gestures of the owner, response to other dogs, behaviour toward other dogs	No	NA	Both	0.01–0.22	601		356
Hare and Thomas (2009)	USA	Labrador Retriever	Detection of drugs	Chase retrieve, physical possession, independent possession, mental possession	Yes	NA	Both	0.16–0.37			
Wijga et al. (2009)	Netherlands	Labrador Retriever	Guide dog	Success, puppy test	No, Yes	No, Yes	Both	0.09–0.11	6744		
Schiefelbein (2012)	USA	German Shepherd Dog, Golden Retriever, Labrador Retriever	Guide dog	Aggression, trainability, chasing, fear, anxiety, separation-related behaviour, pain sensitivity, excitability, attachment/attention-seeking, training and obedience, miscellaneous	No	NA, No, Yes	Both	0.04–0.22	12,287		
Arvelius and Klemetsdal (2013)	Sweden, Norway	English Setter	Hunting	Speed, style, hunting drive, search width, quartering, cooperation	No	NA, No	Both	0.066–0.183	10,795		
Arvelius et al. (2013)	Sweden	Border Collie	Herding	Affability toward humans, social behaviour toward dogs, trainability without livestock, trainability with livestock, ability to relax, balance, natural working distance, effective working distance, pace, natural ability, focus, power, oscillating movements (speed, softness), eye, outrun, lift, grip, handler relation, cooperation, work ethic, courage, style, activity, lift do drive	No	NA, No	M, F	0.03–0.5	2614		
Meyer et al. (2012)	Switzerland	German Shepherd Dog	Behavioural test	Self-confidence, nerve stability, hardness, temperament, sharpness, defence drive, reaction to gunfire	No	NA, No	Both	0.05–0.2	5020		

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006

Table 2
Classification of the measures of behavioural traits into the five functional categories (Environment, Herding, Hunting, Play, Psychical and Psychical characteristic) according to the focus of study by the author and indices which contained.

Category in this study	Original term	Source study
Hunting	Nose	Geiger (1973) cited in Mackenzie et al. (1986), Bartlett (1976), Goddard and Beilharz (1983), Schmutz and Schmutz (1998)
	Prey drive	Wilsson and Sundgren (1997), Boenigk et al. (2005), van der Waaij et al. (2008), Arvelius and Klemetsdal (2013)
	Hunting affinity	Boenigk et al. (2006a, 2006b)
	Hunting eagerness	Vangen (1990), Houpt and Willis (2001), Brenøe et al. (2002)
	Ability to work, hunting style	Vangen (1990), Brenøe et al. (2002)
	Bird finder index	Brenøe et al. (2002)
	Fetch, retrieve	Scott and Bielfelt (1976), Fält et al. (1982), Goddard and Beilharz (1985), Vangen and Klementsdal (1988), Lindberg et al. (2004), Courreau and Langlois (2005), Hare and Thomas (2009)
	Biting	Courreau and Langlois (2005)
	Tug of war	Fält et al. (1982), Saetre et al. (2006), Hare and Thomas (2009)
	Tracking, pursuit, chase	Geiger (1973) cited in Mackenzie et al. (1986), Pfleiderer-Högner (1979), Vangen and Klemetsdal (1988), Schmutz and Schmutz (1998), Houpt and Willis (2001), Liinamo (2004), Strandberg et al. (2005), Saetre et al. (2006), Schiefelbein (2012)
	Seek, search, quest, quartering	Geiger (1973) cited in Mackenzie et al. (1986), Vangen (1990), Kreiner et al. (1992), Karjalainen et al. (1996), Schmutz and Schmutz (1998), Liinamo (2004), Lindberg et al. (2004), Arvelius and Klemetsdal (2013)
	Guarding, focus on a handler hiding the object	Hare and Thomas (2009)
	Self defence	Reuterwall and Ryman (1973), Houpt and Willis (2001)
	Water retrieving, water work	Schmutz and Schmutz (1998), Houpt and Willis (2001), Lindberg et al. (2004)
	Barking	Vangen (1990), Karjalainen et al. (1996)
	Following	Vangen and Klemetsdal (1988), Karjalainen et al. (1996)
	Positive value, behaviour on dead deer, welding work schweissarbeit, scent	Kreiner et al. (1992)
	Tongue, ghost	Liinamo (2004)
	Check work	Liinamo et al. (1997)
	Marking, pointing	Vangen (1990), Schmutz and Schmutz (1998), Lindberg et al. (2004)
	Reaction when throwing the game, grip	Lindberg et al. (2004)
	Man work	Pfleiderer-Högner (1979)
	Fighting in a playful manner, playfulness	Reuterwall and Ryman (1973), Strandberg et al. (2005)
	Defence	Wilsson and Sundgren (1997), Ruefenacht et al. (2002), van der Waaij et al. (2008), Meyer et al. (2012)
	Play interest, grabbing	Saetre et al. (2006)
Environment	Ear sensitivity, sound shy	Bartlett (1976), Scott and Bielfelt (1976), Goddard and Beilharz (1983)
	Strange people, strange environments, strange object, irrelevant stimuli	Reuterwall and Ryman (1973), Bartlett (1976), Scott and Bielfelt (1976), Fält et al. (1982), Goddard and Beilharz (1985), Wilsson and Sundgren (1998), Houpt and Willis (2001), Boenigk et al. (2006a), Saetre et al. (2006), Buse et al. (2009)
	Acoustic and optical influences	Boenigk et al. (2005, 2006a)
	Appearance assessment	Boenigk et al. (2005, 2006a), Mäki et al. (2005)
	Acoustical influences	Goddard and Beilharz (1985), Boenigk et al. (2006a), Saetre et al. (2006)
	Shoot	Reuterwall and Ryman (1973), Goddard and Beilharz (1985), Kreiner et al. (1992), Ruefenacht et al. (2002), Lindberg et al. (2004), Boenigk et al. (2006a), van der Waaij et al. (2008), Meyer et al. (2012)
	Optical influences	Boenigk et al. (2006a)
	Dispositional forget unpleasant incidents	Houpt and Willis (2001)
	Traffic	Scott and Bielfelt (1976)
Play	Play instinct	Boenigk et al. (2006a)
Herding	Herding-traits	Arvelius et al. (2009)
	Outrun, lift, fetch, drive, fangen, pen, shed	Hoffmann (2000), Hoffmann et al. (2002, 2003a)
	Disqualification	Hoffmann et al. (2003a, 2003b)
	Retired, bite sheep, get lost from sheep	Hoffmann et al. (2003b)
	Eye, outrun, lift, grip, style	Arvelius et al. (2013)
Psychical characteristics	Body sensitivity	Bartlett (1976), Scott and Bielfelt (1976), Goddard and Beilharz (1983)
	Intelligence, energy, self-right	Bartlett (1976)
	Contact	Fält et al. (1982), Wilsson and Sundgren (1998), Boenigk et al. (2005), Saetre et al. (2006), van der Waaij et al. (2008)
	Temperament	Mackenzie et al. (1985), Wilsson and Sundgren (1997), Houpt and Willis (2001), Ruefenacht et al. (2002), Boenigk et al. (2005, 2006a, 2006b), van der Waaij et al. (2008), Meyer et al. (2012)
	Speed	Vangen and Klemetsdal (1988), Liinamo et al. (1997), Brenøe et al. (2002), Arvelius and Klemetsdal (2013)
	Independence, seeking width (from handler)	Brenøe et al. (2002)
	Response to dominance gestures	Buse et al. (2009)
	Response to other dogs	Goddard and Beilharz (1982), Goddard and Beilharz (1983), Buse et al. (2009)
	Jumping, following the owner, guarding an object	Courreau and Langlois (2005)
	Obedience	Geiger (1973) cited in Mackenzie et al. (1986), Scott and Bielfelt (1976), Pfleiderer-Högner (1979), Kreiner et al. (1992), Liinamo et al. (1997), Courreau and Langlois (2005), Schiefelbein (2012)

