

eScholarship

International Journal of Comparative Psychology

Title

Thinking Pigs: A Comparative Review of Cognition, Emotion, and Personality in *Sus domesticus*

Permalink

<https://escholarship.org/uc/item/8sx4s79c>

Journal

International Journal of Comparative Psychology, 28(1)

ISSN

0889-3675

Authors

Marino, Lori
Colvin, Christina M

Publication Date

2015

DOI

10.46867/ijcp.2015.28.00.04

Copyright Information

Copyright 2015 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed



Thinking Pigs: A Comparative Review of Cognition, Emotion, and Personality in *Sus domesticus*

Lori Marino^{1,2} & Christina M. Colvin³

*The Kimmela Center for Animal Advocacy¹, The Someone Project²
Emory University, USA³*

While relatively little is known about the psychology of domestic pigs, what is known suggests that pigs are cognitively complex and share many traits with animals whom we consider intelligent. This paper reviews the scientific evidence for cognitive complexity in domestic pigs and, when appropriate, compares this literature with similar findings in other animals, focusing on some of the more compelling and cutting-edge research results. The goals of this paper are to: 1) frame pig cognition and psychology in a basic comparative context independent of the livestock production and management setting; and 2) identify areas of research with pigs that are particularly compelling and in need of further investigation. We summarize and discuss several areas of comparative psychology, including nonsocial and social cognition, self-awareness, emotion, and personality. We conclude that there are several areas of research in which the findings are suggestive of complex psychology in pigs. We conclude by calling for more noninvasive cognitive and behavioral research with domestic pigs in non-laboratory settings that allow them to express their natural abilities.

The animal cognition literature is rich in information about certain types of animals, including primates, rodents, birds, and, increasingly, dogs. From the standpoint of our basic understanding of the range of cognition in the animal kingdom, pigs, as even-toed ungulates, are a taxonomic group that is not as well represented in the comparative psychology literature as these other groups. In fact, no ungulate groups are well-studied compared with the aforementioned animals who are, in contrast, frequently considered. Because of their status as an under-represented ungulate group, there exists a very basic need to bring together what we do know about pigs in order to build on our current understanding and gain further insights into the distribution of various cognitive and behavioral levels of sophistication in mammals and other taxa.

The scientific literature on pig psychology and behavior has been dominated by applied themes and settings relating to welfare in intensive farming. These kinds of applied frameworks likely impact and shape our understanding of pigs from both a

Please send correspondence to Dr. Lori Marino, The Kimmela Center for Animal Advocacy. USA.

(Email:lorimarino@kimmela.org)

<https://doi.org/10.46867/ijcp.2015.28.00.04>

scientific and public perspective. While some studies have been done that do not frame pigs within an applied setting, these are far less numerous than those with direct reference to behavioral management in an agricultural or laboratory setting.

This paper examines both categories of research - applied and basic - in an effort to begin to fill out and reframe our understanding of pig intelligence, cognition, and overall psychology on a basic comparative-evolutionary level. We also identify research findings that are particularly promising and interesting from the point of view of revealing complex abilities of pigs. We do not purport to offer an exhaustive review of all studies of cognition and emotion in pigs. Instead, we have chosen to focus on the more complex capacities in pigs that are arguably at the leading edge of intelligence and sentience and to identify compelling and promising areas of cognition, emotion, and sociality which, we contend, should be investigated in future studies.

Species-specific Factors to Consider When Assessing Findings on Pig Behavior and Cognition

Evolution and History of Domestication

As with any group, species-specific factors need to be considered when interpreting cognitive, emotional, and social capacities in pigs, as well as when comparing their capacities to other species. It is especially important to keep in mind that not all domesticated animals are bred for the same characteristics. For instance, while dogs were selected for traits promoting human companionship and work, pigs were selected for the ability to produce meat.

Domestic pigs descended from wild boars (*Sus scrofa*), a gregarious species that underwent the first phase of domestication in the Near East about 9,000 years ago (Giuffra, Kijas, Amarger, Carlborg, Jeon & Andersson, 2000). Multiple smaller domestication events occurred over time, with much crossbreeding between Asian and European groups (Giuffra et al., 2000; Larson, Dobney, Albarella, Fang, Matisoo-Smith, Robins, & Cooper, 2005). Importantly, although during domestication there was some artificial selection for an easy temperament, most of the selective breeding of pigs has been for production traits, especially growth and reproduction. As a result, modern domesticated pigs are not too dissimilar, cognitively and behaviorally, from ancestral and modern wild boars (Held, Cooper, & Mendl, 2009).

This is especially true of their social behavior; for both domesticated pigs and wild boars, the basic social unit is several females and their offspring, with strong parallels in reproductive behavior, parenting, and development (Graves, 1984; Jensen, 1986). Preliminary comparisons of cognition and learning in wild boars and domestic pigs indicate that often ontogeny and early experience have more of an impact on these processes than selection during domestication (Albiach-Serrano, Brauer, Cacchione, Zickert, & Amici, 2012). Therefore, the capacities and behaviors of domesticated pigs appear to have been developed through adaptations based in the physical and social environment of their wild ancestors and relatives.

Sensory Abilities

Assessments of cognitive capacity in any species are dependent upon using stimuli and settings appropriate to the sensory capabilities of that species, i.e., those that resemble the mass of sensory information the animal is adapted to perceiving and processing (Geiling, Nordquist, & van der Staay, 2011). Therefore, it is critical to recognize that domestication has not substantially altered the type of environmental information domesticated pigs are capable of detecting (Held et al., 2009; Jensen, 1986). They use a wide range of stimuli both in their physical and social environments.

It should not come as a surprise, considering the gregarious nature of their wild counterparts, that pigs are highly social animals and that tactile information plays an important role in their behavior. The highest density of tactile receptors is found in the pig's snout (Kruska, 1988), as they use their snouts to engage in highly manipulative behaviors such as rooting, carrying and pushing, and social interactions (Stolba & Wood-Gush, 1989). Olfaction is the pig's keenest sense. Thus, they learn olfactory discriminations more easily than discriminations in other modalities (Croney, 1999). As opportunistic omnivores, they rely heavily on odors and flavors to find appropriate food items when foraging (Croney, Adams, Washington, & Stricklin, 2003). Furthermore, their sensitivity in the olfactory domain is not limited to foraging for food, but is used heavily in the social domain in a wide range of contexts, including discriminating social identity (Mendl, Randle, & Pope, 2002), sexual state (Signoret, Baldwin, Fraser, & Hafez, 1975) and the emotional state of other pigs in aggressive encounters (McGlone, 1990), as well as in creating dominance hierarchies (Mendl, Randle, & Pope, 2002).

Audition is used by pigs in many social contexts, including communication. Identity and arousal state can be conveyed through vocalizations (Manteuffel, Puppe, & Schon, 2004), and these are used extensively in mother-offspring interactions (Weary, Lawson, & Thompson, 1996; Weary, Ross, & Fraser, 1997). The hearing range of pigs spans from 42-40,500 Hz (Heffner & Heffner, 1992), making them sensitive in the ultrasound range.

Pigs typically use vision along with other senses, particularly olfaction and touch, to discriminate objects in the natural environment (Arave, 1996; Lomas, Piggins, & Phillips, 1998). Nevertheless, they are capable of discriminating objects by vision alone in the absence of other cues (Koba & Tanida, 2001). Moreover, both vision and audition are used more than olfaction when discriminating between humans (Tanida & Nagano, 1998).

The Scientific Literature

Research Methods

Here we present a summary of cognitive, emotional, personality and social characteristics of pigs from a comprehensive review of the scientific literature. We conducted online Google-based direct searches through all of the major peer-reviewed journals in these areas (Table 1). We used familiar and broad terms relevant to intelligence, cognition, and behavior and key terms from existing papers (e.g., intelligence, cognition, behavior, learning, memory, sociality, self-awareness, self-recognition, etc.). We also used more specific search terms, e.g., spatial memory,

navigation, deception, etc., within these broader categories when necessary. Additionally, we used these terms to search on ScienceDaily for relevant news items and the peer-reviewed papers they described. We also conducted a complete search of the websites of the major authors in these fields for all of their relevant projects. Finally, we searched the reference section of each paper to find additional papers in additional miscellaneous journals (not listed in Table 1) and ensured that our search was comprehensive. We included books, book chapters, and dissertation theses as well as both empirical and review papers (which provided further description and interpretation of the empirical data) and included both the basic comparative psychology literature and the applied literature. We did not place time restrictions on articles, but we did give priority to more recent papers when appropriate. The reference section shows the full breadth of the sources we consulted.

We divide our findings into five broad categories: Nonsocial Cognition, Social Cognition, Self-awareness, Emotion, and Personality, with sub-categories within some.

Findings from the Literature

Nonsocial Cognition

Nonsocial cognition refers to how animals perceive, mentally represent, and process physical components of their environment. It includes problem solving in the physical realm, object discrimination, spatial cognition, and other elements of learning and memory in the physical/object domain, including time perception. In this paper we distinguish nonsocial from social cognition for the sake of presentation but do not presume that all aspects of social and nonsocial cognition are mutually exclusive.

Table 1. List of major peer-reviewed journals searched

Journals	
<i>Animal Behavior</i>	<i>Domestic Animal Endocrinology</i>
<i>Animal Cognition</i>	<i>Hormones and Behavior</i>
<i>Animal Welfare</i>	<i>International Journal of Comparative Psychology</i>
<i>Applied Animal Behavior Science</i>	<i>Journal of Animal Science</i>
<i>Applied Animal Behavior Ethology</i>	<i>Journal of Comparative Psychology</i>
<i>Behaviour</i>	<i>Journal of Mammalogy</i>
<i>Behavioural Brain Research</i>	<i>Nature</i>
<i>Behavioural Processes</i>	<i>Physiology and Behavior</i>
<i>Brain, Behavior and Evolution</i>	<i>Public Library of Science (PLoS) Biology and PLoS One</i>
<i>Current Biology</i>	<i>Science</i>

Object discrimination learning. Object discrimination learning involves the ability to learn to discriminate stimuli or objects on the basis of various attributes of those stimuli through differential reinforcement contingencies (Kehoe, 2008). Clearly, object discrimination is a necessary foundation for other forms of cognition. Object discrimination makes categorization and concept formation possible; these capacities, in turn, can provide cognitive scaffolding for other complex capacities. All animals possess some ability to learn to discriminate objects, and these capacities range from discriminations of simple concrete stimuli to complex and even abstract concepts.

