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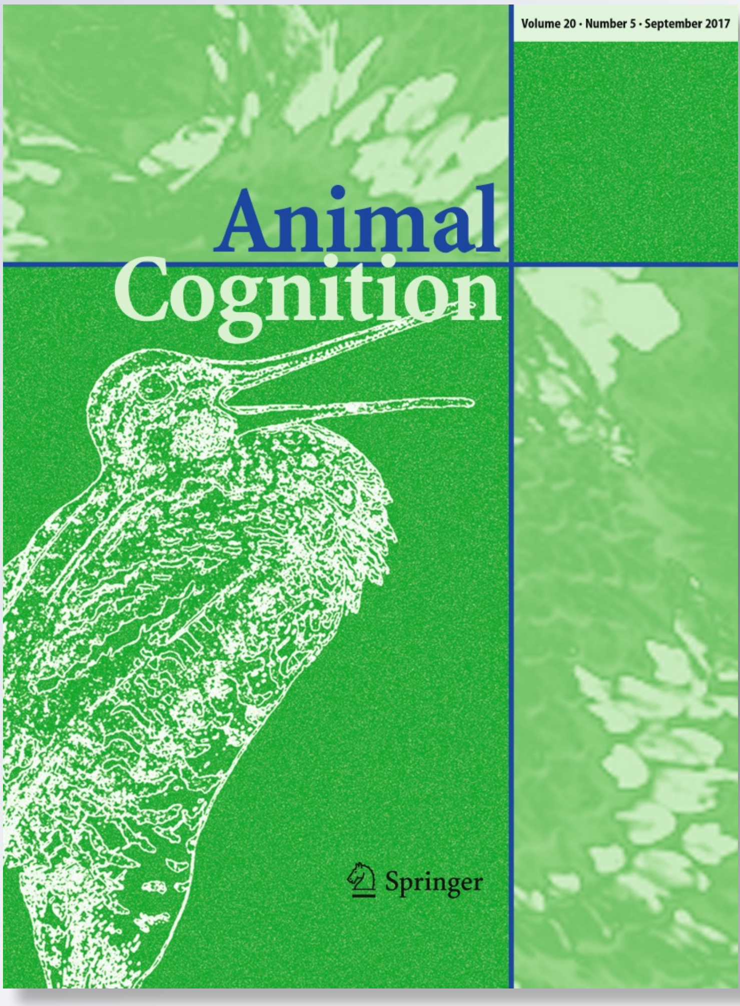
Animal Cognition

ISSN 1435-9448
Volume 20
Number 5

Anim Cogn (2017) 20:923-939
DOI 10.1007/s10071-017-1112-8



Springer

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DOI 10.1007/s10071-017-1112-8

ORIGINAL PAPER

Temperament and problem solving in a population of adolescent guide dogs

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Received: 12 April 2017 / Revised: 2 July 2017 / Accepted: 4 July 2017 / Published online: 10 July 2017

Abstract It is often assumed that measures of temperament within individuals are more correlated to one another than to measures of problem solving. However, the exact relationship between temperament and problem-solving tasks remains unclear because large-scale studies have typically focused on each independently. To explore this relationship, we tested 119 prospective adolescent guide dogs on a battery of 11 temperament and problem-solving tasks. We then summarized the data using both confirmatory factor analysis and exploratory principal components analysis. Results of confirmatory analysis revealed that a priori separation of tests as measuring either temperament or problem solving led to weak results, poor model fit, some construct validity, and no predictive validity. In contrast, results of exploratory analysis were best summarized by principal components that mixed temperament and problem-solving traits. These components had both construct and predictive validity (i.e., association with success in the guide dog training program). We conclude that there is complex interplay between tasks of "temperament" and "problem solving" and that the study of both together will be more informative than approaches that consider either in isolation.

Keywords Temperament · Cognition · Problem solving · Behavior · Canine · Guide dogs

Introduction

Temperament and cognition, or problem solving, are often regarded as distinct phenomena. Although each is difficult to define, temperament is usually associated with affect, or "the probability of experiencing and expressing the primary emotions and arousal" (Goldsmith et al. 1987, p. 510). It is presumed to be genetically based and present from a young age (Goldsmith et al. 1987). An animal's temperament is generally considered to affect performance in tasks that are emotionally charged and/or occur in unfamiliar situations. In practice, temperament is often measured by gauging the animal's reaction to startling events (e.g., King et al. 2003) or willingness to engage with novel environments (e.g., Brown et al. 2005; Greenberg 1984). Cognition, in contrast, is typically associated with "all processes involved in acquiring, storing, and using information from the environment" (Shettleworth 2013, p. 1). Cognition is thought to influence performance in tasks that require behavioral flexibility, innovation, and insight, such as novel tool use (e.g., Taylor et al. 2010), decision making (e.g., Dill 1987), problem solving (e.g.,

Electronic supplementary material The online version of this article (doi:10.1007/s10071-017-1112-8) contains supplementary material, which is available to authorized users.

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Benson-Amram et al. 2016), and inhibitory control (e.g., MacLean et al. 2014).

If temperament and problem-solving skills truly correspond to distinct mental processes, we might expect an individual's performance on a task purporting to test temperament to be more similar to other tasks ostensibly drawing on this same ability than to cognitive tasks that involve problem solving. Indeed, there is evidence that individual performance on tasks within these domains is associated with one another. Tasks of cognition correlate to other tasks of cognition in studies of dogs, rodents, and male bowerbirds (Arden and Adams 2016; Isden et al. 2013; Matzel and Kolata 2010). Similarly, temperament traits (e.g., aggression, activity, and boldness) often co-occur together in "behavioral syndromes" (Sih et al. 2004). These findings leave open the scenario that temperament and cognition are easily separable constructs, but importantly do not explicitly test for it because they're only ever looking at half of the picture.

And in fact, several authors challenge such a strict dichotomy. One of the earliest examples originates from Pavlov, who proposed that aspects of temperament, or "types of nervous systems," were determinants of cognition, as measured by individual differences in the speed of acquisition of classical conditioning (Carere and Locurto 2011; Pavlov 1935; Strelau 1997). More recent work supports the connection between temperament and problem-solving skills (Guillette et al. 2017; Rowe and Healy 2014). For example, several studies of innovative problem solving—a putative cognitive skill (Morand-Ferron et al. 2015; Reader 2003)—suggest that certain attributes associated with temperament (e.g., neophobia, exploration) play a nontrivial role in affecting animals' success (Auersperg et al. 2011; Benson-Amram and Holekamp 2012; Guido et al. 2017; Overington et al. 2011; Webster and Lefebvre 2001). In other words, animals that are bold and exploratory in their interactions with a problem-solving apparatus increase their opportunities to solve it, whereas animals that are too timid even to approach the apparatus greatly diminish their chance of success. In other examples of the interconnectedness between the two domains, point-following in domesticated foxes is affected by selection for temperament traits (e.g., willingness to approach a human) (Hare et al. 2005), and dogs' performance on a detour task involving inhibitory control varies based on temperament (Bray et al. 2015).

Large-scale studies purporting to measure problem-solving performance across species have typically not attempted to account for the possible contributions of temperament. For example, several studies have attempted to measure the relationship between brain size and putative cognitive skills in different species of birds (response to novel environments: Sol et al. 2005), carnivores (problem solving: Benson-Amram et al. 2016), and both birds and mammals (inhibitory control: MacLean et al. 2014). None, however, included analyses about the possible contributions of attributes like motivation and neophobia to performance. Similarly, Svartberg and Forkman (2002) conducted a behavioral study of temperament in over 15,000 dogs, but did not collect measures on problem solving within the same animals. While each of these studies is useful in its own right, there has been a lack of large-scale empirical studies in which animals are given multiple behavioral tasks designed to measure *both* what we might call temperament and cognition (Carere and Locurto 2011; Griffin et al. 2015). It seems apparent both that temperament and problem solving refer to functionally distinct domains, and also that they interact: however, the degree to which temperament and problem solving depend upon one another remains an open question.

For theoretical and practical reasons, dogs are an ideal species in which to study the intersection of these two domains. The utility of dogs in herding, hunting, detecting, serving, and guiding depends on specific behaviors and skills (Hart and Yamamoto 2017; Lord et al. 2017). Many studies have explored cognition in dogs (e.g., Kaminski and Marshall-Pescini 2014; Miklósi 2015) and temperament (e.g., Riemer et al. 2016; Serpell and Hsu 2001)—however, it is rare to see cognition and temperament explicitly examined in the same study (but see Bray et al. 2015; Marshall-Pescini et al. 2008; Passalacqua et al. 2013). The need for such a synthesis is beginning to be acknowledged (Marshall-Pescini et al. 2017). Finally, high levels of community interest facilitate the recruitment of canine participants for behavioral testing (e.g., Riemer et al. 2014) and the collection of survey responses from caretakers (Hsu and Serpell 2003).

Here, we subjected a large sample of prospective adolescent guide dogs to a battery of tasks. Some tasks were designed to elicit responses that we assumed, based on past literature and intuition, would be primarily affected by measures of temperament, such as boldness, reactivity, neophobia, distraction, and fearfulness (e.g., Goddard and Beilharz 1986; Pfaffenberger et al. 1976; Wilsson and Sundgren 1998). Others, we assumed, would elicit responses influenced mainly by problem-solving skills, such as impulse control,[1] innovation, and behavioral flexibility (e.g., Barrera et al. 2015; Benson-Amram and Holekamp 2012; Bray et al. 2014). We also measured three

[1] Perhaps speaking to the inherent difficulty in separating temperament and cognition, impulse control is sometimes grouped in the 'temperament' category within the human literature (e.g., Duckworth and Allred 2012), although acknowledged to relate to executive control. However, we adhered to the convention in the animal literature, where it is considered a 'cognitive' ability (e.g., Amici et al. 2008; Dettmer et al. 2017; MacLean et al. 2014).

dependent variables in order to validate our behaviorally derived factors: subjective assessments of behavior as measured by questionnaires, a physiological measure of stress as measured by salivary cortisol, and success as measured by outcome in the guide dog training program.