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006

Table 2 (*Continued*)

Category in this study	Original term	Source study
	Reaction to separation	Fält et al. (1982), Wilsson and Sundgren (1998), Schiefelbein (2012)
	Activity	Fält et al. (1982), Wilsson and Sundgren (1998), Arvelius et al. (2013)
	Suitability as guide dog	Goddard and Beilharz (1982)
	Fear, fearfulness	Goddard and Beilharz (1982), Goddard and Beilharz (1983), Schiefelbein (2012)
	Excitability	Goddard and Beilharz (1982), Schiefelbein (2012)
	Nervousness	Goddard and Beilharz (1983), Houpt and Willis (2001)
	Suspicion, willingness	Goddard and Beilharz (1983)
	Concentration	Goddard and Beilharz (1983), Liinamo et al. (1997)
	Courage	Houpt and Willis (2001), Reuterwall and Ryman (1973), Wilsson and Sundgren (1997), van der Waaij et al. (2008), Arvelius et al. (2013)
	Leash, heel	Scott and Bielfelt (1976), Kreiner et al. (1992)
	Sharpness	Kreiner et al. (1992), Wilsson and Sundgren (1997), Ruefenacht et al. (2002), van der Waaij et al. (2008), Meyer et al. (2012)
	Behaviour	Liinamo et al. (1997), Mäki et al. (2005)
	Cooperation	Vangen and Klemetsdal (1988), Liinamo et al. (1997), Wilsson and Sundgren (1997), Schmutz and Schmutz (1998), Brenøe et al. (2002), Lindberg et al. (2004), van der Waaij et al. (2008), Arvelius and Klemetsdal (2013), Arvelius et al. (2013)
	Aggression	Strandberg et al. (2005), Pérez-Guisado et al. (2006), Saetre et al. (2006), van den Berg et al. (2006a), Liinamo et al. (2007), Schiefelbein (2012)
	Waiting passively in a group	Lindberg et al. (2004)
	Character	Pfleiderer-Högner (1979)
	Affability	Reuterwall and Ryman (1973), Wilsson and Sundgren (1997), Arvelius et al. (2013)
	Disposition for forgetting unpleasant incidents	Reuterwall and Ryman (1973)
	Self confidence	Ruefenacht et al. (2002)
	Nerve stability, hardness	Wilsson and Sundgren (1997), Ruefenacht et al. (2002), Meyer et al. (2012), van der Waaij et al. (2008)
	Trained response, willing in training, willing new experience	Scott and Bielfelt (1976)
	Desire to work	Schmutz and Schmutz (1998)
	Curiosity/fearlessness	Strandberg et al. (2005)
	Fetching, retrieving, tug of war, reaction to the ball -puppy test	Wilsson and Sundgren (1998)
	Success, puppy test-guide dog	Wijga et al. (2009)
	Trainability, pain sensitivity, attachment/attention, miscellaneous	Schiefelbein (2012)
	Social behaviour toward dogs, trainability with and without livestock, ability to relax, balance, natural and effective working distance, pace, natural ability, focus, power, oscillating movements, handler relation, work ethic, lift to drive	Arvelius et al. (2013)

could not be used due to the missing sample size (Fält et al., 1982; Houpt and Willis, 2001).