Pigeons and other bird species are capable of categorizing and differentiating various stimuli, e.g., distinguishing between photos with and without humans (Huber, Apfalter, Steurer, & Prossinger, 2005). Many mammals, including rodents and primates, are capable of rather complex discriminations (Fagot, 2000; Matsuzawa, 2001; Zentall & Wasserman, 2006). And dogs are able to classify color photographs of natural stimuli such as other dogs and landscapes (Range, Aust, Steurer, & Huber, 2008).

When it comes to robust object discrimination capacities, pigs are no exception. Complex object discrimination has been demonstrated in pigs in a range of situations requiring a robust memory (Croney et al, 2003; Hemsworth, Verge, & Coleman, 1996; Tanida & Nagano, 1998). In one study in which the spontaneous response of pigs to novel and familiar objects was assessed, after exposure to a sample object for two days, pigs remembered the object for at least five days and showed a preference for novel objects over familiar ones (Gifford, Sylvie Cloutier, & Newberry, 2007), demonstrating their capacity for long-term memory.

Moreover, pigs can prioritize *important* memories, such as the requirements of a food-searching task. When given the opportunity to access only one of two food sources, they regularly preferred the one with more food and remembered that site (Held, Baumgartner, Kilbride, Byrne, & Mendl, 2005). Pigs can also use either or both visual and olfactory cues while foraging. Rather than rely on the spatial placement of a location that previously contained food, pigs can follow both certain colors and food extract odors to find a food source, showing that they can make discriminations in both modalities, that is, between colors and odors (Croney et al. 2003).

Some of the most compelling studies on object discrimination with pigs were designed to parallel the *symbolic language comprehension* research with dolphins (*Tursiops truncatus*, Herman, 1980, 1987; Herman, Hovanick, Gory, & Bradshaw, 1989) and sea lions (*Zalophus californianus*, Schusterman, 1993). These marine mammals can utilize visual (gestural) and auditory stimuli to successfully process semantic (meaning) and syntactic (sequential) components of an artificial language. When given a similar task, two Vietnamese potbellied pigs (*Sus scrofa domesticus*) demonstrated comprehension of gestural and verbal symbols representing objects (frisbee, ball, dumbbell) and actions (sit, fetch, jump). They were also able to distinguish these items from one another (Cerbulis, 1994). Moreover, they learned to comprehend a combination of symbols for actions and objects (e.g., *fetch the frisbee*), discriminating among three objects, and, like dolphins and sea lions, performed the action-object task presented to them. Although there has been controversy over whether these kinds of

responses to symbols represent more than stimulus response-learning, the pigs, like the dolphins, exhibited complex three-choice object discrimination and three-object, one action combination discrimination as well. These capacities lend support to the view that their performance on the task may require a more complex explanation. The basic ability to appropriately respond to symbols representing objects and actions in pigs suggests that further studies of this kind would be worth pursuing in order to explore the differences and similarities in levels of cognitive complexity in this situation between pigs and marine mammals.

Time perception. One area of longstanding interest in comparative cognition is time perception, i.e., the ability to detect the passage of time and anticipate the future. Basic time perception is not entirely synonymous with, but is arguably a basis for, more sophisticated mental time travel, the conscious ability to mentally represent the past and the future. That is, when coupled with an episodic memory system, time perception may become part of an autobiographical sense of self in the past, present and future.

There is substantial evidence that other animals have internal timing mechanisms that help them know the time of day and predict when events will occur (Gallistel, 1994). Western scrub jays (*Aphelocoma californica*) are able to anticipate future events and act accordingly during food-caching episodes (Raby, Alexis, Dickinson, & Clayton, 2007). Chimpanzees (*Pan troglodytes*) and other great apes clearly possess an autobiographical self, as they are able to prepare themselves for future actions (e.g., tool use), even as much as a day in advance (Beran, Pate, Washburn, & Rumbaugh 2004, 2012; Mulcahy & Call, 2006; Osvath & Osvath, 2008) and demonstrate a capacity for episodic memory. They can remember highly specific contextual elements, that is, the *what, where and when* of events when hours, weeks and even years have passed (Martin-Ordas, Berntsen, & Call, 2013; Martin-Ordas, Haun, Colmenares, & Call, 2010).

Although there has been no conclusive work on time perception in pigs, the research that has been done is intriguing and points toward the value of further work in this area. In one study female pigs were given a choice between two crates that differed mainly with respect to the duration of confinement they imposed, which was either 30 min (short) or 240 min (long). The pigs showed an overall preference for confinement in crates associated with short durations instead of those associated with longer durations, demonstrating that they were sensitive to differences in elapsed time in the two crates. Furthermore, the pigs used a variety of sensory cues (visual patterns and direction) to make that decision (Spinka, Duncan, & Widowski, 1998). However, the pigs in this study did not show all the behaviors expected from the time perception hypothesis. That is, there was no measurable hesitancy to enter crates where they would be confined for long duration. One would hypothesize that if the pigs strongly preferred short-duration to long-duration crates that they would hesitate to enter the long-duration crates. The authors concluded, however, that although there was a preference the long duration period was not very aversive for the pigs. Also, the apparatus used was not symmetrical and the pigs initially showed some bias towards one side versus the other. This bias had to be overcome by modifications in the apparatus. Therefore, there were a number of components of the study that need to be explored more closely before it can be taken as definitive evidence of time perception.

Another study used an operant set-up requiring a foot lever press by six female, pre-adolescent mini-pigs who performed tasks thought to measure some aspect of timing behavior through temporal response differentiation requiring the pigs to hold down a lever for a specific number of seconds. The authors concluded that the cognitive aspects of the task were likely to be within the capacity of the pigs but that the required physical response was too difficult, i.e., their hooves slipped off the lever and many of the pigs tried to respond with their snouts instead of feet, showing that they likely understood the cognitive requirements of the task, despite the physical limitations (Ferguson, Gopee, Paule, & Howard, 2009).

In another study, pigs were able to anticipate positive and negative situations (Imfeld-Mueller, van Wezemaela, Stauffachera, Gygax, & Hillmann, 2011). Pigs were kept in a waiting box and cued with tones signaling whether they would be able to go into a room with a bowl of popcorn (positive) or cross a ramp provoking a visual cliff response (negative). When anticipating the negative situation, the proportion of pigs uttering high-frequency vocalizations was significantly higher, pigs turned around more often, and the latency to move was longer after door opening, than when waiting for the positive situation. However, heart rate, heart rate variability and locomotive activity were not influenced by the valence of the situation but differed depending on the phase (waiting, tone, anticipation and end) of the trial. Although the authors considered the high-pitched vocalization to be the most sensitive parameter of the pigs' emotional responses, the results demonstrate various behaviors indicative of an emotional response in anticipation of two different events.

Although there is insufficient data to draw definitive conclusions regarding the complexity of time perception in pigs, the research described above suggests that further research on time perception, anticipation, and, if these abilities turn out to be robust in pigs, perhaps even planning (which is based upon these capacities), in pigs would be promising.

Spatial learning and memory. Spatial cognition (learning and memory) refers to the ability to acquire knowledge of, remember, organize and utilize information about spatial aspects of one's environment, including navigation and learning to discriminate and prioritize the locations of objects. Spatial learning is highly dependent upon mental representations in both short and long-term memory and often forms the basis of complex cognitive maps of the environment, providing the foundation for many other social and non-social strategic behaviors during such tasks as foraging and traveling.

The complex spatial abilities of food-caching birds are well known (Balda & Kamil, 2002; Shettleworth, 2002) and many other species display sophisticated navigational and spatial foraging capacities as well, including rodents (Bird, Roberts, Abrams, Kit, & Crupi, 2013) and fish (Brown, 2015). Dogs, too, show complex spatial navigational and search capacities indicating use of cognitive maps. For instance, while navigating toward desired locations and searching for hidden objects, dogs appear to develop novel spatial shortcuts based on their knowledge of previously used paths (Bensky, Gosling, & Sinn, 2013, for a review). Chimpanzees and other nonhuman primates also possess sophisticated spatial-navigational memory and learning capacities in some cases, on a par with four-year old humans (Garber & Dolins, 2014).

Pigs, as foraging animals, are especially good at using spatial information; they are highly competent at learning to navigate mazes and other spatial arrangements (e.g., de Jon et al., 2000; Siegford, Rucker, & Zarella, 2008), although many of these tests are done in highly artificial settings, such as water mazes. Arguably more relevant and revealing are studies of spatial abilities in a foraging context. One of the most ethologically valid and productive methods used to study spatial learning and memory and other cognitive capacities in pigs is the *holeboard* procedure (van der Staay, Gieling, Pinzon, Nordquist, & Ohl, 2012). The holeboard is an open-field arena with numerous holes (or wells) in it that can be baited. This apparatus and procedure allow pigs to *forage* using their snouts as they do in the natural setting. The holeboard protocol has been used to study spatial behavior in a wide variety of species and has been used extensively to study a range of dimensions of spatial behavior, including working memory and foraging strategies. Pigs perform quite well in this spatial discrimination setting, and their performance is robust as it is not affected by an acute social stress, e.g., the presence of a strange pig (Arts, van der Staay, & Ekkel, 2009). For instance, pigs rapidly learn spatial discriminations that depend upon working and reference memory (Bolhuis et al., 2013; Gieling, Arts, Nordquist, & van der Staay, 2012; Gieling et al., 2013; Nawroth & von Borell, 2014).

Pigs also remember the location, content, and relative value of previously discovered sites that contained stimuli of interest. Across 10-minute and 2-hour retention intervals, pigs successfully used spatial memory to search areas for food and to avoid areas previously found to be empty (Mendl, Laughlin, & Hitchcock, 1997). Another experiment showed that pigs were able to learn a win-shift (searching elsewhere after finding food) foraging task faster and with a higher degree of accuracy than a win-stay (returning to the location of previously-discovered food) foraging task, suggesting that pigs have a predisposition to forage in previously unexplored areas (Laughlin & Mendl, 2000). These studies show that pigs can use spatial memory flexibly; they can be trained to either return to a location where they previously found food or to use the memory of a previously discovered food site to forage elsewhere.