We initially performed a confirmatory factor analysis to model the data, permitting us to identify a priori which tasks would load onto two separate factors, named *Problem solving* and *Temperament*. When this analysis yielded poor results, we next applied exploratory principal components analysis. This is a data-driven approach in which variables load onto factors based on patterns of correlation within the data without any a priori framework (e.g., Musek 2007). Using these alternative approaches allowed us to ask which mode of analysis best fit our data, and which led to factors that were most valid, as assessed through construct and predictive validity.

We assessed construct validity—i.e., that we were measuring what we intended to—in two different ways. First, we tested whether our behavior-based factors were associated with subjective ratings of similar constructs obtained from puppy-raiser questionnaires. Subjective human ratings have successfully predicted the behavior that they are intended to capture in studies of dogs (Barnard et al. 2016; Foyer et al. 2014; Gosling et al. 2003; Svartberg 2005; although see Brucks et al. 2017b) and other animals (e.g., rhesus macaques: Bolig et al. 1992; baboons: Carter et al. 2012a; gray langurs: Konečná et al. 2008; and horses: Lloyd et al. 2007).

As a second measure of construct validity, we tested whether our behavior-based factors were associated with a physiological measure known to vary across individuals: in this case, cortisol. Cortisol concentration in dogs reflects HPA axis activity and is related to other measures of stress-related behaviors (Beerda et al. 1999; Carrier et al. 2013; Dreschel and Granger 2005; Hydbring-Sandberg et al. 2004). Several past studies have found an association between cortisol levels and various measures of canine temperament (Batt et al. 2009; De Palma et al. 2005; Dreschel and Granger 2005; Hennessy et al. 2001; King et al. 2003; Siniscalchi et al. 2013). In other species, cortisol has been specifically linked to measures of temperament: high levels are associated with excitability in cattle (Burdick et al. 2011; Curley et al. 2006) and fearfulness in primates (Buss et al. 2003; Kalin et al. 1998).

Finally, we tested whether our factors had predictive validity by examining associations between them and later success in the guide dog program. Past studies of working dogs have implicated measures of temperament in successful completion of training (Duffy and Serpell 2012; Harvey et al. 2016; McGarrity et al. 2016; Sinn et al. 2010). One study has also found a measure of problem solving to be predictive (Bray et al. in press).

On the assumption that measures of temperament and problem solving are separable through behavioral testing, we predicted that the confirmatory approach would produce two factors that fit the data well and had strong construct and predictive validity. Specifically, we expected the "temperament" factor to correspond with ratings of excitability, nonsocial fear, and separation-related behaviors, and the "problem-solving" factor to correspond with ratings of trainability and impulsivity. We hypothesized that salivary cortisol concentrations would be associated with the "temperament" factor, and that both factors should be associated with success in the program. Under the same assumption, we predicted that the exploratory approach would reveal similar results, with temperament tasks loading only onto factors with other temperament tasks, and the same with problem-solving tasks.

However, if aspects of temperament and problem solving are more deeply intertwined, then the confirmatory approach should fit poorly, lack associations with previous measures, and fail to be associated with outcome. Additionally, the exploratory approach should reveal factors that do not sort easily into putative temperament and problem-solving categories, but instead reflect a combination of each. Furthermore, these components should correspond to questionnaire and biological (stress-related) measures of temperament and problem solving. They should also be associated with outcome in the program.

General methods

Subjects

Subjects were the same as those described in Bray et al. (in press). Participating dogs were recruited through The Seeing Eye, Inc. (Morristown, NJ, USA), a philanthropic non-profit organization that breeds, raises, and trains guide dogs for the blind and visually impaired. The Seeing Eye granted informed consent to all aspects of the study. All dogs were whelped at the breeding station, weaned at five weeks, and then sent to volunteer puppy raisers at seven weeks. These families were responsible for basic obedience training, taking their puppies to regular meetings with families and dogs in the same geographic region, and exposing their puppies to a wide array of people, animals, locations, and experiences. Between 14 and 17 months, dogs were recalled to headquarters to begin professional training. All testing procedures adhered to regulations set forth by the University of Pennsylvania Institutional Animal Care and Use Committee (Protocol #805210).

We tested 133 young adult dogs from May–October of 2015. However, 14 dogs had to be excluded for missing test scores on at least one task due to video malfunction

($n = 2$) or failure to complete warm-up trials on the memory problem solving, multistep problem solving, and/or cylinder tasks ($n = 12$). The 26 dogs that were Lab-Golden crosses were assigned to the breed that contributed over 50% of their genes if applicable, and in all other cases to the breed of their mother. Thus, our final sample consisted of 119 dogs (46 German Shepherds, 55 Labrador Retrievers, and 18 Golden Retrievers) from 21 different litters (Table S1).

Questionnaires

Puppy raisers filled out two online questionnaires when the dogs were approximately one year old and had not yet returned to headquarters. They first completed the Canine Behavioral Assessment and Research Questionnaire (C-BARQ©, www.cbarq.org), a behavioral survey designed and validated by Hsu and Serpell (2003) (Appendix A of electronic supplementary material). C-BARQ data were obtained for 114 of the 119 dogs that went on to complete young adult testing (Table S1).

Puppy raisers also completed a 13-item attention deficit hyperactivity disorder (ADHD) rating scale (RS), modified from a human questionnaire (DuPaul et al. 1998) and applied to and validated in dogs (Lit et al. 2010; Vas et al. 2007; Wan et al. 2013) (Appendix B of electronic supplementary material). Puppy raisers read phrases such as "(S)he is quick to break his/her 'rest' command" and "(S)he follows simple commands easily, such as 'sit', but (s)he often has difficulties with more complicated commands, such as 'go to your place', even if (s)he knows them and has practiced them often." They were then asked to rate the frequency (never, sometimes, often, or very often) with which these statements applied to their dog. Dog-ADHD RS data were obtained for 105 of the 119 dogs that went on to complete young adult testing (Table S1).

Salivary cortisol collection

The transition from puppy-raiser homes to a kennel environment is recognized as a particularly stressful time for dogs (Hennessy et al. 1997, 2001; Rooney et al. 2007). We collected saliva after the dogs returned to headquarters and entered the kennels, either one ($n = 1$), two ($n = 102$), or three ($n = 13$) days postarrival and prior to participation in young adult testing. Collection occurred between 7:40 and 8:50 h, at least 1.5 h after the dog's morning meal. Collection followed previously published methods (Bray et al. 2017; Dreschel and Granger 2009). Briefly, one to two experimenters held the dog while the main experimenter (EB), wearing latex gloves, held a Salimetrics® Children's Swab under the dog's tongue and in the dog's cheek pouches, avoiding contact with the gums, for 1–5 min (Coppola et al. 2006). The swab was gently moved around the dog's mouth throughout sampling.

Postcollection, all samples ($n = 116$, Table S1) were stored in a plastic Salimetrics® tube and either immediately refrigerated (at 4 °C) or placed in a freezer (at −20 °C). If samples were refrigerated first, they were frozen no more than 40 min later. One to five months later, samples were mailed on dry ice to Arizona State University's Institute for Interdisciplinary Salivary Bioscience Research, where they were thawed and assayed for cortisol using ELISA technology and an enzyme immunoassay kit (Salimetrics, Carlsbad, CA). All samples were assayed in duplicate using 25 µL of saliva, and the average of these two measures was used in subsequent analyses. The lower limit of detection was 0.007 µg/dL, and there was an average intra-assay coefficient of variation of less than 10% and an average inter-assay coefficient of variation of less than 15%. To ensure accuracy, analysis was repeated for 18 samples that had a coefficient of variation greater than 15%.

Young adult testing

All testing sessions occurred during the initial weeks of return, before each dog was assigned to a professional trainer. Our test battery (described in Bray et al. in press) consisted of 11 tasks designed to capture aspects of dogs' temperament and problem solving. All dogs were tested on the entire battery twice: they participated in the first testing within the first week of returning to headquarters for training [mean = 2.3 days postarrival, median = 2 days, interquartile range (IQR) = 0 days, range = 1–6 days], and the second testing within a week of undergoing anesthesia for neutering and/or hip X-rays, which occurred over a more variable period after initial return [mean = 12.9 days postarrival, median = 10 days, IQR = 6 days, range = 5–35 days].

On the testing day, tasks were administered over two sessions. Session one lasted approximately one hour, and consisted of the first seven tasks. Dogs were then given at least an hour break before completing session two, which lasted around 30 min and consisted of the final four tasks. For the sake of consistency and intra-individual comparison (MacLean et al. 2017), dogs completed all tasks in the same order.

Dogs ($n = 119$) were tested at The Seeing Eye® headquarters in an empty 11′ × 7′ tiled exam room located within an unoccupied kennel wing, near the kennel in which the dogs were housed. All tasks took place in the testing room, except for the distraction task, which was conducted in a 44′ × 4′ empty hallway within the same kennel. Testing took place between 7:30 and 17:30 h. For all tasks that required a reward, dogs worked for Zuke's® mini naturals roasted chicken treats. A main experimenter and a dog handler were always present. At any given time, these roles were filled by two of five females of similar age, with the first author (EB) acting as the main experimenter in 87% of sessions. Aside from positioning the dog, the handler did not interact with the dog during testing. Testing sessions were videotaped using Sony video cameras (HDR-PJ230, HDR-CX405) mounted on tripods.

Below, we briefly describe each task in the order in which it was presented to the dogs. For further details, see SI methods of electronic supplementary material.

Isolation

This task measured a dog's comfort level when placed alone in an unfamiliar environment (similar to Gazzano et al. 2008; Wilsson and Sundgren 1998). The handler released the dog into the empty lighted testing room, then left for 2 min. The dependent measures were number of times the dog switched between quadrants of the room over the course of the session and duration of time spent near exit, vocalizing, active, and rearing up on hind legs, respectively. Based on classification in past animal literature (e.g., Kazlauckas et al. 2005; Prut and Belzung 2003; Seaman et al. 2002), we considered this to be primarily a temperament test, measuring activity and anxiety.