2.2. Meta-analysis

We computed an effect size and variance for each trait within each category, and then computed a random-effects model with a weighted mean of these effect sizes using Comprehensive Meta-Analysis (Biostat, Englewood, NJ) according to Hedges and Olkin (1985) and Borenstein et al. (2005).

Correlation coefficients were used as effect size. Because the variance strongly depends on the correlation, all correlations were converted to the Fisher z metric for syntheses. This Fisher z metric should not be confused with the z statistic used to test hypotheses.

$$zr_i = \frac{1}{2}\log_e\left(\frac{1+r_i}{1-r_i}\right)$$

The standard error (SE) of this metric is determined solely by sample size (n):

$$\mathrm{SE}(zr_i) = \sqrt{\frac{1}{n_i - 3}}$$

The transformed effect sizes were used to calculate an average z in which each effect size is weighted. With the logic of the analysis that effect sizes have been sampled from a distribution of effect sizes with a true effect that could vary from study to study, a random effects model was used.

$$\bar{z}_r = \frac{\sum_i w_i zr}{\sum_i w_i}$$

where w_i is the weighing factor for the ith study, which is $1/(\mathrm{SE}^2 + v)$ (within-and between-study variances) in a random effects model.

The between-study variance (v) was calculated as:

$$v = \frac{Q - (n-1)}{c}$$

The Q value is defined, assuming a weighing factor for a fixed effect model, as:

$$Q = \sum_i w_i (zr_i - \bar{z}_r)^2$$

and c calculated as:

$$c = \sum_i w_i - \frac{\sum_i (w_i)^2}{\sum_i w_i}$$

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006

Estimates for Fisher z were converted back to correlation units using:

$$r_i = \frac{e^{(2zi)} - 1}{e^{(2zi)} + 1}$$

Each category was grouped according to breed of dog in order to see the differences between the breeds, by sex, by whether the analysis was based on multifactorial approach, and finally by whether the behavioural trait has to be trained or not. We have calculated a separate meta-analysis for each grouping. As not all studies distinguished heritability according sex and noted whether a multiple analysis was applied, these grouping were based on an adequate data. Since the number of rows (heritability coefficients entering the analysis) in all categories except Play, are too many to present; only overall and grouped results are shown. Where appropriate and the results for breeds were sufficient to be presented graphically, a random effect model plot showing relative weights of the studies grouped by breed was used (Borenstein et al., 2009). Random effect models, which include within- and between-study variances, eliminate the use of methods to evaluate risk of bias, such as those presented by publication bias. Confidence interval level is 95%.

3. Results

The overall weighted means of heritability were generally low (Table 3). The Herding category was based on five studies and Play only on one (Table 2) and each contained just one breed. No estimate according to sex was done in these two categories. Training did not show any variation within these categories either. Therefore, no grouping for Herding and Play was applicable. The results for the category Environment are shown in Tables 3 and 4, and Fig. 1; for Herding in Table 3; for Hunting in Tables 3 and 4, and Fig. 2; for Play in Table 3; and for Psychical characteristic in Tables 3 and 4, and Fig. 3. Values of heritability were low for grouping according to breed (Figs. 1–3). Where there were fewer subjects, there was a trend for values to be higher compared with those having many subjects. Heritability coefficients reached moderate values when grouped according to sex and whether or not the authors applied a multifactorial approach in the Environment category (Table 4). No significant differences, indicated by the confidence intervals, were detected either between males and females or whether or not the behavioural traits could be trained. The only exception was higher heritabilty of Psychical characteristics in which training was not needed in comparison with those in which training was needed (Table 4).

4. Discussion

In accordance with previous studies (Mackenzie et al., 1986; Willis, 1995; Houpt and Willis, 2001; Houpt, 2007; Hall and Wynne, 2012), also the present meta-analysis has shown low general heritability of the categorised behavioural traits analysed. When compared with the previous reports, the novelty of this study lies in the fact that individual high values of heritability reported either for individual trait or traits within a study (e.g., Fält et al., 1982; Goddard and Beilharz, 1985; Kreiner et al., 1992; Schmutz and Schmutz, 1998; Wilsson and Sundgren, 1998; van den Berg et al., 2006b; Liinamo et al., 2007), or for a single dog breed (Kreiner et al., 1992; Schmutz and Schmutz, 1998) disappeared when statistical synthesis of the data across studies was applied. The occasional high values of heritability, shown for example in Figs. 1–3, were usually based on a small number of animals involved and reported in a single study. It is unlikely that one behavioural trait would be highly heritable in one population and/or breed, while having low heritability in others. Where analysed, a shared genetic component behind most of the examined behavioural traits was found

Table 3
Heritability, confidence interval, z-value, number of heritability coefficients entering the analysis, and total sample size for the categories Environment, Herding, Hunting, Play and Psychical characteristics.

Category	Heritability	Lower limit	Upper limit	z-Value	p-Value	Number of heritability coefficients	Total sample size
Environment	0.154	0.141	0.166	23.831	0.000	119	197,258
Herding	0.099	0.067	0.132	5.993	0.000	99	26,175
Hunting	0.154	0.141	0.166	23.831	0.000	247	521,741
Play	0.093	0.057	0.130	4.961	0.000	2	2,811
Psychical characteristic	0.123	0.114	0.132	26.762	0.000	1232	1,890,613

Table 4
Heritability, confidence interval, z-value, number of heritability coefficients entering the analysis, and total sample size for Environment, Hunting and Psychical characteristic grouped according to sex, whether training was needed and if the original analysis used a multifactorial approach by category.