In another particularly interesting experiment, pigs were presented with two different food sites that were baited with unequal amounts of food. When made to choose between one of the two locations in a foraging context, pigs showed a preference for visiting the site containing the larger amount of food (Held et al., 2005). These findings suggest that pigs are able to discriminate between and remember the locations of food sites of different relative value. Although it is possible that the pigs were subitizing, a form of pattern recognition that is used to rapidly assess small quantities of items (Cutini & Bonato, 2012), these findings do suggest some level of numerosity in pigs. Of course, more research could be focused on determining the exact cognitive mechanism underlying this ability.

Novelty Seeking, Inquisitiveness and Play. Play is related to creativity and innovation and, therefore, forms the basis for complex object-related and social abilities (Bateson, 2015) in humans and other animals.

Exposure to novelty enhances learning experiences, and responses to novelty can have an impact on performance in other cognitive tasks as well (Kaulfuss & Mills, 2008). Social play, which involves creating new interactions and situations, has an important role in the development of canids and other social mammals (Bekoff, 1974,

2014). Therefore, curiosity and the preference for novelty are, arguably, related to cognitive complexity and certain personality traits (see below).

Play is found most predominantly in the most cognitively complex and adaptable nonhuman species, such as primates (Bencke, 2015), dogs (Bekoff, 2015), dolphins (Janik, 2015) and birds (Emery & Clayton, 2015). However, play behavior also exists in fish and reptiles (Burghardt, 2015), and the most cognitively complex invertebrates, such as the octopus (Zylinski, 2015). Therefore, play appears to be a marker of cognitive complexity.

Pigs, too, are playful animals (Donaldson, Newberry, Spinka, & Cloutier, 2002; Olsen, Simonsen, & Dybkjaer, 2002; Newberry, et al. 1988; Wood-Gush and Vestergaard, 1991, 1993), exhibiting a wide range of behaviors in this domain. A recent study of play behavior in pigs shows that they engage in quite complex types of play that include social play and object play (Horback, 2014). Common object play behaviors in pigs include shaking or carrying an object such as a ball or stick or tossing straw (Bolhuis, Schouten, Schrama, & Wiegant, 2005; Dudink, Simonse, Marks, de Jonge, & Spruijt, 2006; Newberry et al., 1988). Locomotor play includes waving/tossing of the head, scampering, jumping, hopping, pawing, pivoting, and gamboling (energetic running), flopping on the ground, and hopping around (Martin, Ison, & Baxter, 2015). Social play in pigs includes play fighting, pushing and running after each other (Horback, 2014). Many of these categories of play are combined and the behaviors are similar to play behavior in dogs and other mammals.

Play in pigs not only satisfies a need for exploration and discovery, it also is critical for healthy development. Play is best stimulated by diverse, complex, *hands on*, and renewable objects and materials (Martin, et al., 2015; Studnitz, Jensen, & Pedersen, 2007; Telkanranta, Bracke, & Valros, 2014). So important is this need that insufficient opportunity to explore leads to behavioral abnormalities (Pedersen et al., 2014; Studnitz et al., 2007; Telkanranta et al., 2014). Young pigs reared in a cognitively challenging and complex environment affording greater interactions with objects and other pigs are more socio-cognitively developed than their counterparts raised in standard farrowing crates (Martin et al., 2014). Olsen et al. (2002) found that when given access to materials allowing for exploration, pigs engaged in more behaviors associated with positive affect, such as play, and especially locomotor play. Also, consistent with these findings is the fact that pigs make more optimistic choices (have a positive bias) when in enriched environments than in others, indicating that they find stimulation rewarding and pleasurable (Douglas, Bateson, Walsh, Bedue, & Edwards, 2012). Therefore, opportunities for play and exploration impact emotional development in pigs as well.

Social Cognition and Complexity

Social cognition is the use of cognitive skills within the social domain and forms the basis for cognitive complexity and intelligence, including culture, across a wide range of species. There is an abundance of empirical evidence showing a positive correlation between various high-level cognitive capacities and measures of social complexity in groups as wide-ranging as primates (e.g., Dunbar, 1998), birds (Burish, Kueh, & Wang, 2004), and cetaceans, e.g., dolphins and whales (Whitehead & Rendell, 2015). Whereas domestic and wild pigs are social animals, relatively little is known

about how these capacities manifest in their natural lives and what cognitive and emotional abilities underwrite their sociality. What is known points to the possibility that pigs are as socially complex as many other highly intelligent animals, possibly sharing a number of cognitive capacities related to social complexity.

Discriminating conspecifics and others. The ability to discriminate among individuals forms the basis for social relationships, hierarchies, and reactions to familiar versus unfamiliar individuals. Individual discrimination is not the same as but is a prerequisite to the more complex capacity for true individual recognition, defined as a mental representation of an individual's identifying characteristics. Thus, individual discrimination is a logical beginning for investigating a species' general social recognition abilities.

A number of animals can discriminate individuals. Dogs can discriminate between barks of other dogs recorded in different contexts from the same individual, as well as from different individuals in the same context (Molnar, Pongracz, Farago, Doka, & Miklosi, 2009). As another example, elephants are well known for their sophisticated recognition of individual conspecifics even over long distances (McComb, Moss, Sayialel, & Baker, 2000). These kinds of capacities not only underlie the ability to recognize kin from non-kin, and stranger from familiar individual, but also allow for finer discriminations of individual identity within one's social network.

Like these other socially complex animals, pigs discriminate among conspecifics and show a preference for familiar individuals over strangers (de Souza, Jansen, Tempelman, Mendl, & Zanella, 2006; Kristensen, Jones, Schofield, White, & Wathes, 2001; McLeman, Mendl, Jones, White, & Wathes, 2005). McLeman et al. (2005), investigated the ability of 6-week-old female pigs to discriminate between pairs of female conspecifics in a Y-maze using a variety of sensory cues. They found that juvenile pigs base discriminations on learning and can differentiate between two familiar conspecifics when allowed to use all normal social cues. They can even discriminate between closely-related individuals.

Young pigs can also discriminate between both familiar and unfamiliar individuals based on urinary samples alone (Mendl et al, 2002). In one study, pigs were able to use olfactory cues to make social discriminations even after chronic exposure to 36 ppm of ammonia, which degraded their sense of smell (Kristensen et al., 2001). Moreover, this ability to make distinctions lasted at least over a 15-minute period, over which the pigs showed habituation to the same odors. In addition to olfactory discrimination, pigs use auditory cues to distinguish among conspecifics, as do dogs (Molnar, Pongracz, Farago, Doka, & Miklosi, 2009). Consistent with this finding is the evidence for the individuality of vocalizations in pigs (Blackshaw, Jones, & Thomas, 1996; Schön, Puppe, Gromko, & Manteufel, 1999). When listening to a playback of piglet vocalizations, sows responded more strongly when the calls of their own piglets were played than when listening to the calls of unfamiliar piglets, showing that they are able to discriminate their offspring from other litters by voice (Illmann, Schrader, Pinka, & Ustr, 2002). Thus, not unlike canids, pigs appear to have strong abilities to flexibly discriminate among conspecifics using various cues and under a variety of circumstances.

It may be argued that it requires even further cognitive flexibility and learning to differentiate members of another species. Dogs can not only discriminate among

humans but they can tell the difference between a smiling human face and a neutral expression (Nagasawa, Murai, Mogi, & Kikusui, 2011). These kinds of capacities are not surprising in a species with a history of domestication that involved sensitivity to human cues. Yet pigs, too, can discriminate familiar and unfamiliar humans (Koba & Tanida, 1999; Tanida & Nagano, 1998), though perhaps not with the same degree of subtlety. In a study by Tanida and Nagano (1998), young miniature pigs were handled gently and fed treats for five weeks and then allowed to choose between the handler and a stranger in a Y-maze. The results showed that these pigs were able to discriminate between the handler and a stranger and there were a range of individual differences in the kinds of cues (e.g., olfactory, visual and auditory) each pig used. Surprisingly, olfaction appeared to be the least useful for the pigs in differentiating stranger from familiar handler. In general, this study showed that the pigs were able to use prior experience to discriminate between two humans.

Interestingly, there is some evidence that pigs in commercial settings handled in a negative manner do not discriminate between handlers as they are handled roughly by all handlers in this setting (Hemsworth, Coleman, Cox, & Barnett, 1994), a result that shows that pigs respond adaptively to different kinds of previous treatment. In another set of choice studies similar to those above, Koba and Tanida (1999) found that pigs can discriminate between humans by differences in body size and some aspects of the face when repeatedly exposed to people wearing the same clothes. The pigs' abilities were more attuned to differences in body size than facial characteristics, but these results suggest that pigs may be sensitive, at some level, to facial characteristics in humans. More research is clearly needed to clarify and refine our understanding of these capacities.

Perspective-taking. The ability to take the perspective of another individual is considered a complex mental capacity that may form the basis of a specific kind of social cognition known as Machiavellian Intelligence (Byrne & Whiten, 1988; Humphrey, 1976; Whiten & Byrne, 1997). Machiavellian intelligence is defined by political maneuvering, e.g., deceit and manipulation, and is hypothesized to be a major driver of intelligence in primates and some other species, such as dogs (Humphrey, 1976; Whiten & Byrne, 1997, 1988).

Throughout the general comparative literature and across a variety of species, perspective-taking has been associated with a number of other cognitive capacities, including self-awareness, theory of mind, intentional deception and empathy (Bullock, Boysen, & Furlong, 2008; de Waal, 2005, 2008a; Gallup, 1998; Towner, 2010, for a comprehensive review of these issues). Even the most basic forms, attention to visual cues and visual perspective-taking, require taking a stance other than one's own and usually using that information to one's advantage. Although responsiveness to cues, such as pointing, is not equivalent to perspective-taking, it can be categorized in a very general way as sensitivity toward some indicating act on the part of another. In this section, we will explore the continuum of cue use and perspective-taking in pigs.

A number of species have demonstrated well-developed capacities in the realm of conspecific perspective-taking, including chimpanzees (Krachun & Call, 2009), and dogs (Bräuer, Bös, Call, & Tomasello, 2013), and Western scrub jays (Clayton, Dally, & Emery, 2007). Pigs exhibit behaviors and patterns of interaction with one another that may be comparable to what has been observed in primates and some birds.