Distraction

This task measured a dog's ability to ignore salient distractors in favor of approaching an encouraging human (Goddard and Beilharz 1984; Harvey et al. 2016). The experimenter called the dog from the other end of a hallway. Initially, the hallway was empty. In subsequent trials, toy and treat distractors were placed along the dog's route. The dependent measures were time to walk down an empty hallway, number of toys touched, and number of treats eaten. We also calculated a difference score by subtracting each dog's initial time from her "distraction" time, so that a bigger difference indicated a longer time to complete the "distraction" trials. Based on classification in past animal literature (e.g., Jones and Gosling 2005; Murphy 1998; Weiss and Greenberg 1997), we considered this to be primarily a temperament test, measuring distractibility.

Sustained attention

This task measured a dog's attentiveness to a human in the absence of a reward. The experimenter commanded the dog to sit and then stood silently facing the dog. The trial started when the dog sat and ended when the dog turned away from the experimenter, capped at 2 min. The dependent measures were the amount of time that the dog remained oriented toward the experimenter on trials one and two. Based on classification in past animal literature (e.g., De Palma et al. 2005; Murphy 1998; Serpell and Hsu 2001; Vas et al. 2007), we considered this to be primarily a temperament test, measuring attentiveness and interest toward humans.

Memory problem solving

This task measured a dog's ability to remember and efficiently recover hidden treats (similar to Barrera et al. 2015). We used the Nina Ottosson Dog Magic puzzle toy for this task. The dog watched the experimenter place treats in four equidistant wells, then cover the four baited wells along with five empty ones. The dog was given a maximum of 2 min to find the hidden treats. The dependent measures were amount of time to uncover all four treats, the number of correct wells uncovered, accuracy, and persistence. Based on classification in past animal literature (e.g., Barrera et al. 2015; MacLean et al. 2017), we considered this to be primarily a problem-solving test.

Multistep problem solving

This task measured a dog's ability to solve a problem that required completion of two steps in a precise order (similar to Benson-Amram and Holekamp 2012; Marshall-Pescini et al. 2008). Successful performance also depended on the dog's ability to avoid perseverating at a tempting but fruitless option (i.e., fixating on the physical location of a hidden treat despite having to manipulate the apparatus in a different location to gain access). We used the Nina Ottosson Dog Tornado puzzle game for this task. The dog watched as the experimenter baited a well, twisted the top part of the apparatus to cover the treat, and then placed a plastic bone in an empty adjacent well, thereby rendering the apparatus unable to spin until the bone was dislodged. The dog was given a maximum of 2 min to recover the treat. The dependent measures were amount of time to successfully uncover the treat, amount of time gazing to the experimenter, and amount of time perseverating (interacting with the part of the apparatus covering the baited area while the plastic bone was still in the adjacent well). We also measured persistence. Based on classification in past animal literature (e.g., Griffin and Guez 2014), we considered this to be primarily a problem-solving test.

Cylinder

This task measured a dog's ability to inhibit perseverating at a visible but inaccessible treat directly in front of it in favor of making a temporary detour to the side to retrieve the treat (Bray et al. 2014; MacLean et al. 2014). Dogs first completed familiarization trials with an opaque cylinder, where they learned to retrieve a treat from an open side of the apparatus without touching the front of it. In ten test trials, dogs faced an identical problem with the same solution, except that the cylinder was transparent so the food reward was readily visible throughout. The dependent measure was the number of test trials in which the dog correctly retrieved the reward on her first attempt. Based on classification in past animal literature (Hauser et al. 2002; Müller et al. 2016; Vlamings et al. 2010), we considered this to be primarily a problem-solving test.

Detour problem solving

This task measured a dog's ability to detour around a barrier in order to reach a reward (similar to Fox and Stelzner 1966; Osthaus et al. 2010). The experimenter stood at the end of a Z-shaped maze and called the dog over for three trials. In the first two, she stood diagonally opposite to the dog, requiring the dog to make two turns around barriers to reach her. In the final trial, the experimenter moved directly in front of the dog but still remained behind the barrier, necessitating the same amount of detouring but with the additional challenge of inhibiting the counterproductive urge to approach directly. The dependent measures were solving times for trials one through three, as well as a test trial score (number of trials solved within the time limit). Based on classification in past animal literature (e.g., Frank and Frank 1982; Kohler 1925; Thompson and Heron 1954), we considered this to be primarily a problem-solving test.

Greeting

This task measured a dog's emotional reaction to the appearance of a strange figure (similar to Goddard and Beilharz 1986). The experimenter knocked and then silently entered the room in a hunched position, draped in a felt cape. After 15 s, the experimenter then encouraged the dog to approach in a friendly tone, and patted the dog if in reach. The trial ended after 45 s. The dependent measures were latency to initially approach and amount of time spent interacting with the experimenter. Based on classification in past animal literature (e.g., Jones and Gosling 2005; Murphy 1998; Svartberg and Forkman 2002), we considered this to be primarily a temperament test, measuring fear and confidence.

Ball play

This task measured a dog's willingness to play fetch with a human (similar to Slabbert and Odendaal 1999; Wilsson and Sundgren 1998). The experimenter remained stationary and threw a ball, encouraging the dog to retrieve it. She continued throwing the ball as many times as the dog brought it back within 1 min. The dependent measure was the sum of a dog's retrieval score over two trials. Based on classification in past animal literature (e.g., Jones and Gosling 2005; Valsecchi et al. 2011; Wilsson and Sundgren 1998), we considered this to be primarily a temperament test, measuring cooperative willingness.

Novel object

This task measured a dog's emotional stability when placed alone in a room with novel objects (similar to King et al. 2003; Marshall-Pescini et al. 2017). The experimenter turned on two motion-activated toy cats, which produced erratic noises and movement, and then released the dog alone into the testing room with them for 2 min. The dependent measures were time to first approach the mechanical cats, time spent in contact with them, time spent orienting toward them, and latency to first vocalize. Based on classification in past animal literature (e.g., Barnard et al. 2016; Herrmann et al. 2007; Réale et al. 2007), we considered this to be primarily a temperament test, measuring neophobia.

Umbrella-opening

This task measured a dog's initial reaction and subsequent recovery to a startling event (Sherman et al. 2015; van der Borg et al. 1991). The experimenter faced the dog and released an auto-open umbrella, which the dog was then given 45 s to explore. If the dog was not near the umbrella at predetermined time intervals, the experimenter first verbally coaxed the dog to approach, and then if needed the handler gently led the dog toward the umbrella. The dependent measures were the dog's initial reaction score (which accounted for movement and body position), the time frame within which the dog subsequently approached the umbrella, and the amount of time spent exploring the umbrella. Based on classification in past animal literature (e.g., Foyer et al. 2014; Taylor and Mills 2006), we considered this to be primarily a temperament test, measuring reactivity and recovery.

Program outcome

Program outcome was coded as a binary variable: dogs either succeeded (became guide dogs or breeders) or were released (did not pass the program and were adopted by families). Breeders had to successfully complete two months of guide dog training and then were selected to enter the breeding program based on their health and behavior. Dogs could be released at any point from the program, although only 4% of our sample ($n = 5$) was released prior to returning to headquarters for training. The primary reasons that dogs were released from the program were behavioral, including but not limited to lack of confidence, excitability, inability to focus, lack of initiative, body or noise sensitivity, and suspiciousness. Dogs could also be released for medical concerns or because they were transferred to an external organization. We were only interested in dogs that were released for behavioral reasons (e.g., Batt et al. 2008; Duffy and Serpell 2012). Of the 119 dogs that completed young adult testing, 20% were released for medical concerns ($n = 23$) or transfer ($n = 1$). Of the 95 remaining dogs, 63 succeeded (66%) and 32 were released due to behavioral concerns (34%) (Table S1).

Data processing and statistical analysis

All statistical analyses were carried out in R version 3.3.0 (R Development Core Team 2016).

EB or a research assistant involved in the study coded the following variables from video: perseveration during the multistep problem-solving task, initial response during the umbrella-opening task, and all variables from the isolation and novel object tasks. A separate coder then coded 20% of randomly selected trials, and interrater reliability of these variables was calculated using Spearman's rho for continuous variables and Cohen's Kappa for categorical variables. Interrater agreement was strong (McHugh 2012): all correlations were greater than 0.83 and the Kappa for initial reaction to umbrella-opening was 0.83. All other behavioral variables were coded live (see SI methods of electronic supplementary material).

We first examined the 34 standardized variables from the 11 tasks and used reverse coding where necessary to ensure that a positive score always indicated that the dog solved problems more effectively (e.g., more quickly) or acted in a more desirable way (e.g., confident, engaged, comfortable), whereas a negative score showed the opposite (see Table 1). We then removed those variables which did not contribute to a compact pattern of correlations, as indicated by Kaiser–Meyer–Olkin (KMO) measures of sampling adequacy that were less than 0.50 (Field et al. 2012).

Next, we used intraclass correlation coefficients estimated from variance components of a generalized linear model to determine rank-order stability of individual scores on behavioral measures between the first and second testing sessions, using the R package "rptR" (Stoffel et al. 2017). Evidence of repeatability over time is a prerequisite of temperament and cognitive traits (Brust and Guenther 2017; Carere and Locurto 2011; Guillette et al. 2017).

Then, in a hypothesis-driven approach, we applied confirmatory factor analysis (CFA), fit using the R package "lavaan" (Rosseel 2012). Tasks were placed in a factor based on how they had been previously categorized in the literature (see "General Methods" section). The "temperament" factor included tasks that measured dogs' reactions to novel and/or startling environments, objects, and situations, their patterns of attention and distractibility, and their interactions with humans. The "problem solving" factor included tasks that measured dogs' problem solving, memory, behavioral flexibility, and impulse control. Both factors were estimated jointly from the observed variance–covariance matrix, and parameters were estimated using maximum likelihood. Goodness of fit was evaluated using the comparative fit index (CFI: values >0.95 indicate good fit; Hooper et al. 2008), the root-mean-square error of approximation (RMSEA: values <0.08 indicate acceptable fit; Hu and Bentler 1998), and the standardized root-mean-square residual (SRMR: values <0.08 indicate acceptable fit; Hu and Bentler 1999).