Category	Level	Heritability	Lower limit	Upper limit	z-Value	p-Value	Number of heritability coefficients	Total sample size
Sex								
Environment	F	0.210	0.156	0.262	7.552	0.000	12	14,219
	M	0.161	0.103	0.218	5.363	0.000	10	11,166
Hunting	F	0.210	0.156	0.262	7.552	0.000	35	28,689
	M	0.161	0.103	0.218	5.363	0.000	38	34,176
Psychical characteristic	F	0.202	0.179	0.225	16.731	0.000	321	76,477
	M	0.226	0.204	0.248	19.445	0.000	321	79,311
Training needed for the behavioural trait tested								
Environment	Not applicable	–	–	–	–	–	–	–
Hunting	No	0.176	0.152	0.199	14.161	0.000	36	124,699
	Yes	0.148	0.108	0.188	7.122	0.000	7	13,316
Psychical characteristic	No	0.147	0.134	0.160	21.499	0.000	1232	1,260,713
	Yes	0.061	0.047	0.074	8.743	0.000	134	204,250
Multifactorial analysis								
Environment	No	0.301	0.099	0.479	2.881	0.004	20	9,170
	Yes	0.229	0.198	0.259	14.305	0.000	111	177,447
Hunting	No	0.127	0.094	0.159	7.571	0.000	44	39,923
	Yes	0.158	0.144	0.171	22.632	0.000	242	471,177
Psychical characteristic	No	0.153	0.118	0.188	8.512	0.000	22	17,520
	Yes	0.122	0.113	0.131	26.297	0.000	1236	1,888,655

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006

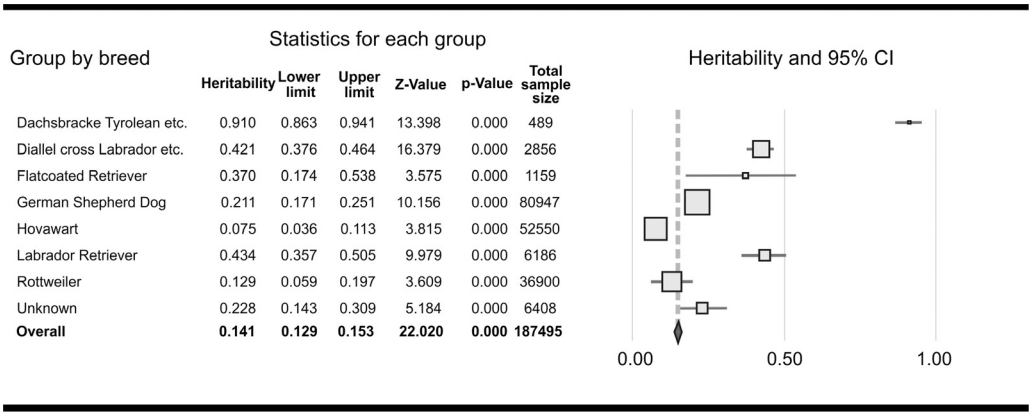

Fig. 1. Heritability for the category Environment grouped by breed is represented by a box (proportional in area to that breed's weight in the analysis), which is bounded by the confidence interval 95% for the effect size in that breed. The summary line in a plot uses a diamond to depict the mean effect size (the centre of the diamond) and its confidence interval (the width of the diamond).

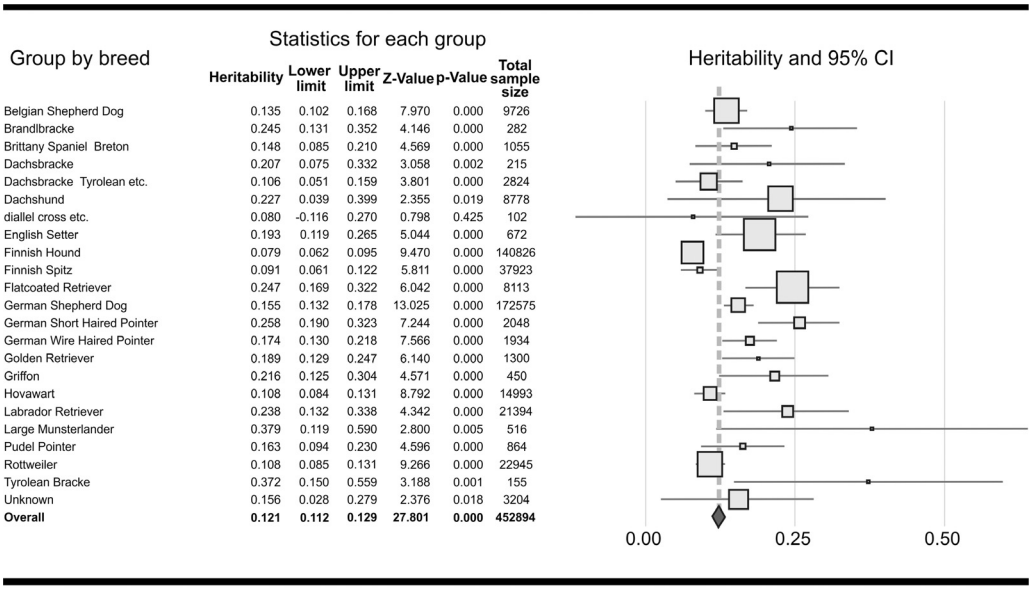

Fig. 2. Heritability for the category Hunting grouped by breed is represented by a box (proportional in area to that breed's weight in the analysis), which is bounded by the confidence interval 95% for the effect size in that breed. The summary line in a plot uses a diamond to depict the mean effect size (the centre of the diamond) and its confidence interval (the width of the diamond).