For example, pigs exhibit complex abilities to utilize and manipulate conspecifics to their advantage in social foraging situations. In a protocol requiring pigs to forage in pairs for hidden food, when one pig was informed as to the location of the food and the other was naïve (a scrounger), the latter was able to exploit the knowledge of the informed pig by following him to the food source and displacing him, thus reducing the time it took for the naïve pig to find food on his own (Held, Mendl, Devereux, & Byrne, 2000). Moreover, exploited pigs altered their behavior in response to this exploitation in competitive foraging trials; foraging behavior of individuals who were previously exploited changed to match the circumstances and to decrease the chances of being exploited. For instance, subordinates were more likely to show food-directed behavior when the chances of arriving at the food ahead of their exploiters was high (Held, Mendl, Devereux, & Byrne, 2002; Held, Mendl, Laughlin, & Byrne, 2002). In a similar study, subordinates increased their foraging speed to stay ahead of exploiters (Held et al., 2010).

These kinds of strategic behaviors and counter-behaviors are described as tactical deception when observed in great apes (Bräuer, Call, & Tomasello, 2007; Byrne & Whiten, 1988, 1992), and these observations in pigs suggest that pigs may have a complex level of perspective-taking. As one of the authors stated: “Our results suggest that pigs can develop quite sophisticated social competitive behavior, similar to that seen in some primate species.” (Mendl, 2002, British Association for the Advancement of Science conference). Like primates, the ability to take the perspective of another is most apparent in competitive situations in pigs.

Some other species, such as apes (Hostetter, Russell, Freeman, & Hopkins, 2007), dogs (Gacsi, Miklosi, Varga, Topalo, & Csanyi, 2004; Kaminski, Brauer, Call, & Tomasello, 2009) and horses (Proops & McComb, 2010) are sensitive to the attentional state of humans. This capacity is not surprising in dogs and horses, as these species were selected for purposes of interacting with humans, and these factors enhanced their skills in reading human communicative cues. Apes and other primates quite naturally use visual cues in their social interactions with conspecifics.

But pigs, domesticated mainly for meat production, are also sensitive to the attention state of humans. In a paradigm requiring active choice between two humans, Nawroth, Ebersbach, and von Borell (2013a, b) found that young pigs are quite skillful at utilizing human head cues to discriminate between different attention states in humans (Nawroth et al., 2013a). They prefer humans who are being attentive to those who are not. Additionally, pigs can use pointing by humans (under certain circumstances) to lead them to a food reward (Nawroth et al., 2013b). There are some differences in these capacities between dogs and pigs. For instance, pigs had more trouble with distant rather than proximal pointing, but it is notable that pigs can be meaningfully engaged in these kinds of perspective-taking tasks and do relatively well under some circumstances. These findings suggests that sensitivity to human visual perspective and indicators in pigs may be extensions of the complexity of their natural social interactions with conspecifics to humans (Nawroth et al., 2013b).

Self-awareness

Self-awareness is a component of cognition that has to do with sense of self in both the physical and mental domains. In the physical domain, ethologists have traditionally tested self-awareness by determining if an animal recognizes himself in a mirror (i.e., mirror self-recognition, MSR); however, some authors suggest that this method might not be a suitable test of self-recognition for all species (Coren, 2004).

In the mental realm, self-awareness takes the form of metacognition, the ability to think about one's own thoughts and feelings. Both involve having an autobiographical self—a sense of “I” - on some level (Marino, 2010). Although the mirror test tends to create the impression that self-awareness is unitary, it is probably more accurately understood as a continuum of subtle and complex abilities (Bekoff & Sherman, 2004).

MSR is usually tested by determining whether an animal uses a mirror to investigate a part of his own body and is usually demonstrated in a controlled setting by placing a mark on a part of the body not visible without a mirror and determining whether a mirror-experienced subject exhibits mark-directed behaviors at the mirror. To date, mirror self-recognition has been convincingly demonstrated in all great apes (Anderson & Gallup, 2011 for a review of this literature), Asian elephants (*Elephas maximus*) (Plotnik, de Waal & Reiss, 2006) bottlenose dolphins (*Tursiops truncatus*) (Reiss & Marino, 2001), and magpies (*Pica pica*) (Prior, Schwarz, & Gunturkun, 2008). In chimpanzees, for instance, MSR is tested by providing mirror-naïve individuals with a mirror to determine if they show indications that they understand the mirror image is not another chimpanzee and begin to use the mirror to investigate their body. The definitive test is to apply a non-tactile mark to their forehead or ear while they are unaware and determine whether they later use the mirror to investigate the new mark on their own body. European magpies show MSR by pecking at the mark with their beaks, elephants by investigating the mark with their trunks, and dolphins by maneuvering in front of the mirror to expose the newly marked part of their body.

On the other hand, some animals, such as monkeys, do not show definitive evidence of MSR but are able to use mirrors as a tool to find hidden items. For instance, Japanese monkeys (*Macaca fuscata fuscata*) found hidden apples that were only visible in a mirror (Itakura, 1987).

When confronted with a mirror, pigs, like many other animals, do not display clear indicators of mirror self-recognition. However, there is evidence that they are able to use mirrors as a tool to find hidden items. Broom, Sena, and Moynihan (2009) exposed young pigs to a mirror and found that seven out of eight mirror-experienced pigs were able to use the mirror to find hidden food (i.e., mirror-mediated spatial localization); the eighth pig looked behind the mirror for the food.

After 5 h spent with a mirror, the pigs were shown a familiar food bowl, visible in the mirror but hidden behind a solid barrier. Seven out of eight pigs found the food bowl in a mean of 23s by going away from the mirror and around the barrier. Naïve pigs shown the same, looked behind the mirror. (Broom, 2010, p. 5)

Moreover, upon encountering a mirror for the first time, some of the pigs in this study made repetitive movements while apparently watching themselves in the mirror.

After initially encountering the mirror the pigs moved back from the mirror surface, oriented nose and eyes towards it apparently looking at it and made movements looking again from different angles. Three pigs showed some weaving movements. (Broom, 2009, p. 1039)

These behaviors are interesting because they are similar to the contingency-checking behaviors displayed by other animals e.g., elephants, dolphins and chimpanzees (Plotnik et al., 2006; Reiss & Marino, 2001), who pass the definitive mark test, suggesting the pigs could have been monitoring their own movements in the mirror.

As compelling as these findings are, another study showed that these results are not as robust as they may seem. That is, in a similar situation with similar research subjects, only two pigs out of eleven in the first study and one pig out of eleven in a second study used the mirror to find food (Geiling et al., 2014). The authors suggest that mirror use may not be robust in pigs and/or that differences in the findings between the two studies might be due to the use of different genetic lines of pigs. Clearly, more research is needed to determine the robustness of mirror-mediated spatial capacities in pigs and to determine if they engage in any behaviors suggesting they are testing the relationship between their own body and the mirror image.

From a comparative perspective, similar unclear results are found in dogs. Howell and Bennett (2011) found that when placed in front of a mirror with their human guardian standing behind them, only two out of 40 dogs were able to understand the actual location of the human. Howell, Toukhsati, Conduit, and Bennett (2013) adapted a similar paradigm to that used by Broom et al. (2009) to dogs and found that more dogs could find the location of hidden food reflected in an angled mirror than those in a control group without a mirror. These responses to mirrors and the ability to use the mirror as a tool to locate hidden items is very similar to the level of understanding of mirrors found in monkeys. Like rhesus macaques (Rajala, Reininger, Lancaster, & Populin, 2010), pigs and dogs can use mirrors to solve problems and may understand something about how they are spatially oriented in relationship to other objects. But the cognitive foundation and robustness of these interesting capacities require much more elucidation.

Pigs have also demonstrated another compelling behavior that may be related to self-awareness. Croney (1999) found that pigs were able to manipulate a modified joystick in order to move an on-screen cursor. In a study designed to assess how well pigs would acquire this kind of task to obtain an on-screen target, Croney (1999) found that all pigs in the study were able to acquire the task, despite dexterity and visual-capacity constraints of the joystick task. Dogs, however, did not do as well on the same tasks (Croney, 2014). Manipulating a joystick to attain a target arguably requires a complex capacity known as self-agency: the ability to recognize actions caused by oneself. Self-agency is a fundamental component of autonomy and purposeful behavior. Pigs may share this capacity with chimpanzees, who are able to distinguish a computer cursor controlled by themselves from motion caused by someone else (Kaneko & Tomonaga, 2011). Again, much more research is needed to determine the exact nature of the pigs' responses to this task and whether it overlaps in any way with self-awareness and self-agency.

Emotion

Emotions are comprised of behavioral, neurophysiological, cognitive and conscious subjective processes (Mendl & Paul, 2004; Paul, Harding, & Mendl, 2005) and can interact with other processes by shaping attention, decision-making, and memory. Emotions, themselves, are influenced by such cognitive abilities as situational awareness and sensitivities to the experience of others. Emotions and cognition, therefore, are often intimately tied together in a complex interplay e.g., recollection of memories can generate strong emotions and, in turn, modulate one's response to various stimuli (Mendl, Burman, Parker, & Paul, 2009; Ohl, Arndt, & van der Staay, 2008; Paul et al., 2005).

It may be that an exact definition of emotion is impossible, based on the complexity and *fuzzy boundaries* of the concept. If so, then description, rather than categorization and labeling, will be more illustrative of animal capacities. Regardless, emotional experience is a felt blend of mood, current responses, cognitive biases, and memory, as becomes clear when looking at the literature of emotion, regardless of species. Murphy, Nordquist, and van der Staay (2014) reviewed behavioral methods used to study pig cognition and emotion and suggested a list of eight criteria by which these studies can be assessed. The authors came to the conclusion that, among other important factors, such as replicability, a major dimension that is often overlooked in studies of pig emotion is ethological validity, which, in many ways, sets the context for other important criteria, such as the ability of the animal to express natural and spontaneous behaviors. For instance, findings in many classical comparative psychology tests of emotion, especially anxiety and fear, are often inconsistent and difficult to interpret and may not be ethologically valid for pigs, as many have been developed for testing laboratory-reared rats.

Emotions tend to influence more than one individual in a group. For instance, they can be shared through a process known as emotional contagion, the arousal of emotion in one individual upon witnessing the same emotion in another individual (Hatfield, Cacioppo, & Rapson, 1993). Emotional contagion is considered, by some investigators, to be a simple form of empathy, the ability to feel the emotional state of another from the other's perspective (de Waal, 2008b). Emotional contagion may be the phylogenetically oldest level of empathy and a building block of more complex forms of empathy; it is difficult to imagine the capacity for empathy without the ability to share or match emotional experience at some level. de Waal (2008b) suggests that emotional contagion forms the basis of sympathetic concern (which involves some perspective-taking) and these lead to empathy-based altruism. Therefore, it is important to follow this line of reasoning and determine, first, if a species is capable of emotional contagion.