Next, in a data-driven approach, we applied exploratory principal components analysis (PCA) with an orthogonal, varimax rotation to identify latent factors or attributes. We determined the number of components to retain by using parallel analysis (Horn 1965), fit using the R package "paran" (Dinno 2012), as well as the scree test (Cattell 1966) and the Comparison Data technique (Ruscio and Roche 2012).

In an effort to compare the factors obtained from the competing approaches, we looked for construct validity. First, we determined the associations between factors and questionnaire measures of temperament and impulsivity collected prior to testing. C-BARQ subscales were calculated when at least 80% or more of the values that made up the subscale were present (Duffy and Serpell 2012). Specifically, we were interested in associations with the excitability, nonsocial fear, trainability, and separation-related behavior subscales (see Appendix A of electronic supplementary material). Following Vas et al. (2007), we also calculated an activity-impulsivity score for each dog by taking the average score on items 4, 5, 6, 8, 9, 11, and 13 on the Dog-ADHD RS (see Appendix B of electronic supplementary material). All questionnaire ratings were then standardized. We used a General Estimating Equations version of a general linear regression model (GEE-GLM) to estimate all associations of interest. Because breed, sex, birth season, and age at return have been controlled for in previous studies due to their effect on behavior (e.g., Bray et al. in press), each of these was included as a covariate. We used a Gaussian error distribution with litter as the unit of analysis. Variances estimates for the statistical tests on the regression coefficients were adjusted for clustering due to litter effects using generalized estimating equations (Liang and Zeger 1993). All models were fit using the R package "geepack" (Halekoh et al. 2006). For all

Table 1 Final set of young adult testing variables used in analyses

Task	Variable	Description	Positive score equates to
Isolation	Proximity to exit	Time spent near the door leading out of the room	Less time near exit
Isolation	Vocal	Time spent vocalizing	Less time vocalizing
Isolation	Mobile	Time spent mobile (i.e., not sitting/laying/standing in same spot, but actively moving)	More mobile
Distraction	Toy contact	# of toys a dog contacts while being called down the hallway, averaged over two trials	Less toys contacted
Sustained attention	Trial 1	Time facing the experimenter before turning away during trial 1	More attentive
Memory problem solving	Solve	Amount of time to successfully uncover and eat all four treats	Quicker to solve
Memory problem solving	Correct	Number of correct (i.e., baited) indentations uncovered in 120 s	More correct
Memory problem solving	Persist	Amount of time engaging with the apparatus divided by total session time	More persistent
Multistep problem solving	Solve	Amount of time to successfully uncover and eat treat	Quicker to solve
Multistep problem solving	Persist	Amount of time engaging with the apparatus divided by total session time	More persistent
Multistep problem solving	Gaze	Amount of time gazing at human divided by total session time	Less time gazing
Detour	Trial 2	Latency to solve trial 2	Quicker to solve
Detour	Trial 3	Latency to solve trial 3	Quicker to solve
Detour	Score	Number of trials solved within the time limit (1–3)	More trials solved
Greeting	Interact	Amount of time interacting with experimenter	More interaction
Retrieval	Score	Retrieval score summed over trials 1 and 2 (where 1 = no interest in ball and 5 = dog retrieves and brings back to experimenter 3+ times)	Better at retrieval
Novel object	Latency to vocalize	Latency to first vocalize	Slow to vocalize
Umbrella-opening	Reaction	Initial reaction to umbrella-opening (where 1 = no detectable reaction and 4 = rapid avoidance response)	Less reactive
Umbrella-opening	Approach	Latency to first approach umbrella	Quicker to approach
Umbrella-opening	Contact	Amount of time contacting umbrella	More contact

models, 2-sided p-values <0.05 were considered statistically significant.

As a second test of construct validity, we examined the associations between factors and salivary cortisol collected upon the dogs' return to headquarters (see above). We applied a natural log transformation to the cortisol measurements and then used GEE-GLMs as above.

Finally, to investigate the predictive validity of our factors, we used GEE-GLMs to estimate which factors were associated with success in the guide dog program. Models were the same as described above, except that they used a binomial error distribution.

Results

Model fit

We first conducted a KMO test on the 34 behavioral variables from the 11 tasks described above. The sampling adequacy was KMO = 0.52, barely above the acceptable limit of 0.5 (Field et al. 2012), so the 14 variables with individual KMO values <0.50 were removed from further consideration. Rerunning the test using 20 behavioral variables (Table 1) yielded a sampling adequacy of KMO = 0.66 and KMO values for all remaining individual variables ≥ 0.55.

We next verified that the 19 behavioral variables showed consistency across time (the novel object variable was excluded because the objects were no longer novel at the second time of testing) (Table 2). The majority of variables were strongly positively correlated across testing sessions. Thus, all subsequent analyses used data from the first testing, due to greater consistency in the time of first testing and probable ceiling effects in some tasks at the time of second testing (see SI methods of electronic supplementary material). Table S2 presents means, modes, standard deviations, and ranges of the raw scores from the first time of testing.

We first applied confirmatory factor analysis (CFA) to the 20 variables from young adult testing. Given our a priori hypothesis, we designated two latent constructs: *Problem solving* and *Temperament* (Table 3). The two factors were not correlated with one another ($r = 0.08$, $p = 0.40$). However, results were below our threshold for acceptable fit, $\chi^2(169,\ n = 119) = 509$, $p < 0.001$ (RMSEA = 0.130 [0.117–0.143]; CFI = 0.393; SRMR = 0.142). Given the poor fit and the fact that many of our tasks failed to load on either factor at a strength >0.32, we concluded that our first hypothesized categorization of tasks was not optimal.

We then applied exploratory PCA to the same 20 variables. Bartlett's test, $\chi^2(190) = 771$, $p < 0.001$, indicated that correlations between items were sufficiently large for PCA. Parallel analysis using 5000 iterations indicated retaining four principal components, as did inflexions in the scree plot and the comparison data technique (Ruscio and Roche 2012). The four components were orthogonally rotated. All components were uncorrelated. The total variance explained by all four components was 50%. We then examined loadings of each behavior onto the four components (Table 4), paying particular attention to loadings $\geq |0.32|$ (Tabachnik and Fidell 2007).

Individuals who scored high on component 1 (for ease of discussion, *Confident flexibility*) were quick to solve a detour, even when the parameters changed slightly, were comfortable around the umbrella, mobile and exploratory during the isolation task, interactive during greeting, and proficient at playing fetch.

Individuals who scored high on component 2 (for ease of discussion, *Calm + engaged*) were adept at the memory problem-solving task: they solved quickly, searched in the correct locations, and appeared very engaged (i.e., persistent). They also did not have large startle responses to the umbrella.

Individuals who scored high on component 3 (for ease of discussion, *Independent problem solving*) exhibited superior performance on the multistep problem-solving task. They were quick to solve, highly focused on the task, and rarely looked to the experimenter.

Individuals who scored high on component 4 (for ease of discussion, *Quiet investigation*) rarely vocalized during the isolation and novel object tasks. They also seemed curious toward their immediate environment: they were mobile and exploratory during the isolation task, attentive to the toys during the distraction task, and focused on the experimenter during the first trial of the sustained attention task.

Thus, the exploratory PCA fit well and produced four components, all of which had behavioral loadings that combined aspects of temperament and problem solving. Taken together, the poor fit of the CFA and the superior fit of the PCA support the premise that temperament and problem solving are deeply interrelated.

Table 2 Repeatability between scores at young adult postarrival (PA) and postsurgery (PS) testing, using intraclass correlation coefficients estimated from variance components of a generalized linear model

Test	Variable	Repeatability
Isolation	Proximity to exit	0.00
Isolation	Vocal	0.54***
Isolation	Mobile	0.00
Distraction	Toy contact	0.33***
Sustained attention	Trial 1	0.19**
Memory problem solving	Solve	0.32***
Memory problem solving	Correct	0.07
Memory problem solving	Persist	0.08*
Multistep problem solving	Solve	0.22*
Multistep problem solving	Persist	0.00
Multistep problem solving	Gaze	0.00
Detour	Trial 2	0.00
Detour	Trial 3	0.33
Detour	Score	0.00
Greeting	Interact	0.27**
Retrieval	Score	0.76***
Umbrella-opening	Reaction	0.65***
Umbrella-opening	Approach	0.33***
Umbrella-opening	Contact	0.52***

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Construct validity

Table S3 presents means, modes, standard deviations, and ranges of the raw questionnaire ratings for the relevant C-BARQ and Dog-ADHD RS items.

To test our predictions regarding construct validity, we developed separate GEE-GLM models with the dog's

Table 3 CFA standardized loadings ($\geq$0.32 bolded) and standard errors in a two-factor model of young adult testing

Observed variable	Latent construct	β	Standard error
Memory problem solving solve	*Problem solving*	**0.76**	0.08
Memory problem solving correct	*Problem solving*	**0.73**	0.08
Multistep problem solving solve	*Problem solving*	0.10	0.10
Detour trial 2	*Problem solving*	0.18	0.10
Detour trial 3	*Problem solving*	0.11	0.08
Detour score	*Problem solving*	0.00	0.10
Memory problem solving persist	*Problem solving*	**0.88**	0.08
Multistep problem solving persist	*Problem solving*	0.26	0.10
Multistep problem solving gaze	*Problem solving*	0.21	0.09
Isolation proximity to exit	*Temperament*	**0.79**	0.10
Isolation vocal	*Temperament*	**0.51**	0.10
Isolation mobile	*Temperament*	**0.68**	0.10
Distraction toy contact	*Temperament*	−0.19	0.11
Sustained attention trial 1	*Temperament*	0.17	0.10
Greeting interact	*Temperament*	0.09	0.11
Retrieval score	*Temperament*	0.11	0.10
Novel object latency to vocalize	*Temperament*	0.14	0.11
Umbrella-opening reaction	*Temperament*	−0.05	0.11
Umbrella-opening approach	*Temperament*	0.14	0.10
Umbrella-opening contact	*Temperament*	**0.32**	0.10

$n = 119$ dogs

questionnaire rating or salivary cortisol concentration as the predictor and individual factors (CFA- or PCA-derived) as the dependent variable. Models included breed, birth season, sex of puppy, and age at return as covariates, and assumed outcomes were correlated within litter. Results are summarized in Table 5.