(Saetre et al., 2006). The common problem with genetic estimates like this is that heritability studies are usually only relevant to the population from which they were derived and for the period of time when they were assessed (Willis, 1995). Moreover, breed differences in behaviour are influenced by both genetics, and by the environment and experience (Mehrkam and Wynne, 2014).

Recent studies dealing with single behavioural traits, such as aggression (Takeuchi and Houpt, 2003) still suggest an existence of potentially useful selection criteria based on behavioural traits. On the other hand, the general low heritability of the behavioural traits analysed in the present study are not surprising either. Reasons for such results may be due to the multiple origins of such traits (e.g., Meyer et al., 2012; Mehrkam and Wynne, 2014). First of all, dog behaviour in adulthood may be significantly modified by a number of factors such as quality of milk or solid food for the young (Malm and Jensen, 1996); timing of weaning (Mogi et al., 2011); conditions during the period of socialization (De Meester et al., 2005); early experience (Scott and Fuller, 1965; McMillan et al., 2011, 2013; Mehrkam and Wynne, 2014), etc. The conditions in which dog breeders raise and sell puppies rarely meet the recommendations espoused in the scientific literature. A survey on this revealed that in the breeding kennels deviations from the conditions recommended in the literature were common (De Meester et al., 2005). Moreover, evaluations of the behavioural traits are often difficult due to the lack of testing repeatability between and also within judges. Performance testing is usually subjective as significantly different scores are given by the judges as shown, for example, in Finnish Spitz (Karjalainen et al., 1996).

The heritability values were two to more than 6 times higher when the results were from a simple analysis in comparison with those based on multifactorial analysis (Table 2). Still, these differences did not reach the level of statistical significance in the meta-analysis as indicated by the confidence intervals. This may be due to fact that according to total sample size across the

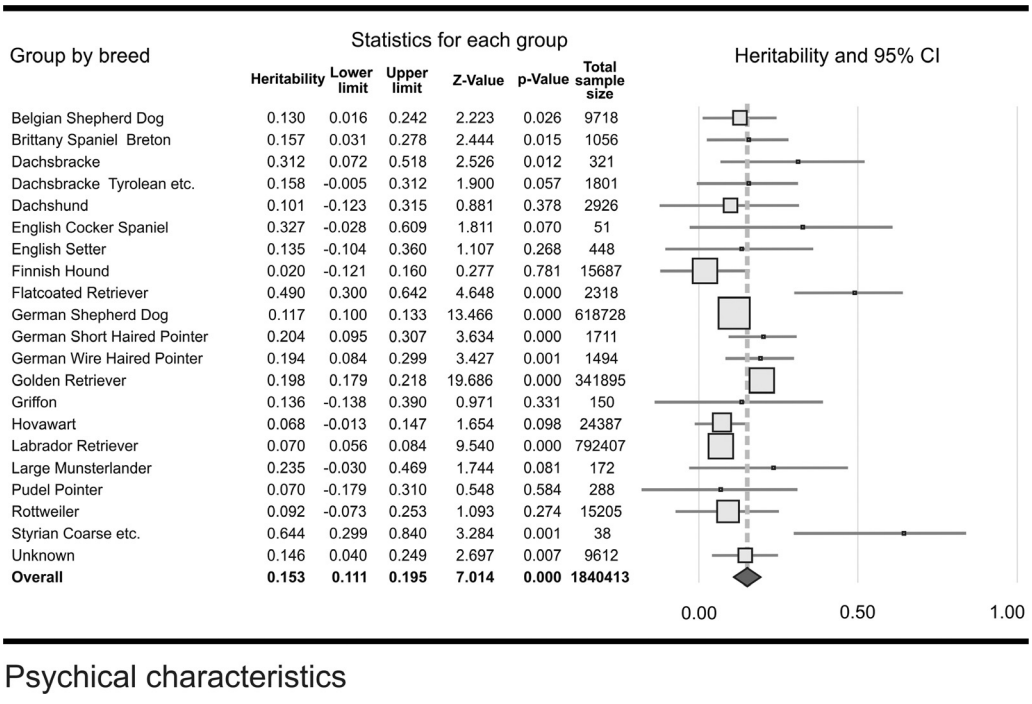

Fig. 3. Heritability for the category Psychical characteristic grouped by breed is represented by a box (proportional in area to that breed's weight in the analysis), which is bounded by the confidence interval 95% for the effect size in that breed. The summary line in a plot uses a diamond to depict the mean effect size (the centre of the diamond) and its confidence interval (the width of the diamond).

studies analysed, multifactorial analysis was used in a sample 10 times larger than a simple analysis. This is also most likely the reason why we detected that gender had almost no effect across the five categories and whether the trait needed training or not (Table 4). The only significant difference, the higher heritabilty of Psychical characteristics, in which training was not needed, compared to those in which training was needed, was negligible despite the fact the trend corresponded with expectation.

Moderate values based on separate meta-analyses, applying grouping according to sex and whether or not the authors applied a multifactorial approach (Table 4) are due to the between-study variance in random effects models. As such they should not be taken as increased heritability. This procedure was applied only to see whether these effects could affect the resulting heritabilities, which appeared not to be the case.