Emotional contagion has been demonstrated in many socially complex groups such as dogs (Joly-Mascheroni, Senju, & Shepherd, 2008), wolves (*Canis lupus*) (Romero, Ito, Saito, & Hasegawa, 2014), great apes (Anderson, Myowa-Yamakoshi, & Matsuzawa, 2004; Palagi, Norscia & Demuru, 2014) and only a few other nonhuman species, including pigs. Emotional contagion, like other proximate psychological mechanisms, serve the ultimate purpose of providing a way for social animals, including pigs, to take in social cues about important circumstances and respond accordingly.

Some of the more interesting studies demonstrating emotional contagion in pigs involve responses to other pigs' anticipation of positive or negative events, revealing the importance of social factors in emotion.

In one study, naïve test pigs were exposed to pen mates who had been trained to anticipate upcoming rewarding events (receiving straw and chocolate raisins) or aversive events (social isolation). When the naïve pigs were placed in the company of the trained pigs they adopted the same emotional anticipatory behaviors (e.g., ear and tail postures, increased cortisol release) as the trained pigs with the direct experience. These findings show that not only can pigs connect with the emotions of other pigs, but they can also do so with pigs who are responding emotionally in anticipation of future events (Reimert, Bolhuis, Kemp, & Rodenburg, 2013).

In a recent extension of this study, Reimert, Bolhuis, Kemp, and Rodenburg (2014) housed pigs in groups of six and trained two of the pigs from each group to anticipate something positive (food) or something negative (social isolation and handling). They did this by training the pigs to associate a piece of music with one of the two outcomes - for half of the training pigs Bach was played for the positive event and a military march for the negative event and for the other half the opposite was the case. All the naïve pigs were then played the music that held meaning to the trained pigs. A few of the trained pigs showed that they learned what the music predicted for them, showing either *happy* behaviors (play behavior, wagging their tail and barking) or stress (standing *alert*, putting their ears back, urinating and defecating). The authors wanted to determine if the naïve pigs would react to the behavior of the trained pig when they heard the music predicting a positive or negative outcome. They found that when a naïve pig was near a trained pig that was acting stressed, the naïve pig also became more alert and also put her ears back. This happened to a much greater degree than when naïve pigs were paired with pigs that acted *happy*. The researchers could be sure that the naïve pigs were reacting to the behavior of the other pigs and not just the sound of the music because when they just played music, this had no effect on their behavior at all. This study indicates that pigs are sensitive to the emotions of other pigs even when the other pigs are responding to a learned cue about a positive or negative outcome. This and the study above provide promising evidence for emotional contagion in pigs. Further work could help to better explicate the parameters of this response and help to clarify the degree to which it is related to empathy.

Finally, Murphy et al. (2014) suggest that play could be useful for the study of emotion in pigs. As mentioned above, pigs engage in a range of play behaviors and Murphy et al. (2014) suggest that object play, and most (but not all) forms of social play, are motivated by positive affect and are indirect indicators of emotion. Indeed, naïve pigs in the studies above showed increases in play behavior when anticipating a positive event, even when the event was only happening to the trained pigs. The study of both positive, especially play, behavior and negative responses, in naturalistic settings will likely prove to elucidate more dimensions of emotional responses in pigs.

Personality

Personality is a complex phenomenon with ambiguous boundaries. Even in the human domain there is no consensus on a single definition of personality. However,

one definition that captures the phenomenon for purposes of comparison is: “Those characteristics of individuals that describe and account for temporally stable patterns of affect, cognition, and behavior” (Gosling, 2008, p. 986). However, personality adds a dimension of complexity to assessments of comparative psychology and is critically important for understanding that other animals, as humans, are individuals with their own combination of psychological and behavioral characteristics.

The study of personality in other animals is not only important because it is necessary for understanding and dealing with inter-individual variability in research subjects, but, from a more theoretical point of view, personality in other animals demonstrates a basic psychological continuity across species and with humans. Acknowledgement of personality in other animals becomes a path by which individuality can be recognized and other animals can be viewed not as one-dimensional interchangeable members of a species, but rather as more complex individuals. Personality interacts with cognition and emotion and is, therefore, an important dimension in understanding behavior and intelligence in any animal.

Studies of personality in nonhuman animals have shown that personality traits are ubiquitous in the animal kingdom; a wide range of fish, birds, and mammals show persistent individual differences that can be organized along core personality dimensions, many of which overlap with those found in humans (Gosling, 2008; Gosling & John, 1999). Although some authors prefer to refer to *behavioral syndromes* or *temperament* in other animals, there is little distinction between these phenomena and personalities as observed and documented (Gosling, 2008). The different labels refer, with only slight variation of meaning, to the same category of phenomena.

Given the wide range of species that possess personality traits, an analysis of comparative traits profits most from a discussion of how these traits are structured. Debate exists over the number and types of dimensions needed to characterize personality variation in most species of animals (Gosling, 2008). In humans, there is broad agreement on a five-factor model of personality that includes the dimensions of openness, conscientiousness, extraversion, agreeableness, and neuroticism (McCrae & Costa, 2008). Some studies of personality in other animals indicate fewer or more personality traits than have been identified in humans. However, much of this issue has to do with how much one combines or separates behavioral traits. Personality studies of pigs are important for understanding what traits pigs share with other species, including humans, as well as for better understanding individual variability in cognitive performance (Carere & Locurto, 2011; Sih & Bell, 2008).

Pigs display consistent behavioral and emotional characteristics that have been described variously as personality. e.g., coping styles, response types, temperament, and behavioral tendencies (Brown et al., 2009; D'Eath, 2002; D'Eath & Burn, 2002; Hessing et al., 1993; Ijichi, Collins, & Elwood, 2013; Janczak, Peddersen, & Bakken, 2003; Lawrence, Terlouw, & Illius, 1991; Melotti, Oostindger, Bolhuis, Held, & Mendl, 2011; Ruis et al., 2000 van Erp-van der Kooij et al, 2002). Individual differences tend to be consistent over time. A number of studies have found personality profiles, dimensions, and structure in pigs comparable to other species (Forkman, Furuhaug, & Jensen, 1995; Gosling & John, 1999).

Ruis et al. (2000) found that when put in a group-feeding competition setting, individual aggression emerged as a stable personality feature of female pigs. In another illustrative example, Forkman et al. (1995) examined how piglets respond to different situations (being held down for several seconds, social isolation, contact with an unfamiliar piglet, and the introduction of novel objects) and measured various behaviors, including vocalization, aggression, approaches, and others. Using principal component analysis to determine which factors were closely correlated with others, the authors derived at least three personality factors in pigs: aggression, sociability, and exploration. Forkman, Furuhaug, and Jensen noted that these personality factors are very similar to those identified in many other species. Moreover, Gosling and John (1999) suggested that the factors revealed by Forkman et al. (1995) map onto the human dimensions of agreeableness, extraversion, and openness. All of these studies point to the presence of stable individual behavioral traits that reveal a complex personality in pigs that overlaps with that of other animals, including humans. As with any comparative scientific issue, the study of personality in pigs and how it interacts with their other characteristics is critical for a full understanding of who they are.

Conclusion

In this paper we have identified a number of findings from studies of pig cognition, emotion, and behavior which suggest that pigs possess complex ethological traits similar, but not identical, to dogs and chimpanzees. The main conclusion from this review is that essentially every domain of research with pigs would profit from further explanation as many of the current findings are promising but only suggestive. In general, the study of pig psychology lags behind comparative research with some other species (e.g., dogs, chimpanzees, elephants, cetaceans). Therefore, in order to investigate the leading edges of cognition in pigs, in a comparative framework, we recommend the following for further research areas:

- 1) Discrimination and comprehension of symbolism and the meaning of various combinations and sequences of symbolic cues.
- 2) The ability to not only anticipate an event but to prepare or plan for an event behaviorally.
- 3) The capacity for numerical understanding, particular in a foraging situation.
- 4) Play and exploration and how different forms are combined and are related to social relationships.
- 5) Level of sophistication in social discriminations of conspecifics and humans, including the nature and subtlety of cues used in these circumstances.
- 6) Whether discrimination of individuals is also accompanied by true recognition of conspecifics and/or humans.
- 7) Taking the perspective of a conspecific or human, including understanding eye and head orientation as it relates to attention.
- 8) Understanding and using pointing and other indicating actions by humans.
- 9) The question of contingency-checking behaviors at a mirror and, especially, the robustness and parameters of mirror-mediated behaviors.
- 10) Parameters of emotional contagion and the presence of cognitive empathy
- 11) Personality structure as it compares with other species, including humans.

Acknowledgments

We wish to thank Donald Broom, Bruce Friedrich, Mark Bekoff, Joyce D'Silva and Hope Ferdowsian, and two anonymous reviewers for their guidance and suggestions for improving this manuscript.