The CFA factor *Problem solving* was positively associated with C-BARQ trainability (estimate = 0.08, Wald = 9.93, $p = 0.002$): dogs rated by their puppy raisers as quick learners, obedient, and attentive to their owner did well on tasks that were cognitive in nature. Furthermore, *Problem solving* was negatively associated with activity-impulsivity (estimate = −0.23, Wald = 9.73, $p = 0.002$): dogs rated as very active and impulsive by their puppy raisers did poorly on cognitive tasks. All hypothesized associations between questionnaire measures and the CFA factor temperament failed to reach statistical significance. Therefore, using puppy-raiser ratings, we found only partial support for construct validity of our CFA factors—*Problem solving* was associated with trainability and impulsivity, but *Temperament* was not associated with excitability, nonsocial fear, or separation, as we would have expected.

We found stronger support using puppy-raiser ratings for construct validity within our PCA factors: three of the four were associated with at least one questionnaire measure. The PCA factor *Calm + engaged* was negatively associated with excitability (estimate = −0.18, Wald = 12.28, $p < 0.001$): dogs rated as more excitable on the C-BARQ performed poorly on the memory problem-solving task and reacted strongly to the umbrella-opening. The PCA factor *Quiet investigation* was also negatively associated with excitability (estimate = −0.13, Wald = 7.70, $p = 0.006$): dogs high in excitability were vocal during the isolation and novel object tasks and curious about their immediate surroundings in the distraction and sustained attention tasks. The PCA factor *Independent problem solving* was negatively associated with both separation-related behaviors (estimate = −0.32, Wald = 8.36, $p = 0.004$) and activity-impulsivity (estimate = −0.23, Wald = 15.13, $p < 0.001$). Dogs low in separation anxiety and impulsivity were most effective at solving a multistep problem, persisting at the task and not looking to the experimenter.

As a second way of assessing construct validity, we examined salivary cortisol concentrations. Here, as predicted, *Temperament* was negatively associated with high levels of salivary cortisol (estimate = −0.26, Wald = 9.90, $p = 0.002$). In other words, dogs that scored low on *Temperament*—exhibiting anxious behaviors when left alone and wariness of the umbrella—had higher cortisol concentrations. By this measure, *Temperament* therefore had construct validity.

The PCA factor *Confident flexibility* was also negatively associated with salivary cortisol levels (estimate = −0.14,

Table 4 Components and loadings (≥0.32 bolded) of the PCA over the variables from young adult testing

Observed variable	*Confident flexibility*	*Calm + engaged*	*Independent problem solving*	*Quiet investigation*
Detour trial 2	**0.75**	0.11	−0.07	0.18
Detour score	**0.65**	−0.13	−0.04	0.29
Detour trial 3	**0.63**	0.07	0.10	−0.11
Umbrella-opening approach	**0.59**	0.01	−0.01	−0.15
Greeting interact	**0.48**	−0.05	0.11	−0.08
Umbrella-opening contact	**0.38**	0.16	0.06	0.12
Retrieval score	**0.35**	−0.07	0.25	0.05
Memory problem solving solve	−0.02	**0.86**	0.08	−0.05
Memory problem solving persist	0.09	**0.84**	0.16	0.10
Memory problem solving correct	0.01	**0.81**	−0.04	0.05
Umbrella-opening reaction	**0.32**	**0.33**	−0.12	−0.30
Multistep problem solving persist	0.00	0.13	**0.90**	−0.08
Multistep problem solving gaze	0.07	0.07	**0.89**	0.00
Multistep problem solving solve	0.12	0.00	**0.72**	0.13
Isolation vocal	0.05	−0.17	0.04	**0.77**
Isolation proximity to exit	**0.36**	0.01	−0.10	**0.64**
Isolation mobile	**0.44**	0.06	−0.15	**0.60**
Novel object latency to vocalize	−0.27	−0.26	0.06	**0.45**
Distraction toy contact	0.11	−0.28	−0.11	**−0.42**
Sustained attention trial 1	−0.04	0.18	0.05	**0.40**
Eigenvalue	2.76	2.50	2.33	2.20
Percent variance explained	14%	13%	12%	11%

$n = 119$ dogs

Wald = 4.21, $p = 0.04$). Dogs with higher cortisol concentrations ended up being less proficient at solving the detour task and wary during multiple tests of temperament. *Quiet investigation* tended toward a negative association with salivary cortisol as well (estimate = −0.18, Wald = 3.17, $p = 0.075$). Thus, when using association with cortisol to distinguish between the *Temperament/Problem solving* factors and the PCA factors, the data were less conclusive as there was evidence for construct validity for both.

Predictive validity

To determine the predictive ability of the different factors, we built separate GEE-GLM models for the association between each factor and program outcome. Models included breed, birth season, sex of puppy, and age at return as covariates, and assumed outcomes were correlated within litter. Results are summarized in Table 5.

Importantly, neither *Problem solving* nor *Temperament* were significantly associated with outcome in the program. Thus, neither of the CFA factors demonstrated predictive validity, once again suggesting that results do not support a clear distinction between tests of problem solving and temperament.

In contrast, the exploratory PCA produced two factors that were associated with outcome. *Confident flexibility* (estimate = −0.36, Wald = 4.57, $p = 0.03$) was negatively associated with release from the program, indicating that dogs that scored less favorably on the detour, greeting, umbrella, isolation, and retrieval tasks were more likely to be released [Odds Ratio (OR) 0.70]. We also found a significant association for *Independent problem solving* (estimate = −0.51, Wald = 6.07, $p = 0.01$): dogs that were unengaged and performed poorly on the multistep problem-solving task were more likely to be released (OR 0.60). The other two PCA components, *Calm + engaged* and *Quiet investigation*, were not significantly associated with program outcome. In sum, when taken as a whole, the PCA factors demonstrated more evidence for both construct and predictive validity than did the CFA factors.

Discussion

Based on their assumed underlying differences and separation in much of the literature, we posited that putative temperament and problem-solving characteristics might correlate more among themselves than between each other.

Table 5 Construct and predictive validity for the young adult testing factors derived from CFA and PCA

Factors	Construct validity												Predictive validity		
	C-BARQ excitability[a]		C-BARQ nonsocial fear[b]		C-BARQ trainability[a]		C-BARQ separation[a]		ADHD activity-impulsivity[c]		Salivary cortisol[d]		Release from program[e]		
	Est.	*p*	Est.	*p*	Est.	*p*	Est.	*p*	Est.	*p*	Est.	*p*	OR	Est.	*p*
CFA: *Problem solving*	NA	NA	NA	**NA**	**0.08**	**0.002**	NA	**NA**	**−0.23**	**0.002**	NA	NA	1.05	0.05	0.86
CFA: *Temperament*	−0.05	0.30	0.06	0.50	NA	NA	−0.06	0.52	NA	NA	**−0.26**	**0.002**	1.05	0.05	0.84
PCA: *Confident flexibility*	NA	NA	0.03	0.78	0.00	0.96	NA	NA	NA	NA	**−0.14**	**0.04**	**0.70**	**−0.36**	**0.03**
PCA: *Calm + engaged*	**−0.18**	**<0.001**	NA	NA	NA	NA	−0.10	0.52	NA	NA	−0.13	0.20	1.42	0.35	0.25
PCA: *Independent problem solving*	NA	NA	NA	NA	−0.02	**0.48**	**−0.32**	**0.004**	**−0.23**	**<0.001**	NA	**NA**	**0.60**	**−0.51**	**0.01**
PCA: *Quiet investigation*	**−0.13**	**0.006**	0.03	0.76	NA	NA	NA	NA	NA	NA	−0.18	0.08	1.08	0.08	0.75

Associations that reached significance ($p < 0.05$) are bolded

[a] $n = 114$ dogs

[b] $n = 112$ dogs

[c] $n = 105$ dogs

[d] $n = 118$ dogs

[e] $n = 95$ dogs

When we conducted a CFA in which we forced the temperament and problem-solving variables to load onto separate factors, we found some evidence for construct validity: *Problem solving* was associated with questionnaire measures of trainability and impulsivity, and *Temperament* was associated with salivary cortisol concentrations. However, the CFA factors fell short on all other criteria. They fit the data poorly, with some tasks loading at such low levels that they were not represented by either factor. Furthermore, both CFA factors were not significantly associated with outcome in the guide dog program.

By contrast, the exploratory PCA was an open-ended analysis that searched for the combination of measures into principal components that best accounted for variation in the data. Presumably, if there had been two underlying components (temperament and problem solving) each giving rise to observed measures of its trait, the exploratory PCA would have identified them, but it did not. Rather, when we conducted exploratory PCA with no imposed structure, variables naturally sorted into four factors, each representing a different type of competence that included both problem-solving and temperament measures: *Confident flexibility*, *Calm + engaged*, *Independent problem solving*, and *Quiet investigation*. These factors fit the data well and were associated with related questionnaire and endocrine measures. Moreover, two of the factors, *Confident flexibility* and *Independent problem solving*, were significantly associated with success in the guide dog program.

Taking all the evidence together, we conclude that a specified dichotomy of problem solving versus temperament is a less informative approach to describing our data. Rather, a bottom-up method that blends features of problem solving and temperament offers a more accurate picture of our results. Of course, one reason that our bottom-up factors fit the data better than a prespecified, two-factor dichotomy is that they were derived from this particular sample. The best test of the validity of our four principal components will come when they are applied to a completely new sample. For the moment, however, our results strongly support the hypothesis that temperament and cognition are difficult to disentangle.

For example, we found that a temperament trait (separation anxiety, as evaluated through the C-BARQ) was associated with *Independent problem solving*, a factor consisting mainly of skills that have traditionally been conceptualized as cognitive (i.e., innovation and impulse control). Additionally, both problem-solving (detour skills) and temperament (e.g., approach and exploratory behavior) variables loaded strongly onto *Confident flexibility*. Similarly, both cognitive (memory problem solving) and temperament (reactivity) variables loading strongly onto *Calm + engaged*. Finally, problem-solving ability, largely regarded as a cognitive skill, loaded together with persistence, which is usually associated with temperament, on two of our factors (*Calm + engaged* and *Independent problem solving*), corroborating findings from meerkats (Thornton and Samson 2012), hyenas (Benson-Amram and Holekamp 2012), and birds (Lermite et al. 2017).