5. Conlcusion

In summary, various estimates of dog behavioural ability have a low heritability, indicating that such performance scores are not an accurate reflection of the animal's genetic potential. Reproduction based on such criteria can in rare cases only significantly improve the ability of the progeny (Schmutz and Schmutz, 1998; Meyer et al., 2012). Therefore, the commonly used behaviour tests for many breeds, to determine the dog's eligibility for reproducing, traditionally required by many associations, when breeders are usually unable to maintain standard, comparable breeding conditions, is not supported by the present results of the meta-analysis.

Conflict of interest statement

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

Acknowledgements

The study has been supported by the Ministry of Interior of the Czech Republic (VG20132015133), Czech University of Life Sciences (GA FAPPZ 2011213703198), and the Ministry of Agriculture of the Czech Republic (MZERO0714). The authors thank their colleagues from the Department of Animal Science and Ethology of Animals for their advices. The authors also gratefully acknowledge assistance of Gudrun Illmann for deciphering the specific terms used in the German scientific literature and Madelene Crook for help in improving the language.

References

Arvelius, P., Klemetsdal, G., 2013. How Swedish breeders can substantially increase the genetic gain for the English Setter's hunting traits. J. Anim. Breed. Genet. 130, 142–153.
Arvelius, P., Malm, S., Svartberg, K., Strandberg, E., 2009. Genetic analysis of herding behavior in Swedish Border Collie dogs. J. Vet. Behav. Clin. Appl. Res. 4, 237.
Arvelius, P., Malm, S., Svartberg, K., Strandberg, E., 2013. Measuring herding behavior in Border Collie—effect of protocol structure on usefulness for selection. J. Vet. Behav. Clin. Appl. Res. 8, 9–18.
Bartlett, C.R., 1976. Heritabilities and Genetic Correlations Between Hip Dysplasia and Temperament Traits of Seeing-Eye Dogs. Rutgers University, New Brunswick, NJ (Masters Thesis).
Boenigk, K., Hamann, H., Distl, O., 2005. Genetic analysis of the outcome of behavioural tests in puppies of the Hovawart dog. Dtsch. Tierarztl. Wochenschr. 112, 265–271.
Boenigk, K., Hamann, H., Distl, O., 2006a. Analysis of environmental and genetic influences on the outcome of the juvenile and breeding performance tests for behaviour traits in Hovawart dogs. Berl. Munch. Tierarztl. Wochenschr. 119, 258–269.
Boenigk, K., Hamann, H., Distl, O., 2006b. Genetic influences on the outcome of the progeny tests for behaviour traits in Hovawart dogs. Dtsch. Tierarztl. Wochenschr. 113, 182–188.

Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R., 2005. Comprehensive Meta-analysis Version 2. Biostat. Engelwood, NJ, USA.
Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R., 2009. Introduction to Meta-analysis. John Wiley & Sons, Ltd, Chichester, UK.
Brenøe, U.T., Larsgard, A.G., Johannessen, K.R., Uldal, S.H., 2002. Estimates of genetic parameters for hunting performance traits in three breeds of gun hunting dogs in Norway. Appl. Anim. Behav. Sci. 77, 209–215.
Buse, C., Stock, K.F., Hamann, H., Distl, O., 2009. Population genetic analysis of behaviour traits in Hovawart dogs. Berl. Munch. Tierarztl. Wochenschr. 122, 108–115.
Charney, E., 2012. Behavior genetics and postgenomics. Behav. Brain Sci. 35, 331–358.
Courreau, J.F., Langlois, B., 2005. Genetic parameters and environmental effects which characterise the defence ability of the Belgian shepherd dog. Appl. Anim. Behav. Sci. 91, 233–245.
De Meester, R., Moons, C., Van Bree, H., Coopman, F., 2005. Critical evaluation of the environment in Belgian dog breeding kennels during the puppies' socialization period. Vlaams Diergeneeskd. Tijdschr. 74, 364–374.
Fält, L., Swenson, L., Wilsson, E., 1982. Mentalbeskrivning av valpar. Statens Hundskola, Sveriges Lantbruksuniversitet and Stockholms Universitet, Stockholm.
Geiger, G., 1973. In: Mackenzie, S.A., Oltenacu, E.A.B., Houpt, K.A. (Eds.), Canine behavioral genetics—a review. Applied Animal Behaviour Science, p. 379.
Goddard, M.E., Beilharz, R.G., 1982. Genetic and environmental factors affecting the suitability of dogs as guide dogs for the blind. Theor. Appl. Genet. 62, 97–102.
Goddard, M.E., Beilharz, R.G., 1983. Genetics of traits which determine the suitability of dogs as guide-dogs for the blind. Appl. Anim. Ethol. 9, 299–315.
Goddard, M.E., Beilharz, R.G., 1985. A multivariate-analysis of the genetics of fearfulness in potential guide dogs. Behav. Genet. 15, 69–89.
Hall, N.J., Wynne, C.D.L., 2012. The canid genome: behavioral geneticists' best friend? Genes Brain Behav. 11, 889–902.
Hare, E., Thomas, S.G., 2009. Heritability of motivation-related traits in Labrador Retriever detector dogs. J. Vet. Behav.: Clin. Appl. Res. 4, 238–239.
Hedges, L.V., Olkin, I., 1985. Statistical Methods for Meta-analysis. Academic Press, Orlando, San Diego, New York, London, Toronto, Montreal, Sydney, Tokyo.
Hoffmann, U., 2000. Umweltbedingte und genetische Einflüsse auf Merkmale der Leistungsprüfung beim Koppelgebrauchshund Border Collie. Hannover, Stockholm, pp. 70–118.
Hoffmann, U., Hamann, H., Distl, O., 2002. Genetic analysis of traits of the working test for Border Collies. Zuchtungskunde 74, 213–231.
Hoffmann, U., Hamann, H., Distl, O., 2003a. Genetic analysis of traits of the working test for herding dogs 1st communication: performance traits. Berl. Munch. Tierarztl. Wochenschr. 116, 81–89.
Hoffmann, U., Hamann, H., Distl, O., 2003b. Genetic analysis of traits of the working test for herding dogs 2nd communication: undesired behaviour traits. Berl. Munch. Tierarztl. Wochenschr. 116, 90–95.
Houpt, K.A., 2007. Review article genetics of canine behavior. Acta Vet. Brno 76, 431–444.
Houpt, K.A., Willis, M.B., 2001. Genetics of behaviour. In: Ruvinsky, A., Sampson, J. (Eds.), The Genetics of the Dog. CAB, International, New York, NY, pp. 271–400.
Karjalainen, L., Ojala, M., Vilva, V., 1996. Environmental effects and genetic parameters for measurements of hunting performance in the Finnish Spitz. J. Anim. Breed. Genet. 113, 525–534.
Kis, A., Bence, M., Lakatos, G., Pergel, E., Turcsan, B., Pluijmakers, J., Vas, J., Elek, Z., Brúder, I., Földi, L., Sasvari-Szekely, M., Miklósi, A., Rónai, Z., Kubinyi, E., 2014. Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (*Canis familiaris*). PLoS ONE 9 (1), e83993, http://dx.doi.org/10.1371/journal.pone.0083993
Kreiner, M., Stur, I., Mayrhofer, G., Müller, S., 1992. Heritability and phenotypic correlations of behavior trails of 4 Austrian Bracken breeds. J. Anim. Breed. Genet. 109, 425–432.
Liinamo, A.-E., Karjalainen, L., Ojala, M., Vilva, V., 1997. Estimates of genetic parameters and environmental effects for measures of hunting performance in Finnish Hounds. J. Anim. Sci. 75, 622–629.
Liinamo, A.E., 2004. Genetic trends in hunting behaviour in the Finnish Hound. In: 55th Annual meeting of EAAP, Bled, 5 – 9 September 2004. Animal Science Group, Wageningen, pp. 1–5.
Liinamo, A.E., van den Berg, L., Leegwater, P.A.J., Schilder, M.B.H., van Arendonk, J.A.M., van Oost, B.A., 2007. Genetic variation in aggression-related traits in Golden Retriever dogs. Appl. Anim. Behav. Sci. 104, 95–106.
Lindberg, S., Strandberg, E., Swenson, L., 2004. Genetic analysis of hunting behaviour in Swedish Flatcoated Retrievers. Appl. Anim. Behav. Sci. 88, 289–298.
Lit, L., Belanger, J.M., Boehm, D., Lybarger, N., Oberbauer, A.M., 2013. Differences in behavior and activity associated with a Poly(A) expansion in the dopamine transporter in Belgian Malinois. PLoS ONE 8 (12), e82948, http://dx.doi.org/10.1371/journal.pone.0082948
Mackenzie, S.A., Oltenacu, E.A.B., Houpt, K.A., 1986. Canine behavioral genetics - a review. Appl. Anim. Behav. Sci. 15, 365–393.
Mackenzie, S.A., Oltenacu, E.A.B., Leighton, E., 1985. Heritability estimate for temperament scores in German shepherd dogs and its genetic correlation with hip dysplasia. Behav. Genet. 15, 475–482.
Mäki, K., Liinamo, A.E., Groen, A.F., Bijma, P., Ojala, M., 2005. The effect of breeding schemes on the genetic response of canine hip dysplasia, elbow dysplasia, behaviour traits and appearance. Anim. Welf. 14, 117–124.
Malm, K., Jensen, P., 1996. Weaning in dogs: within- and between-litter variation in milk and solid food intake. Appl. Anim. Behav. Sci. 49, 223–235.