References

- Albiach-Sewrrano, A., Brauer, J., Cacchione, T., Zickert, N., & Amici, F. (2012). The effect of domestication and ontogeny in swine cognition (*Sus scrofa scrofa* and *S. s. domestica*). *Applied Animal Behavior Science*, *141*, 25-35.
- Anderson, J. R. & Gallup, Jr., G. G. (2011). Which primates recognize themselves in mirrors? *PLoS Biology*, *9*, e1001024. doi:10.1371/journal.pbio.1001024.
- Anderson, J. R., Myowa-Yamakoshi, M., & Matsuzawa, T. (2004). Contagious yawning in chimpanzees. *Proceedings of the Royal Society, B* *271*(Suppl. 6), S468-S470.
- Arave, C. W. (1996). Assessing sensory capacity of animals using operant technology. *Journal of Animal Science* *74*, 1996-2009.
- Arts, J. W. M., van der Staay, F. J., & Ekkel, E. D. (2009). Working and reference memory of pigs in the spatial holeboard discrimination task. *Behavioural Brain Research*, *205*, 303-306.
- Balda, R. P. & Kamil, A. C. (2002). Spatial and social cognition in corvids: An evolutionary approach. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal* (pp.129-134). Cambridge, MA: MIT Press.
- Bekoff, M. (2015). Playful fun in dogs. *Current Biology*, *25*(1), R4-R7.
- Bekoff, M. (2014). The significance of ethological studies: Playing and peeing. In A. Horowitz (Ed.), *Dog Behavior and Cognition* (pp. 59-78). New York, NY: Springer.
- Bekoff, M. (1974). Social play and play-soliciting by infant canids. *American Zoology*, *14*, 323-340.
- Bekoff, M., & Sherman, P. W. (2004). Reflections on animal selves. *Trends in Ecology and Evolution*, *19*, 176-180.
- Bencke, I. (2015). Play in the Peter Pan ape. *Current Biology*, *25*(1), R24-R27.
- Bensky, M. K., Gosling, S. D., & Sinn, D. L. (2013). The world from a dog's point of view: A review and synthesis of dog cognition research. *Advances in the Study of Behavior*, *45*, 209-406.
- Beran, M., Pate, J., Washburn, D., & Rumbaugh, D. (2004). Sequential responding and planning in chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Behavior Processes*, *30*, 203-212.
- Blackshaw, J. K., Jones, D. N., & Thomas, F. J. (1996). Vocal individuality during suckling in the intensively housed domestic pig. *Applied Animal Behaviour Science*, *50*, 33-41.
- Bird, L. R., Roberts, W. A., Abrams, B., Kit, K. A., & Crupi, C. (2003). Spatial memory for food hidden by rats (*Rattus norvegicus*) on the radial maze: studies of memory for where, what, and when. *Journal of Comparative Psychology* *117*, 176-187.
- Bolhuis, J. E., Oostindjer, M., Hoeks, C. W. F., de Haas, E. N., Bartels, A. C., Ooms, M., & Kemp, B. (2013). Working and reference memory of pigs (*Sus scrofa domesticus*) in a holeboard spatial discrimination task: The influence of environmental enrichment. *Animal Cognition*, *16*, 845-850.

- Bolhuis, J. E., Schouten, W. G. P., Schrama, J. W., & Wiegant, V. M. (2005). Behavioural development of pigs with different coping characteristics in barren and substrate-enriched housing conditions. *Applied Animal Behavior Science*, *93*, 213-228.
- Bräuer, J., Bös, M., Call, J., & Tomasello, M. (2013). Domestic dogs (*Canis familiaris*) coordinate their actions in a problem-solving task. *Animal Cognition*, *16*, 273-285.
- Bräuer, J., Call, J., & Tomasello, M. (2007). Chimpanzees really know what others can see in a competitive situation. *Animal Cognition*, *10*, 439-448.
- Broom, D. (2010). Cognitive ability and awareness in domestic animals and decisions about obligations to animals. *Applied Animal Behavior Science*, *126*, 1-11.
- Broom, D., Sena, H., & Moynihan, K. L. (2009). Pigs learn what a mirror image represents and use it to obtain information. *Animal Behaviour*, *78*, 1037-1041.
- Brown, C. (2015). Fish intelligence, sentience, and ethics. *Animal Cognition*, *18*, 1-17.
- Brown, J. A., Dewey, C., Delange, C. F. M., Mandell, I. B., Purslow, P. P., Widowski, T. M. (2009). Reliability of temperament tests on finishing pigs in group-housing and comparison to social tests. *Applied Animal Behaviour Science*, *118*, 28-35.
- Bulloch, M. J., Boysen, S. T., & Furlong, E. E. (2008). Visual attention and its relation to knowledge states in chimpanzees, *Pan troglodytes*. *Animal Behaviour*, *76*, 1147-1155.
- Burghardt, G. (2015). Play in fishes, frogs and reptiles. *Current Biology*, *25*(1), R9-R10.
- Burish, M. J., Kueh, H. Y., & Wang, S. H. (2004). Brain architecture and social complexity in modern and ancient birds. *Brain, Behavior and Evolution*, *63*, 107-124.
- Byrne, R. W. & Whiten, A. (1988) *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford , England: Oxford University Press.
- Byrne, R. W. & Whiten, A. (1992). Cognitive evolution in primates: evidence from tactical deception. *Man*, *27*, 609-627.
- Carere, C., & Locurto, C. (2011). Interaction between animal personality and animal cognition. *Current Zoology*, *57*, 491-498.
- Cerbulis, I. G. (1994). Cognitive abilities of the domestic pig (*Sus scrofa*), Thesis in Department of Psychology, Ohio State University, 1-108.
- Clayton, N. S., Dally, J. M., & Emery, N. J. (2007). Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 507-522.
- Coren, S. (2004). *How dogs think: Understanding the canine mind*. New York, NY: Free Press.
- Crone, C. C. (1999). *Cognitive abilities of domestic pigs*. Thesis in Animal Science, The Pennsylvania State University, College of Agricultural Sciences, 1-105.
- Crone, C. C., Adams, K. M., Washington, C. G., & Stricklin, W. R. (2003). A note on visual, olfactory and spatial cue use in foraging behaviour of pigs: indirectly assessing cognitive abilities. *Applied Animal Behaviour Science*, *83*, 303-308.
- Cutini, S., & Bonato, M. (2012). Subitizing and visual short-term memory in human and nonhuman species: A common shared system? *Frontiers in Psychology*, *3*, 469. doi:10.3389/fpsyg.2012.00469
- D'Eath, R. B. (2002). Individual aggressiveness measured in a resident intruder test predicts the persistence of aggressive behaviour and weight gain of young pigs after mixing. *Applied Animal Behaviour Science*, *77*, 267-283.
- D'Eath, R. B. & Burn, C. C. (2002). Individual differences in behaviour: a test of 'coping style' does not predict resident-intruder aggressiveness in pigs. *Behaviour*, *139*, 1175-1194.

- De Souza, A. S., Jansen, J., Tempelman, R. J., Mendl, M., & Zanella, A. J. (2006). A novel method for testing social recognition in young pigs and the modulating effects of relocation. *Applied Animal Behavior Science*, *99*, 77-87.
- de Waal, F. B. M. (2005). Intentional deception in primates. *Evolutionary Anthropology*, *1*, 86-92.
- de Waal, F. B. M. (2008a). The thief in the mirror. *PLoS Biology* *6*(8), e201.
- de Waal, F. B. M. (2008b). Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology*, *59*, 279-300.
- Donaldson, T. M., Newberry, R. C., Spinka, M., & Cloutier, S. (2002). Effects of early play experience on play behavior of piglets after weaning. *Applied Animal Behaviour Science*, *79*, 221-231.
- Douglas, C., Bateson, M., Walsh, C., Bedue, A. & Edwards, S.A. (2012). Environmental enrichments induces optimistic cognitive biases in pigs. *Applied Animal Behaviour Science*, *139*, 65-73.
- Dudink, S., Simonse, H., Marks, I., de Jonge, F. H., & Spruijt, B. M. (2006). Announcing the arrival of enrichment increases play behavior and reduces weaning-stress-induced behaviours of piglets directly after weaning. *Applied Animal Behaviour Science*, *101*, 86-101.
- Dunbar, R. I. (1998). The social brain hypothesis. *Brain*, *9*(10), 178-190.
- Emery, N. J., & Clayton, N. S. (2015). Do birds have the capacity for fun? *Current Biology* *25*(1), R16-R20.
- Fagot, J. (2000). *Picture Perception in Animals*. East Sussex, England: Psychology Press Ltd.
- Ferguson, S. A., Gopee, N. V., Paule, M. G., & Howard, P. C. (2009). Female mini-pig performance of temporal response differentiation, incremental repeated acquisition, and progressive ration operant tasks. *Behavioural Processes*, *80*, 28-34.
- Forkman, B., Furuhaug, I. L., & Jensen, P. (1995). Personality, coping patterns, and aggression in piglets. *Applied Animal Behaviour Science*, *45*, 31-42.
- Gácsi, M., Miklosi, A., Varga, O., Topal, J., & Csanyi, V. (2004). Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Animal Cognition*, *7*, 144-153.
- Gallistel, C. R. (1994). Space and time. In N. J. Mackintosh (Ed.), *Animal learning and cognition* (pp. 221-253). San Diego, CA: Academic Press.
- Gallup, Jr. G. G. (1998). Self-awareness and the evolution of social intelligence. *Behavioural Processes*, *42*, 239-247.
- Garber, P. A. & Dolins, F. L. (2014). Primate spatial strategies and cognition: Introduction to this special issue. *American Journal of Primatology*, *76*, 393-398.
- Gielsing, E. T., Arts, J., Nordquist, R. E., & van der Staay, F. J. (2012). Measuring spatial discrimination performance in (mini) pigs using the cognitive holeboard task. *Ellegaard Newsletter*, *38*, 4-7.
- Gielsing, E. T., Mijdam, E., van der Staay, F. J., & Nordquist, R. E. (2014). Lack of mirror use by pigs to locate food. *Applied Animal Behavior Science*, *154*, 22-29.
- Gielsing, E. T., Nordquist, R. E., & van der Staay, F. J. (2011). Assessing learning and memory in pigs. *Animal Cognition*, *14*, 151-173.
- Gielsing, E. T., Wehkamp, W., Willigenburg, R., Nordquist, R. E., Ganderup, N. C., & van der Staay, F. J. (2013). Performance of conventional pigs and Gottingen miniature pigs in a spatial holeboard task: Effects of the putative muscarinic cognition impairer Biperidon. *Behavioural and Brain Functions*, *9*, 4- 10.
- Gifford, A., Sylvie Cloutier, K., & Newberry, R. C. (2007). Objects as enrichment: Effects

of object exposure time and delay interval on object recognition memory of the domestic pig. *Applied Animal Behaviour Science*, 107, 206-217.