Surprisingly, none of our factors that involved bold and curious behaviors (*Temperament*, *Confident flexibility*, or *Quiet investigation*) were associated with ratings of nonsocial fear. We think one possible explanation for this inconsistency was that levels of nonsocial fear were quite low in our population (mean = 0.31), with very little inter-individual variation (Table S3).

Previous large-scale studies that have suggested that animal cognition and temperament are separate, stable constructs have typically examined only one of these putative traits. For example, one study in birds reported correlations between three cognitive measures: innovative propensity, initial learning of a discrimination task, and reversal learning of the same task (Griffin et al. 2013). However, traits such as neophobia were not considered. Other studies in dogs (Arden and Adams 2016), mice (Matzel and Kolata 2010), and male bowerbirds (Isden et al. 2013) found evidence for a general cognitive ability that emerged across performance on multiple cognitive tests, but again did not consider the relation of these measures to measures of temperament.

Tests of temperament have also often failed to incorporate measures of problem solving into their analyses. For example, a meta-analysis of personality in dogs suggested that traits associated with temperament were moderately consistent over time (average effect size $r = 0.43$) (Fratkin et al. 2013), but the analysis did not also include measures of cognition. Similarly, a growing literature points to the existence of "behavioral syndromes," or correlated temperament traits (e.g., boldness and aggression), across varying contexts in species as diverse as crickets (Kortet and Hedrick 2007), spiders (Johnson and Sih 2005), fish (Bell and Sih 2007), and birds (Verbeek et al. 1996). Taken together, these studies could be interpreted as implying that cognition and temperament are distinct, reliable constructs in animals. Importantly, however, none of these studies tested both purported temperament and cognitive tasks.

Other data argue against the implicit assumption that cognition and temperament are easily separable. For example, even within a single cognitive domain, like inhibitory control, context affects behavior. As a result, individual tasks meant to measure the same underlying construct are not always correlated (Bray et al. 2014; Brucks et al. 2017a; Fagnani et al. 2016). Similar issues have arisen in the temperament literature. In a study of wild baboons, Carter et al. (2012b) determined that responses to two different stimuli (a threatening stimulus and a novel object) designed to measure "boldness" were not related.

Many other studies acknowledge that cognition and temperament are difficult to disassociate, and perhaps even interdependent (Griffin et al. 2015; Sih and Del Giudice 2012). For instance, while innovation involves the cognitive ability to derive a solution, it also crucially hinges on aspects of temperament like neophilia and exploration (Kaulfuß and Mills 2008; Marshall-Pescini et al. 2017; Reader 2003). Also, numerous smaller-scale studies have successfully uncovered correlations between personality traits and problem solving across taxa (Brust and Guenther 2017; Lermite et al. 2017; Matzel et al. 2017; Nawroth et al. 2017; Schneider et al. 1991; Trompf and Brown 2014).

Two of our PCA factors, *Confident flexibility* and *Independent problem solving*, had predictive validity: scoring high on these components was associated with success in the guide dog program. These results align with prior findings. In a sample of 1067 prospective Seeing Eye® dogs, Serpell and Hsu (2001) reported that lack of confidence was the second most common reason for release from the program. Furthermore, a recent analysis of the same sample used in the current study also found superior performance on the multistep problem-solving task was associated with success (Bray et al. in press). Bray et al. (in press) additionally found a strong connection between latency to vocalize during the novel object task and outcome. However, in the current analysis, latency to vocalize loaded onto *Quiet investigation*, a factor that was not associated with outcome. One possibility for this discrepancy is that the explanatory power of that measure was diluted by the other behaviors that loaded onto this component.

In conclusion, psychological research has a long history of using specific tasks to study an animal's "temperament" or "problem solving" independently, and yet empirical work rarely tests the associations between the two. We aimed to address this deficit by employing a larger-than-usual sample, a battery of both temperament and problem-solving tasks, and robust statistical methods. Our results indicate that forcing tasks into categories assumed to be associated solely with "problem solving" or "temperament" leads to poor fit and factors that do not correlate with other important variables or predict outcome. Alternatively, when a bottom-up approach allows problem solving and temperament to intermingle, the resulting factors reveal that the two domains interact in interesting ways. Furthermore, these factors are associated with questionnaire measures, cortisol, and program outcome.

Thus, by including multiple measures of both temperament and problem-solving skills, future large-scale studies of behavior could provide a more complete and realistic picture while allowing for further elucidation of the ways in which the two domains interact.

Acknowledgements Thanks to S. Bartner, L. Cohen, S. Frommer, M. Ream, and R. Schwartz for dedicating their time and expertise to behavioral testing and video coding. Thanks to Z. Cohen and I. Schamberg for their valuable feedback on drafts. We would also like to thank J. Parker and W. Lundskow from Salimetrics and K. Henning from the Institute for Interdisciplinary Salivary Bioscience Research at Arizona State University for their advice and organization of saliva collection and analysis. We are appreciative of Dr. Dolores Holle for coordinating our work at The Seeing Eye, along with Director of Canine Development Peggy Gibbon and the leadership team of The Seeing Eye. We are also grateful to the training kennel staff for giving us access to their dogs and testing space. Finally, we want to thank the puppy raising families for generously filling out our surveys.

Funding This work was supported in part by the University of Pennsylvania Department of Psychology's Norman Anderson Graduate Student Fund, a University of Pennsylvania University Research Fund award, the Class of 1971 Robert J. Holtz Endowed Fund for Undergraduate Research, the University of Pennsylvania's University Scholars program, and a National Science Foundation Graduate Research Fellowship to EB (DGE-1321851).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

References

Amici F, Aureli F, Call J (2008) Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. Curr Biol 18(18):1415–1419

Arden R, Adams MJ (2016) A general intelligence factor in dogs. Intelligence 55:79–85

Auersperg AMI, von Bayern AMP, Gajdon GK, Huber L, Kacelnik A (2011) Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. PLoS ONE 6(6):e20231

Barnard S, Marshall-Pescini S, Passalacqua C, Beghelli V, Capra A, Normando S, Valsecchi P (2016) Does subjective rating reflect behavioural coding? Personality in 2 month-old dog puppies: an open-field test and adjective-based questionnaire. PLoS ONE 11(3):e0149831

Barrera G, Fagnani J, Carballo F, Giamal Y, Bentosela M (2015) Effects of learning on social and nonsocial behaviors during a problem-solving task in shelter and pet dogs. J Vet Behav 10(4):307–314

Batt LS, Batt MS, Baguley JA, McGreevy PD (2008) Factors associated with success in guide dog training. J Vet Behav 3(4):143–151

Batt LS, Batt MS, Baguley JA, McGreevy PD (2009) The relationships between motor lateralization, salivary cortisol concentrations and behavior in dogs. J Vet Behav 4(6):216–222

Beerda B, Schilder MB, Bernadina W, Van Hooff JA, De Vries HW, Mol JA (1999) Chronic stress in dogs subjected to social and spatial restriction. II. Hormonal and immunological responses. Physiol Behav 66(2):243–254

Bell AM, Sih A (2007) Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecol Lett 10(9):828–834

Benson-Amram S, Holekamp KE (2012) Innovative problem solving by wild spotted hyenas. Proc R Soc Lond B Biol Sci 279(1744):4087–4095

Benson-Amram S, Dantzer B, Stricker G, Swanson EM, Holekamp KE (2016) Brain size predicts problem-solving ability in mammalian carnivores. Proc Natl Acad Sci USA 113(9):2532–2537

Bolig R, Price CS, O'Neill PL, Suomi SJ (1992) Subjective assessment of reactivity level and personality traits of rhesus monkeys. Int J Primatol 13(3):287–306. doi:10.1007/bf02547817

Bray EE, MacLean EL, Hare BA (2014) Context specificity of inhibitory control in dogs. Anim Cogn 17(1):15–31

Bray EE, MacLean EL, Hare BA (2015) Increasing arousal enhances inhibitory control in calm but not excitable dogs. Anim Cogn 18(6):1317–1329. doi:10.1007/s10071-015-0901-1

Bray EE, Sammel MD, Cheney DL, Serpell JA, Seyfarth RM (2017) Characterizing early maternal style in a population of guide dogs. Front Psychol 8:175. doi:10.3389/fpsyg.2017.00175

Bray EE, Sammel MD, Cheney DL, Serpell JA, Seyfarth RM (in press) The effects of maternal investment, temperament, and cognition on guide dog success. Proc Natl Acad Sci USA. doi:10.1073/pnas.1704303114

Brown C, Jones F, Braithwaite V (2005) In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. Anim Behav 70(5):1003–1009

Brucks D, Marshall-Pescini S, Wallis LJ, Huber L, Range F (2017a) Measures of dogs' inhibitory control abilities do not correlate across tasks. Front Psychol 8:849

Brucks D, Soliani M, Range F, Marshall-Pescini S (2017b) Reward type and behavioural patterns predict dogs' success in a delay of gratification paradigm. Sci Rep 7:42459

Brust V, Guenther A (2017) Stability of the guinea pigs personality–cognition–linkage over time. Behav Process 134:4–11

Burdick N, Randel R, Carroll J, Welsh T (2011) Interactions between temperament, stress, and immune function in cattle. Int J Zool 2011:1–9

Buss KA, Schumacher JRM, Dolski I, Kalin NH, Goldsmith HH, Davidson RJ (2003) Right frontal brain activity, cortisol, and withdrawal behavior in 6-month-old infants. Behav Neurosci 117(1):11

Carere C, Locurto C (2011) Interaction between animal personality and animal cognition. Curr Zool 57(4):491–498

Carrier LO, Cyr A, Anderson RE, Walsh CJ (2013) Exploring the dog park: relationships between social behaviours, personality and cortisol in companion dogs. Appl Anim Behav Sci 146(1):96–106

Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G (2012a) Evaluating animal personalities: Do observer assessments and experimental tests measure the same thing? Behav Ecol Sociobiol 66(1):153–160

Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G (2012b) How not to measure boldness: novel object and antipredator responses are not the same in wild baboons. Anim Behav 84(3):603–609

Cattell RB (1966) The scree test for the number of factors. Multivariate Behav Res 1(2):245–276

Coppola CL, Grandin T, Enns RM (2006) Human interaction and cortisol: Can human contact reduce stress for shelter dogs? Physiol Behav 87(3):537–541

Curley K, Paschal J, Welsh T, Randel R (2006) Technical note: exit velocity as a measure of cattle temperament is repeatable and associated with serum concentration of cortisol in Brahman bulls. J Anim Sci 84(11):3100–3103

De Palma C, Viggiano E, Barillari E, Palme R, Dufour AB, Fantini C, Natoli E (2005) Evaluating the temperament in shelter dogs. Behaviour 142(9–10):1307–1328

Dettmer AM, Murphy AM, Guitarra D, Slonecker E, Suomi SJ, Rosenberg KL, Novak MA, Meyer JS, Hinde K (2017) Cortisol in neonatal mother's milk predicts later infant social and cognitive functioning in Rhesus monkeys. Child Dev. doi:10.1111/cdev.12783

Dill LM (1987) Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Can J Zool 65(4):803–811

Dinno A (2012) Paran: Horn's test of principal components/factors. R package version 1.5.1. https://CRAN.R-project.org/package=paran

Dreschel NA, Granger DA (2005) Physiological and behavioral reactivity to stress in thunderstorm-phobic dogs and their caregivers. Appl Anim Behav Sci 95(3):153–168

Dreschel NA, Granger DA (2009) Methods of collection for salivary cortisol measurement in dogs. Horm Behav 55(1):163–168

Duckworth AL, Allred K (2012) Temperament in the classroom. Handbook of temperament. Guilford Press, New York, pp 1–45

Duffy DL, Serpell JA (2012) Predictive validity of a method for evaluating temperament in young guide and service dogs. Appl Anim Behav Sci 138(1):99–109

DuPaul GJ, Power TJ, Anastopoulos AD, Reid R (1998) ADHD rating scale-IV: checklist, norms and clinical interpretation. Guilford Press, New York

Fagnani J, Barrera G, Carballo F, Bentosela M (2016) Is previous experience important for inhibitory control? A comparison between shelter and pet dogs in A-not-B and cylinder tasks. Anim Cogn 19(6):1165–1172

Field A, Miles J, Field Z (2012) Discovering statistics using R. SAGE Publications Ltd, London

Fox MW, Stelzner D (1966) Behavioural effects of differential early experience in the dog. Anim Behav 14(2–3):273–281

Foyer P, Bjällerhag N, Wilsson E, Jensen P (2014) Behaviour and experiences of dogs during the first year of life predict the outcome in a later temperament test. Appl Anim Behav Sci 155:93–100

Frank H, Frank MG (1982) Comparison of problem-solving performance in six-week-old wolves and dogs. Anim Behav 30(1):95–98

Fratkin JL, Sinn DL, Patall EA, Gosling SD (2013) Personality consistency in dogs: a meta-analysis. PLoS ONE 8(1):e54907

Gazzano A, Mariti C, Notari L, Sighieri C, McBride EA (2008) Effects of early gentling and early environment on emotional development of puppies. Appl Anim Behav Sci 110(3–4):294–304

Goddard M, Beilharz R (1984) The relationship of fearfulness to, and the effects of, sex, age and experience on exploration and activity in dogs. Appl Anim Behav Sci 12(3):267–278

Goddard M, Beilharz R (1986) Early prediction of adult behaviour in potential guide dogs. Appl Anim Behav Sci 15(3):247–260

Goldsmith HH, Buss AH, Plomin R, Rothbart MK, Thomas A, Chess S, Hinde RA, McCall RB (1987) Roundtable: what is temperament? four approaches. Child Dev 58(2):505–529

Gosling SD, Kwan VSY, John OP (2003) A Dog's got personality: a cross-species comparative approach to personality judgments in dogs and humans. J Pers Soc Psychol 85(6):1161

Greenberg R (1984) Neophobia in the foraging-site selection of a neotropical migrant bird: an experimental study. Proc Natl Acad Sci USA 81(12):3778–3780

Griffin AS, Guez D (2014) Innovation and problem solving: a review of common mechanisms. Behav Proc 109:121–134

Griffin AS, Guez D, Lermite F, Patience M (2013) Tracking changing environments: innovators are fast, but not flexible learners. PLoS ONE 8(12):e84907

Griffin AS, Guillette LM, Healy SD (2015) Cognition and personality: an analysis of an emerging field. Trends Ecol Evol 30(4):207–214

Guido JM, Biondi LM, Vasallo AI, Muzio RN (2017) Neophobia is negatively related to reversal learning ability in females of a generalist bird of prey, the Chimango Caracara, *Milvago chimango*. Anim Cogn 20(4):591–602

Guillette LM, Naguib M, Griffin AS (2017) Individual differences in cognition and personality. Behav Process 134:1–3. doi:10.1016/j.beproc.2016.12.001

Halekoh U, Højsgaard S, Yan J (2006) The R package geepack for generalized estimating equations. J Stat Softw 15(2):1–11

Hare B, Plyusnina I, Ignacio N, Schepina O, Stepika A, Wrangham R, Trut L (2005) Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. Curr Biol 15(3):226–230

Hart LA, Yamamoto M (2017) Dogs as helping partners and companions for humans. In: Serpell JA (ed) The domestic dog: its evolution, behavior, and interactions with people, 2nd edn. Cambridge University Press, Cambridge, pp 247–270

Harvey ND, Craigon PJ, Sommerville R, McMillan C, Green M, England GC, Asher L (2016) Test-retest reliability and predictive validity of a juvenile guide dog behavior test. J Vet Behav 11:65–76

Hauser MD, Santos LR, Spaepen GM, Pearson HE (2002) Problem solving, inhibition and domain-specific experience: experiments on cottontop tamarins, *Saguinus oedipus*. Anim Behav 64(3):387–396

Hennessy MB, Davis HN, Williams MT, Mellott C, Douglas CW (1997) Plasma cortisol levels of dogs at a county animal shelter. Physiol Behav 62(3):485–490

Hennessy MB, Voith VL, Mazzei SJ, Buttram J, Miller DD, Linden F (2001) Behavior and cortisol levels of dogs in a public animal shelter, and an exploration of the ability of these measures to predict problem behavior after adoption. Appl Anim Behav Sci 73(3):217–233

Herrmann E, Call J, Hernández-Lloreda MV, Hare B, Tomasello M (2007) Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. Science 317(5843):1360–1366

Hooper D, Coughlan J, Mullen MR (2008) Structural equation modelling: guidelines for determining model fit. Electron J Bus Res Methods 6(1):53–60

Horn JL (1965) A rationale and test for the number of factors in factor analysis. Psychometrika 30(2):179–185

Hsu Y, Serpell JA (2003) Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. J Am Vet Med Assoc 223(9):1293–1300

Hu L, Bentler PM (1998) Fit indices in covariance structure modeling: sensitivity to under parameterized model misspecification. Psychol Methods 3(4):424

Hu L, Bentler PM (1999) Cutoff criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives. Struct Equ Modeling 6(1):1–55

Hydbring-Sandberg E, von Walter LW, Hoglund K, Svartberg K, Swenson L, Forkman B (2004) Physiological reactions to fear provocation in dogs. J Endocrinol 180(3):439–448

Isden J, Panayi C, Dingle C, Madden J (2013) Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. Anim Behav 86(4):829–838

Johnson JC, Sih A (2005) Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. Behav Ecol Sociobiol 58(4):390–396

Jones AC, Gosling SD (2005) Temperament and personality in dogs (*Canis familiaris*): a review and evaluation of past research. Appl Anim Behav Sci 95(1–2):1–53

Kalin NH, Larson C, Shelton SE, Davidson RJ (1998) Asymmetric frontal brain activity, cortisol, and behavior associated with fearful temperament in rhesus monkeys. Behav Neurosci 112(2):286

Kaminski J, Marshall-Pescini S (2014) The social dog: behavior and cognition. Elsevier, Amsterdam

Kaulfuß P, Mills DS (2008) Neophilia in domestic dogs (*Canis familiaris*) and its implication for studies of dog cognition. Anim Cogn 11(3):553–556

Kazlauckas V, Schuh J, Dall'Igna OP, Pereira GS, Bonan CD, Lara DR (2005) Behavioral and cognitive profile of mice with high and low exploratory phenotypes. Behav Brain Res 162(2):272–278

King T, Hemsworth P, Coleman G (2003) Fear of novel and startling stimuli in domestic dogs. Appl Anim Behav Sci 82(1):45–64

Kohler W (1925) The mentality of apes. Routledge and Kegan Paul, New York

Konečná M, Lhota S, Weiss A, Urbánek T, Adamová T, Pluháček J (2008) Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: subjective ratings and recorded behavior. J Comp Psychol 122(4):379–389

Kortet R, Hedrick A (2007) A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. Biol J Linnean Soc 91(3):475–482

Lermite F, Peneaux C, Griffin AS (2017) Personality and problem-solving in common mynas (*Acridotheres tristis*). Behav Process 134:87–94. doi:10.1016/j.beproc.2016.09.013

Liang K-Y, Zeger SL (1993) Regression analysis for correlated data. Annu Rev Publ Health 14(1):43–68

Lit L, Schweitzer JB, Iosif A-M, Oberbauer AM (2010) Owner reports of attention, activity, and impulsivity in dogs: a replication study. Behav Brain Funct 6(1):1

Lloyd AS, Martin JE, Bornett-Gauci HLI, Wilkinson RG (2007) Evaluation of a novel method of horse personality assessment: rater-agreement and links to behaviour. Appl Anim Behav Sci 105(1):205–222

Lord K, Schneider RA, Coppinger R (2017) Evolution of working dogs. In: Serpell JA (ed) The domestic dog: its evolution, behavior, and interactions with people, 2nd edn. Cambridge University Press, Cambridge, pp 42–66

MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, Anderson RC, Aurel F, Baker JM, Bania AE, Barnard AM, Boogert NJ, Brannon EM, Bray EE, Bray J, Brent LJN, Burkart JM, Call J, Cantlon JF, Cheke LG, Clayton NS, Delgado MM, DiVincenti LJ, Fujita K, Herrmann E, Hiramatsu C, Jacobs LF, Jordan KE, Laude JR, Leimgruber KL, Messer EJE, Moura ACA, Ostojić L, Picard A, Platt ML, Plotnik JM, Range F, Reader SM, Redd RB, Sandel AA, Santo LR, Schumann K, Seed AM, Sewal KB, Shaw RC, Slocombe KE, Su Y, Takimoto A, Tan J, Tao R, van Schaik CP, Virányi Z, Visalberghi E, Wade JC, Watanabe A, Widness J, Young JK, Zentall TR, Zhao Y (2014) The evolution of self-control. Proc Natl Acad Sci USA 111(20):E2140–E2148

MacLean EL, Herrmann E, Suchindran S, Hare B (2017) Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. Anim Behav 126:41–51

Marshall-Pescini S, Valsecchi P, Petak I, Accorsi PA, Previde EP (2008) Does training make you smarter? The effects of training on dogs' performance (*Canis familiaris*) in a problem solving task. Behav Process 78(3):449–454

Marshall-Pescini S, Virányi Z, Kubinyi E, Range F (2017) Motivational factors underlying problem solving: comparing wolf and dog puppies' explorative and neophobic behaviors at 5, 6, and 8 weeks of age. Front Psychol. doi:10.3389/fpsyg.2017.00180

Matzel LD, Kolata S (2010) Selective attention, working memory, and animal intelligence. Neurosci Biobehav Rev 34(1):23–30

Matzel LD, Kolata S, Light K, Sauce B (2017) The tendency for social submission predicts superior cognitive performance in previously isolated male mice. Behav Process 134:12–21

McGarrity ME, Sinn DL, Thomas SG, Marti CN, Gosling SD (2016) Comparing the predictive validity of behavioral codings and behavioral ratings in a working-dog breeding program. Appl Anim Behav Sci 179:82–94

McHugh ML (2012) Interrater reliability: the kappa statistic. Biochem Med 22(3):276–282

Miklósi Á (2015) Dog behaviour, evolution, and cognition, 2nd edn. Oxford University Press, Oxford

Morand-Ferron J, Hamblin S, Cole EF, Aplin LM, Quinn JL (2015) Taking the operant paradigm into the field: associative learning in wild great tits. PLoS ONE 10(8):e0133821

Müller CA, Riemer S, Virányi Z, Huber L, Range F (2016) Inhibitory control, but not prolonged object-related experience appears to affect physical problem-solving performance of pet dogs. PLoS ONE 11(2):e0147753

Murphy JA (1998) Describing categories of temperament in potential guide dogs for the blind. Appl Anim Behav Sci 58(1):163–178

Musek J (2007) A general factor of personality: evidence for the Big One in the five-factor model. J Res Pers 41(6):1213–1233

Nawroth C, Prentice PM, McElligott AG (2017) Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. Behav Process 134:43–53

Osthaus B, Marlow D, Ducat P (2010) Minding the gap: spatial perseveration error in dogs. Anim Cogn 13(6):881–885

Overington SE, Cauchard L, Côté KA, Lefebvre L (2011) Innovative foraging behaviour in birds: What characterizes an innovator? Behav Process 87(3):274–285

Passalacqua C, Marshall-Pescini S, Merola I, Palestrini C, Previde EP (2013) Different problem-solving strategies in dogs diagnosed with anxiety-related disorders and control dogs in an unsolvable task paradigm. Appl Anim Behav Sci 147(1):139–148

Pavlov I (1935) Obshchie tipy vysshei nervnoi deyatel'nosti zhivotnykh i cheloveka (General types of higher nervous activity in animals and man). Poslednie soobshcheniya po fiziologii i patologii vysshei nervnoi deyatel'nosti (Latest Reports on the Physiology and Pathology of Higher Nervous Activity). Akademiya Nauk SSSR, Moscow (3) 5–41

Pfaffenberger CJ, Scott JP, Fuller JL, Ginsburg BE, Bielfelt SW (1976) Guide dogs for the blind: their selection, development, and training. Elselvier, Amsterdam

Prut L, Belzung C (2003) The open field as a paradigm to measure the effects of drugs on anxiety-like behaviors: a review. Eur J Pharmacol 463(1):3–33

R Development Core Team (2016) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org

Reader SM (2003) Innovation and social learning: individual variation and brain evolution. Anim Biol 53(2):147–158

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. Biol Rev 82(2):291–318

Riemer S, Müller C, Virányi Z, Huber L, Range F (2014) The predictive value of early behavioural assessments in pet dogs—a longitudinal study from neonates to adults. PLoS ONE 9(7):e101237

Riemer S, Müller C, Virányi Z, Huber L, Range F (2016) Individual and group level trajectories of behavioural development in Border collies. Appl Anim Behav Sci 180:78–86

Rooney NJ, Gaines SA, Bradshaw JW (2007) Behavioural and glucocorticoid responses of dogs (*Canis familiaris*) to kennelling: investigating mitigation of stress by prior habituation. Physiol Behav 92(5):847–854

Rosseel Y (2012) Lavaan: an R package for structural equation modeling and more. Version 0.5–12 (BETA). Ghent, Belgium: Ghent University

Rowe C, Healy SD (2014) Measuring variation in cognition. Behav Ecol 25(6):1287–1292

Ruscio J, Roche B (2012) Determining the number of factors to retain in an exploratory factor analysis using comparison data of known factorial structure. Psychol Assess 24(2):282–292

Schneider ML, Moore CF, Suomi SJ, Champoux M (1991) Laboratory assessment of temperament and environmental enrichment in rhesus monkey infants (*Macaca mulatta*). Am J Primatol 25(3):137–155

Seaman S, Davidson H, Waran N (2002) How reliable is temperament assessment in the domestic horse (*Equus caballus*)? Appl Anim Behav Sci 78(2):175–191

Serpell JA, Hsu Y (2001) Development and validation of a novel method for evaluating behavior and temperament in guide dogs. Appl Anim Behav Sci 72(4):347–364

Sherman BL, Gruen ME, Case BC, Foster ML, Fish RE, Lazarowski L, Dorman DC (2015) A test for the evaluation of emotional reactivity in Labrador retrievers used for explosives detection. J Vet Behav 10(2):94–102

Shettleworth SJ (2013) Fundamentals of comparative cognition. Oxford University Press, New York

Sih A, Del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos Trans R Soc Lond B Biol Sci 367(1603):2762–2772

Sih A, Bell AM, Johnson JC, Ziemba RE (2004) Behavioral syndromes: an integrative overview. Q Rev Biol 79(3):241–277

Siniscalchi M, McFarlane J, Kauter K, Quaranta A, Rogers L (2013) Cortisol levels in hair reflect behavioural reactivity of dogs to acoustic stimuli. Res Vet Sci 94(1):49–54

Sinn DL, Gosling SD, Hilliard S (2010) Personality and performance in military working dogs: reliability and predictive validity of behavioral tests. Appl Anim Behav Sci 127(1):51–65

Slabbert J, Odendaal J (1999) Early prediction of adult police dog efficiency—a longitudinal study. Appl Anim Behav Sci 64(4):269–288

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L (2005) Big brains, enhanced cognition, and response of birds to novel environments. Proc Natl Acad Sci USA 102(15):5460–5465

Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol Evol. doi:10.1111/2041-210X.12797

Strelau J (1997) The contribution of Pavlov's typology of CNS properties to personality research. Eur Psychol 2(2):125–138

Svartberg K (2005) A comparison of behaviour in test and in everyday life: evidence of three consistent boldness-related personality traits in dogs. Appl Anim Behav Sci 91(1):103–128

Svartberg K, Forkman B (2002) Personality traits in the domestic dog (*Canis familiaris*). Appl Anim Behav Sci 79(2):133–155

Tabachnik B, Fidell L (2007) Using multivariate statistics. Allyn & Bacon, Boston

Taylor KD, Mills DS (2006) The development and assessment of temperament tests for adult companion dogs. J Vet Behav Clin Appl Res 1(3):94–108

Taylor AH, Elliffe D, Hunt GR, Gray RD (2010) Complex cognition and behavioural innovation in New Caledonian crows. Proc R Soc Lond B Biol Sci 277:2637–2643

Thompson WR, Heron W (1954) The effects of restricting early experience on the problem-solving capacity of dogs. Can J Psychol (Revue canadienne de psychologie) 8(1):17–31

Thornton A, Samson J (2012) Innovative problem solving in wild meerkats. Anim Behav 83(6):1459–1468

Trompf L, Brown C (2014) Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. Anim Behav 88:99–106

Valsecchi P, Barnard S, Stefanini C, Normando S (2011) Temperament test for re-homed dogs validated through direct behavioral observation in shelter and home environment. J Vet Beh Clin Appl Res 6(3):161–177. doi:10.1016/j.jveb.2011.01.002

van der Borg JA, Netto WJ, Planta DJ (1991) Behavioural testing of dogs in animal shelters to predict problem behaviour. Appl Anim Behav Sci 32(2):237–251

Vas J, Topál J, Péch É, Miklósi Á (2007) Measuring attention deficit and activity in dogs: a new application and validation of a human ADHD questionnaire. Appl Anim Behav Sci 103(1):105–117

Verbeek ME, Boon A, Drent PJ (1996) Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. Behaviour 133(11):945–963

Vlamings PHJM, Hare B, Call J (2010) Reaching around barriers: the performance of the great apes and 3–5-year-old children. Anim Cogn 13(2):273–285

Wan M, Hejjas K, Ronai Z, Elek Z, Sasvari-Szekely M, Champagne FA, Kubinyi E (2013) DRD4 and TH gene polymorphisms are associated with activity, impulsivity and inattention in Siberian Husky dogs. Anim Genet 44(6):717–727

Webster SJ, Lefebvre L (2001) Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. Anim Behav 62(1):23–32

Weiss E, Greenberg G (1997) Service dog selection tests: effectiveness for dogs from animal shelters. Appl Anim Behav Sci 53(4):297–308

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(1):151–162