Masuda, K., Hashizume, C., Ogata, N., Kikusui, T., Takeuchi, Y., Mori, Y., 2004. Sequencing of canine 5-hydroxytriptamine receptor (5-HTR) 1B, 2A, 2C genes and identification of polymorphisms in the 5-HTR1B gene. J. Vet. Med. Sci. 66, 965–972.
McMillan, F.D., Duffy, D.L., Serpell, J.A., 2011. Mental health of dogs formerly used as 'breeding stock' in commercial breeding establishments. Appl. Anim. Behav. Sci. 135, 86–94.
McMillan, F.D., Serpell, J.A., Duffy, D.L., Masaoud, E., Dohoo, I.R., 2013. Differences in behavioval characteristics between dogs obtained as puppies from pet stores and those obtained from noncommercial breeders. JAVMA—J. Am. Vet. Med. Assoc. 242, 1359–1363.
Mehrkam, L.R., Wynne, C.D.L., 2014. Behavioral differences among breeds of domestic dogs (*Canis lupus familiaris*): current status of the science. Appl. Anim. Behav. Sci. 155, 12–27.
Meyer, F., Schawalder, P., Gaillard, C., Dolf, G., 2012. Estimation of genetic parameters for behavior based on results of German Shepherd Dogs in Switzerland. Appl. Anim. Behav. Sci. 140, 53–61.
Mogi, K., Nagasawa, M., Kikusui, T., 2011. Developmental consequences and biological significance of mother–infant bonding. Prog. Neuro-Psychopharmacol. Biol. Psychiatry 35, 1232–1241.
Murphree, O.D., Angel, C., Deluca, D.C., 1974. Limits of therapeutic change—specificity of behavior-modification in genetically nervous dogs. Biol. Psychiatry 9, 99–101.
Ogata, N., Hashizume, C., Momozawa, Y., Masuda, K., Kikusui, T., Takeuchi, Y., Mori, Y., 2006. Polymorphisms in the canine glutamate transporter-1 gene: identification and variation among five dog breeds. J. Vet. Med. Sci. 68, 157–159.
Ostrander, E.A., Kruglyak, L., 2000. Unleashing the canine genome. Genome Res. 10, 1271–1274.
Pérez-Guisado, J., Lopez-Rodríguez, R., Muñoz-Serrano, A., 2006. Heritability of dominant-aggressive behaviour in English Cocker Spaniels. Appl. Anim. Behav. Sci. 100, 219–227.
Pfleiderer-Högner, M., 1979. Möglichkeiten der Zuchtwertschätzung beim Deutschen Schäferhund anhand der Schutzhundprüfung I. Ludwig-Maximilians-Universität, Munich, Germany.
Reuterwall, C., Ryman, N., 1973. An Estimate of The Magnitude of Additive Genetic Variation of Some Mental Characters in Alsatian Dogs. Institute of Genetics, University of Stockholm, Sweden.
Ruefenacht, S., Gebhardt-Henrich, S., Miyake, T., Gaillard, C., 2002. A behaviour test on German Shepherd dogs: heritability of seven different traits. Appl. Anim. Behav. Sci. 79, 113–132.
Saetre, P., Strandberg, E., Sundgren, P.E., Pettersson, U., Jazin, E., Bergström, T.F., 2006. The genetic contribution to canine personality. Genes Brain Behav. 5, 240–248.
Scott, J.P., Bielfelt, S.W., 1976. Analysis of the puppy-testing program. In: Pfaffenberger, C.J., Scott, J.P., Fuller, J.L., Ginsberg, B.E., Bielfelt, S.W. (Eds.), Guide Dogs for the Blind: Their Selection, Development and Training. Elsevier, Amsterdam, pp. 39–75.
Scott, J.P., Fuller, J.L., 1965. Genetics and The Social Behavior of The Dog. University of Chicago Press, Chicago.
Schiefelbein, K.M., 2012. Estimation of Genetic Parameters for Behavioral Assessment Scores in Labrador Retrievers, German Shepherd Dogs, and Golden Retrievers. Kansas State University, Manhattan, KS (A thesis).
Schmutz, S.M., Schmutz, J.K., 1998. Heritability estimates of behaviors associated with hunting in dogs. J. Hered. 89, 233–237.
Strandberg, E., Jacobsson, J., Saetre, P., 2005. Direct genetic, maternal and litter effects on behaviour in German shepherd dogs in Sweden. Livest. Prod. Sci. 93, 33–42.
Takeuchi, Y., Houpt, K.A., 2003. Behavior genetics. Vet. Clin. North Am.—Small Anim. Pract. 33, 345–363.
van den Berg, L., Schilder, M.B.H., de Vries, H., Leegwater, P.A.J., van Oost, B.A., 2006a. Phenotyping of aggressive behavior in golden retriever dogs with a questionnaire. Behav. Genet. 36, 882–902.
van den Berg, L., Schilder, M.B.H., de Vries, H., Leegwater, P.A.J., van Oost, B.A., 2006b. Phenotyping of aggressive behavior in golden retriever dogs with a questionnaire. Behav. Genet. 36, 882–902.
van der Waaij, E.H., Wilsson, E., Strandberg, E., 2008. Genetic analysis of results of a Swedish behavior test on German Shepherd Dogs and Labrador Retrievers. J. Anim. Sci. 86, 2853–2861.
Vangen, O., 1990. Genetic analysis on vorsteh dog. In: Proceedigs of The Lecture for Norwegian Vorsteh Dog District Conference, May 1990, 231-214.
Vangen, O., Klementsdal, G., 1988. Genetic studies of Finnish and Norwegian tests results in two breeds of hunting dog. In: VI World Conference of Animal Production, 27 June–1 July 1988. Helsinki, Finland, pp. 380.
Wijga, S., Russenberger, J., van den Berg, S.M., Havlena, B., Heuven, H.C.M., 2009. Genetic parameters for guiding ability in purpose bred dogs. Anim. Genet. 40, 1004.

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006

Willis, M.B., 1995. Genetic aspects of dog behaviour with particular reference to working ability. In: Serpell, J. (Ed.), The Domestic Dog: Its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge, pp. 51–64.
Wilsson, E., Sundgren, P.E., 1997. The use of a behaviour test for selection of dogs for service and breeding.2. Heritability for tested parameters and effect of selection based on service dog characteristics. Appl. Anim. Behav. Sci. 54, 235–241.
Wilsson, E., Sundgren, P.E., 1998. Behaviour test for eight-week old puppies—heritabilities of tested behaviour traits and its correspondence to later behaviour. Appl. Anim. Behav. Sci. 58, 151–162.

Please cite this article in press as: Hradecká, L., et al., Heritability of behavioural traits in domestic dogs: A meta-analysis. Appl. Anim. Behav. Sci. (2015), http://dx.doi.org/10.1016/j.applanim.2015.06.006