- Giuffra, E., Kijas, J. M. H., Amarger, V., Carlborg, O, Jeon, J. T., & Andersson, L. (2000). The origin of the domestic pig: Independent domestication and subsequent introgression. *Genetics*, 154, 1785-1791.
- Gosling, S., & John, O. P. (1999). Personality dimensions in nonhuman animals. *Current Directions in Psychological Science*, 8, 69-75.
- Gosling, S. (2008). Personality in nonhuman animals. *Social and Personality Psychology Compass* 2, 985 - 1001.
- Graves, H. B. (1984). Behavior and ecology of wild and feral swine (*Sus scrofa*). *Journal of Animal Science*, 58, 482-492.
- Hatfield, E., Cacioppo, J. T. & Rapson, R. L. (1993). Emotional contagion. *Current Directions in Psychological Science* 2, 96-9.
- Heffner, H. E. & Heffner, R. S. (1992). Auditory perception. In C.J.C. Phillips & D. Piggins (Eds.), *Farm Animals and the Environment* (pp. 159-184). Wallingford, UK: CABI.
- Held, S., Baumgartner, J., Kilbride, A., Byrne, R.W., & Mendl, M. (2005). Foraging behaviour in domestic pigs (*Sus scrofa*): Remembering and prioritizing food sites of different value. *Animal Cognition*, 8, 114-121.
- Held, S., Byrne, R. W., Jones, S., Murphy, E., Friel, M., & Mendl, M. T. (2010). Domestic pigs, *Sus scrofa*, adjust their foraging behavior to whom they are foraging with. *Animal Behaviour*, 79, 857-862.
- Held, S., Cooper, J. J., & Mendl, M. T. (2009). Advances in the study of cognition, behavioural priorities and emotions. In J. N. Marchant-Forde (Ed.), *The welfare of pigs* (pp. 47-94), Springer Science Business Media B.V.
- Held, S., Mendl, M., Devereux, C., & Byrne, R. W. (2000). Social tactics of pigs in a competitive foraging task: the 'informed forager' paradigm. *Animal Behaviour*, 59, 579-576.
- Held, S., Mendl, M., Devereaux, C., & Byrne, R. W. (2002). Foraging pigs alter their behavior in response to exploitation. *Animal Behaviour*, 64, 157-166.
- Held, S., Mendl, M., Laughlin, K., & Byrne, R. W. (2002). Cognition studies with pigs: Livestock cognition and its implication for production. *Journal of Animal Science*, 80 (E Suppl. 1), E10-E17.
- Hemsworth, P. H., Coleman, G. J., Cox, M. L., & Barnett, J. L. (1994). Stimulus generalization: The inability of pigs to discriminate between humans on the basis of their previous handling experience. *Applied Animal Behavior Science*, 40, 129-142.
- Hemsworth, P. H., Verge, J, & Coleman, G. J. (1996). Conditioned approach avoidance responses to humans: the ability of pigs to associate feeding and aversive social experiences in the presence of humans with humans. *Applied Animal Behaviour Science*, 50, 71-82.
- Herman, L. M. (1980). Cognitive characteristics of dolphins. In L. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 363-429). New York, NY: John Wiley & Sons.
- Herman, L.M. (1987). Receptive competencies of language-trained animals. In J. S. Rosenblatt, C. Beer, M. Busnel, and J. Slater (Eds.), *Advances in the Study of Behavior*, 17, 1-60.
- Herman, L., Hovanick, J. Gory, J., & Bradshaw, G. (1989). Generalization of visual matching by a bottlenose dolphin (*Tursiops truncatus*): Evidence for invariance of cognitive performance with visual and auditory materials. *Journal of Experimental Psychology: Animal Behavior Processes*, 15, 124-136.

- Hessing, M. J. C., Hagelso, A. M., van Beek, J. A. M., Wiepkema, P. R. Schouten, W. G. P., & Krukow, R. (1993). Individual behavioural characteristics in pigs. *Applied Animal Behaviour Science*, *37*, 285-295.
- Hostetter, A. B., Russell, J. L., Freeman, H., & Hopkins, W. D. (2007). Now you see me, now you don't: evidence that chimpanzees understand the role of eyes in attention. *Animal Cognition*, *10*, 55-62.
- Horback, K. (2014). Nosing around: Play in pigs. *Animal Behavior and Cognition*, *1*(2), 186-196.
- Howell, T. J., & Bennett, P. C. (2011). Can dogs (*Canis familiaris*) use a mirror to solve a problem? *Journal of Veterinary Behavior: Clinical Applications and Research*, *6*, 306-312.
- Howell, T. J., Toukhsati, S., Conduit, R., & Bennett, P. (2013). Do dogs use a mirror to find hidden food? *Journal of Veterinary Behavior*, *8*, 425-430.
- Huber, L., Apfalter, W., Steurer, M., & Prossinger, H. (2005). A new learning paradigm elicits fast visual discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *31*, 237-246.
- Humphrey, N. K. (1976). The social function of intellect. *Growing Points in Ethology*, 303-317.
- Illmann, G., Schrader, L., Pinka, M., & Ustr, P. (2002). Acoustical mother-offspring recognition in pigs (*Sus scrofa domesticus*). *Behaviour*, *139*, 487-505.
- Ijichi, C. L., Collins, L. M., & Elwood, R.W. (2013). Evidence for the role of personality in stereotypy predisposition. *Animal Behaviour*, *85*, 1145-1151. Need first initial.
- Imfeld-Mueller, S., Van Wezemaela, L., Stauffachera, M., Gygax, L., & Hillmann, E. (2011). Do pigs distinguish between situations of different emotional valences during anticipation? *Applied Animal Behavior Science*, *131*, 86-93.
- Itakura, S. (1987). Mirror-guided behavior in Japanese macaques (*Macaca fuscata fuscata*). *Primates*, *28*, 149-161.
- Janczak, A. M., Pedersen, L. J., & Bakken, M. (2003). Aggression, fearfulness and coping styles in female pigs. *Applied Animal Behaviour Science*, *81*, 13-28.
- Janik, V. (2015). Play in dolphins. *Current Biology*, *25*(1), R7-R8.
- Jensen, P. (1986). Observations on the maternal behavior of free-ranging domestic pigs. *Applied Animal Behavior Science*, *16*, 131-142.
- Joly-Mascheroni, R. M., Senju, A., & Shepherd, A. (2008). Dogs catch human yawns. *Biology Letters*, *4*, 446-448.
- Kaminski, J., Bräuer, J., Call, J., & Tomasello, M. (2009). Domestic dogs are sensitive to a human's perspective. *Behaviour*, *146*, 979-998.
- Kaneko, T., & Tomonaga, M. (2011). The perception of self-agency in chimpanzees (*Pan troglodytes*). *Proceedings of the Royal Society B.*, *278*, 3694-3702.
- Kaulfuss, P., & Mills, D.S. (2008). Neophilia in domestic dogs (*Canis familiaris*) and its implication for studies of dog cognition. *Animal Cognition*, *11*, 553-556.
- Kehoe, E. J. (2008). Discrimination and generalization. In R. Menzel (Vol. Ed.), *Learning Theory and Behavior*. Vol. 1. of J. Byrne (Ed.), *Learning and memory: A comprehensive reference*, (pp. 123-150). Oxford, United Kingdom: Elsevier.
- Koba, Y., & Tanida, H. (2001). How do miniature pigs discriminate between people? Discrimination between people wearing coveralls of the same colour. *Applied Animal Behaviour Science*, *73*, 45-58.
- Krachun, C., & Call, J. (2009). Chimpanzees (*Pan troglodytes*) know what can be seen from where. *Animal Cognition*, *12*, 317-331.
- Kristensen, H. H., Jones, R. B., Schofield, C. P., White, R. P., & Wathes, C. M. (2001). The

use of olfactory and other cues for social recognition by juvenile pigs. *Applied Animal Behaviour Science*, 72, 321-333.

- Kruska, D. (1988). Mammalian domestication and its effect on brain structure and behavior. In H.J. Jerison & Jerison, I. (Eds.) *Intelligence and evolutionary biology* (pp. 211-250). Berlin, Germany: Springer-Verlag.
- Larson, G., Dobney, K., Albarella, U., Fang, M., Matisoo-Smith, E., Robins, J., & Cooper, A. (2005). Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science*, 307, 1618-1621.
- Laughlin, K., & Mendl, M. (2000). Pigs shift too: foraging strategies and spatial memory in the domestic pig. *Animal Behavior*, 60, 403-410.
- Lawrence, A. B., Terlouw, E. M. C., & Illius, A. W. (1991). Individual differences in behavioural responses of pigs exposed to non-social and social challenges. *Applied Animal Behaviour Science*, 30, 73-86.
- Lomas, C. A., Piggins, D., & Phillips, C. J. C. (1988). Visual awareness. *Applied Animal Behaviour Science*, 57, 247-257.
- Manteuffel, G., Puppe, B., & Schon, P. C. (2004). Vocalization of farm animals as a measure of welfare. *Applied Animal Behavior Science*, 88, 163-182.
- Marino, L. (2010). Sentience. *Encyclopedia of animal behavior*, Vol. 3, M. Breed & J. Moore (Eds.) (pp. 132-138). Oxford: UK: Academic Press.
- Martin, J. E., Ison, S. H., & Baxter, E. M. (2015). The influence of neonatal environment on piglet play behaviour and post-weaning social and cognitive development. *Applied Animal Behaviour Science*, 163, 69-79.
- Martin-Ordas, G., Berntsen, D., & Call, J. (2013). Memory for distant past events in chimpanzees and orangutans. *Current Biology*, 23, 1-4.
- Martin-Ordas, G., Haun, D., Colmenares, F., & Call, J. (2010). Keeping track of time: Evidence for episodic-like memory in great apes. *Animal Cognition*, 13, 331-340.
- Matsuzawa, T. (2001). *Primate Origins of Human Cognition and Behavior*. Tokyo, Japan: Springer
- McComb, K., Moss, C., Sayialel, S., & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. *Animal Behavior*, 59, 1103-1109.
- McCrae, R. R., & Costa, P. T. (2008). The five-factor theory of personality. In O. P. John, R. W. Robins, & L. A. Pervin (Eds.), *Handbook of personality* (pp. 159-181). New York, NY: Guilford Press.
- McGlone, J. J. (1990). Olfactory signals that modulate pig aggressive and submissive behavior. In R. Zayan & R. Dantzer (Eds.), *Social stress in domestic animals*, 86-109. Dordrecht: Kluwer Academic Press.
- McLeman, N. A., Mendl, M., Jones, R. B., White, R., & Wathes, C. M. (2005). Discrimination of conspecifics by juvenile domestic pigs, *Sus scrofa*. *Animal Behavior*, 70, 451-461.
- Melotti, L., Oostindjer, M., Bolhuis, J. E., Held, S., & Mendl, M. (2011). Coping personality type and environmental enrichment affect aggression at weaning in pigs. *Applied Animal Behaviour Science*, 133, 144-153.
- Mendl, M. (2002). British Association for the Advancement of Science Conference.
- Mendl, M., Burman, O., Parker, R. M. A., & Paul, E. S. (2009). Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. *Applied Animal Behavior Science*, 118, 161-181
- Mendl, M., Laughlin, K., & Hitchcock, D. (1997). Pigs in space: spatial memory and its susceptibility to interference. *Animal Behaviour*, 54, 1491-1508.
- Mendl, M., & Paul, E. S. (2004). Consciousness, emotion and animal welfare: insights from cognitive science. *Animal Welfare*, 13, S17-25.

- Mendl, M., Randle, K., & Pope, S. (2002). Young female pigs can discriminate individual differences in odours from conspecific urine. *Animal Behaviour*, *64*, 97-101.
- Molnar, C., Pongracz, P., Farago, T., Doka, A., & Miklosi, A. (2009). Dogs discriminate between barks: The effects of context and identity of the caller. *Behavioural Processes*, *82*, 198-201
- Mulcahy, N. J. & Call, J. (2006). Apes save tools for future use. *Science*, *312*, 1038-1040.
- Murphy, E., Nordquist, R., & van der Staay, F. J. (2014). A review of behavioural methods to study emotion and mood in pigs, *Sus scrofa*. *Applied Animal Behaviour Science*, *159*, 9-28.
- Nagasawa, M., Murai, K., Mogi, K., & Kikusui, K. (2011). Dogs can discriminate human smiling faces from blank expressions. *Animal Cognition*, *14*, 525-533.
- Nawroth, C., Ebersbach, M., von Borell, E. (2013a). Are juvenile domestic pigs (*Sus scrofa domesticus*) sensitive to the attentive states of humans? - The impact of impulsivity on choice behavior. *Behavioral Processes*, *96*, 53-58.
- Nawroth, C., Ebersbach, M., & von Borell, E. (2013b). Juvenile domestic pigs (*Sus scrofa domesticus*) use human-given cues in an object choice task. *Animal Cognition*, *17*, 701-713.
- Nawroth, C., & von Borell, E. (2014). Do young domestic pigs (*Sus scrofa domestica*) rely on object-specific cues in a simultaneous discrimination task?. *PeerJ2*: e281v1.
- Newberry, R. C., Wood-Gush, D. G. M., & Hall, J. W. (1988). Playful behavior in piglets. *Behavioural Processes*, *17*, 205-216.
- Ohl, F., Arndt, S., & van der Staay, F. J. (2008). Pathological anxiety in animals. *Veterinary Journal*, *175*, 18-26.
- Olsen, A. W., Simonsen, H. B., & Dybkjaer, L. (2002). Effect of access to roughage and shelter on selected behavioural indicators of welfare in pigs housed in a complex environment. *Animal Welfare*, *11*, 75-87.
- Osvath, M., & Osvath, H. (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Animal Cognition*, *11*, 661-674.
- Palagi, E., Norscia, I., & Demuru, E. (2014) Yawn contagion in humans and bonobos: emotional affinity matters more than species. *PeerJ2*:e519 <http://dx.doi.org/10.7717/peerj.519>
- Paul, E. S., Harding E. J., & Mendl, M. (2005). Measuring emotional processes in animals: The utility of a cognitive approach. *Neuroscience and Bio-Behavioral Reviews*, *29*, 469-491.
- Pedersen, L. J., Herskin, M. S., Forkman, B., Halekoh, U., Kristensen, K. M., & Jensen, M. B. (2014). How much is enough? The amount of straw necessary to satisfy pigs' need to perform exploratory behavior. *Applied Animal Behavior Science*, *160*, 46-55.
- Plotnik, J. M., de Waal, F. B. M., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences*, *103*, 17052-17057.
- Prior, H., Schwarz, A., & Gunturkun, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biology* *6*: 1642-1650, doi:10.1371/journal.pbio.0060202.
- Proops, L., & McComb, K. (2010). Attributing attention: The use of human-given cues by domestic horses (*Equus caballus*). *Animal Cognition*, *13*, 197-205.
- Raby, C. R., Alexis, D. M., Dickinson, A., Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature*, *445*, 919-921.

- Rajala, A. Z., Reininger, K. R., Lancaster, K. M., & Populin, L. C. (2010). Rhesus monkeys (*Macaca mulatta*) do recognize themselves in the mirror: Implications for the evolution of self-recognition. *PLoS ONE* 5, e12865.
- Range, F., Aust, U., Steurer, M., & Huber, L. (2008). Visual categorization of domestic stimuli by domestic dogs. *Animal Cognition*, 11, 338-347.
- Reimert, I., Bolhuis, J. E., Kemp, B., & Rodenburg, T. B. (2014). Emotions on the loose: emotional contagion and the role of oxytocin in pigs. *Animal Cognition*, 18, 517-532.
- Reimert, I., Bolhuis, J. E., Kemp, B., & Rodenburg, T. (2013). Indicators of positive and negative emotions and emotional contagion in pigs. *Physiology and Behavior*, 109, 42-50.
- Reiss, D., & Marino, L. (2001). Self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences USA* 98, 5937-5942.
- Romero, T., Ito, M., Saito, A., & Hasegawa, T. (2014). Social modulation of contagious yawning in wolves. *PLoS One*, e105963. doi: 10.1371/journal.pone.0105963
- Ruis, M. A. W., Brake, J. H., VandeBurgwal, J. A., deJong, I. C., Blokhuis, H. J., & Koolhaas, J. M. (2000). Personalities in female domesticated pigs: Behavioural and physiological indications. *Applied Animal Behavior Science*, 66, 31-47.
- Schoon, P., Puppe, B., Gromyko, T., & Manteuffel, G. (1999). Common features and individual differences in nurse grunting of domestic pigs (*Sus scrofa*): a multi-parametric analysis. *Behaviour*, 136, 49-66.
- Schusterman, R.J. (1993). Artificial language comprehension in dolphins and sea lions: The essential cognitive skills. *The Psychological Record*, 38, 311-348.
- Shettleworth, S. J. (2002). Spatial behavior, food storing, and the modular mind. In *The Cognitive Animal*. In M. Bekoff, C. Allen, & G.M. Burghardt (Eds.), *The cognitive animal* (pp.123 - 128). Cambridge, MA: MIT Press.
- Siegford, J. M., Rucker, G., & Zanella, A. J. (2008). Effects of pre-weaning exposure to a maze on stress responses in pigs at weaning and on subsequent performance in spatial and fear-related tests. *Applied Animal Behavior Science*, 110, 189-202.
- Signoret, J. P., Baldwin, B. A., Fraser, S., & Hafez, E. S. E. (1975). In E. S. E. Hafez (Ed.), *The behaviour of domestic animals* (pp. 295-329). London, UK: Bailliere, Tindall and Cox.
- Sih, A., & Bell, A. M. (2008). Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior*, 38, 227-281.
- Spinka, M., Duncan, I. J. H., & Widowski, T. M. (1998). Do domestic pigs prefer short-term to medium-term confinement? *Applied Animal Behaviour Science*, 58, 221-232.
- Stolba, A., & Wood-Gush, D. G. M. (1989). The behavior of pigs in a semi-natural environment. *Animal Production* 48, 419-425.
- Studnitz, M., Jensen, M. B., & Pedersen, L. J. (2007). Why do pigs root and in what will they root? A review on the exploratory behavior of pigs in relation to environmental enrichment. *Applied Animal Behavior Science*, 107, 183-197.
- Tanida, H., & Nagano, Y. (1998). The ability of miniature pigs to discriminate between a stranger and their familiar handler. *Applied Animal Behaviour Science* 56, 149-159
- Tanida, H., Senda, K., Suzuki, S., Tanaka, T., Yoshimoto, T. (1991). Color discrimination in weaning pigs. *Animal Science and Technology (Jpn.)*, 62, 1029-1034.

- Telkanranta, H., Bracke, M. B. M., & Valros, A. (2014). Fresh wood reduced tail and ear biting and increases exploratory behavior in finishing pigs. *Applied Animal Behavior Science*, *161*, 51-59.
- Towner, S. (2010). Concept of mind in non-human primates. *Bioscience Horizons*, *3*, 96-104.
- Van der Staay, F. J., Gieling, E. T., Pinzon, N. E., Nordquist, R. E., & Ohl, F. (2012). The appetitively motivated "cognitive" holeboard: A family of complex spatial discrimination tasks for assessing learning and memory. *Neuroscience and Biobehavioral Reviews*, *36*, 379-403.
- Van Erp-van der Kooij, E., Kuijpers, A. H., Schrama, J. W., van Eerdenburg, F. J. C. M., Schouten, W. G. P., & Tielen, M. J. M. (2002). Can we predict behaviour in pigs? Searching for consistency in behaviour over time and across situations. *Applied Animal Behaviour Science*, *75*, 293-305.
- Weary, D. M., Lawson, G. L., & Thompson, B. K. (1996). Sows show stronger responses to isolation calls of piglets associated with greater levels of piglet need. *Animal Behaviour*, *52*, 1247-1253.
- Weary, D. M., Ross, S., & Fraser, D. (1997). Vocalisations by isolated piglets: A reliable indicator of piglet need directed towards the sow. *Applied Animal Behaviour Science*, *53*, 249-257.
- Whitehead, H., & Rendell, L. (2015). *The cultural lives of whales and dolphins*. Chicago, IL: University of Chicago Press.
- Whiten, A., & Byrne, R.W. (1997). Machiavellian intelligence. II. Cambridge, UK: Cambridge University Press.
- Whiten, A., & Byrne, R.W. (1988). Tactical deception in primates. *Behavioural and Brain Sciences*, *11*, 233-273.
- Wood-Gush, D. G. M., & Vestergaard, K. (1993). Inquisitive exploration in pigs. *Animal Behaviour*, *45*, 185-187.
- Wood-Gush, D. G. M., & Vestergaard, K. (1991). The seeking of novelty and its relation to play. *Animal Behaviour*, *42*, 599-606.
- Zentall, T., & Wasserman, E. (2006). *Comparative cognition: Experimental explorations of animal intelligence*. New York, NY: Oxford University Press.
- Zylinski, S. (2015). Fun and play in invertebrates. *Current Biology*, *25*(1), R10-R12.

Financial conflict of interest: This paper was supported by a grant from The Someone Project, an endeavor aimed at raising the public's understanding of farm animal cognition and behavior.

Conflict of interest: No stated conflicts.

Submitted: September 11th, 2014
Revision submitted: May 9th, 2015
Accepted: May 13th, 2015