Social and nonsocial category discriminations in a chimpanzee (*Pan troglodytes*) and American black bears (*Ursus americanus*)

Jennifer Vonk · Zoe Johnson-Ulrich

Published online: 6 June 2014 © Psychonomic Society, Inc. 2014

Abstract One captive adult chimpanzee and 3 adult American black bears were presented with a series of natural category discrimination tasks on a touch-screen computer. This is the first explicit comparison of bear and primate abilities using identical tasks, and the first test of a social concept in a carnivore. The discriminations involved a social relationship category (mother/offspring) and a nonsocial category involving food items. The social category discrimination could be made using knowledge of the overarching mother/offspring concept, whereas the nonsocial category discriminations could be made only by using perceptual rules, such as "choose images that show larger and smaller items of the same type." The bears failed to show above-chance transfer on either the social or nonsocial discriminations, indicating that they did not use either the perceptual rule or knowledge of the overarching concept of mother/offspring to guide their choices in these tasks. However, at least 1 bear remembered previously reinforced stimuli when these stimuli were recombined, later. The chimpanzee showed transfer on a control task and did not consistently apply a perceptual rule to solve the nonsocial task, so it is possible that he eventually acquired the social concept. Further comparisons between species on identical tasks assessing social knowledge will help illuminate the selective pressures responsible for a range of social cognitive skills.

Keywords Chimpanzee · Bears · Social relationship · Category discrimination

Electronic supplementary material The online version of this article (doi:10.3758/s13420-014-0141-2) contains supplementary material, which is available to authorized users.

J. Vonk (⊠) • Z. Johnson-Ulrich Department of Psychology, Oakland University, 2200 North Squirrel Road, Rochester, MI 48309, USA e-mail: vonk@oakland.edu The ability to process social information and form concepts regarding the nature of relationships among others is a critical aspect of social cognition that has become a renewed area of comparative research in recent years. Field research with nonhuman primates indicates that primates recognize the relationships of others, both in terms of dominance and kinship (Seyfarth, Cheney, & Bergman, 2005; Silk, 1999). These field studies have provided rich information regarding the ability of primates to assess third-party relations within their social group (Silk, 1999; Silk, Alberts, & Altmann, 2004). However, knowledge gained and used in a social setting, which is replete with various behavioral cues and past associations between individuals and behaviors, is not necessarily indicative of an underlying concept for various social relationships, such as "family," "parent," "sibling," "mate," that might be generalized outside of one's social group. Cheney and Seyfarth's extensive field studies have led to the conclusion that knowledge of social relationships in baboons emerges from perception of specific traits such as identity, rank, and kinship (Seyfarth et al., 2005). We wanted to determine whether captive subjects of a social species (chimpanzees), and a relatively less social species (black bears) would form concepts of a social relationship (mother/offspring) when this relationship could be abstracted only from two-dimensional stimuli of unfamiliar animals of various species, allowing us to disentangle previous associations from performance. Answering such a question would be informative with regard to the type of social experience and behavioral cues necessary to abstract such concepts.

A small number of laboratory studies have revealed recognition of specific kin relations (Dasser, 1988; Parr & de Waal, 1999), but in these studies, animals may have associated physical features between related pairs and chosen pairs that looked more similar, rather than assessing whether there was something qualitatively special about the relationship between the individuals. Animals as diverse as pigeons (Wilkinson,

Specht, & Huber, 2010), monkeys (Pokorny & de Waal, 2009), and apes (Vonk & Hamilton, 2014) have been shown to have a concept for "familiar" group-mates, but only a single study has addressed the question of whether nonhumans have a general concept of, for example, "mother/offspring" (Vonk, 2002). In this study, orangutans and a gorilla correctly matched stimuli according to four possible relationships: "mother/offspring," "mated pairs," "siblings," and "social groups." Some subjects also showed successful transfer on a two-choice procedure discriminating mother/offspring images from those of other possible relationships. This study focused on the abstraction of general "relationship type" concepts in order to avoid the difficulty of disentangling associations or shared features among particular related pairs from more general concepts. In addition, the study aimed to show the extent to which the relationship concepts could be generalized beyond the individuals' own species. Although this data suggested that apes could acquire such relationships, alternative explanations for the apes' performance could not be ruled out.

Despite the fact that chimpanzees are by far the most studied of the apes, and one of the most highly tested of the nonhuman primates, relatively little experimental work has addressed abstract concept formation in this species. With the exception of Tanaka's (2001) study, previous research has not explicitly examined the extent to which chimpanzees focus on perceptual features rather than overarching concepts in performing concept discriminations. Social concepts, such as differing relationships between individuals, cannot be acquired strictly through the basis of perceptual features, given that the nature of the relationship is not always clear from physical characteristics. That is, no set of visual features alone should be shared among all exemplars of a group sharing the same relationship. However, varying combinations of features such as individuals of different sizes and ages, shared physical features, sex, and behavioral cues, such as affiliative interactions and relaxed postures, can contribute to the ability to abstract the relationship from images. That is, all abstractions must be abstracted from a lower level, such as analysis of perceptual features, but the abstraction differs conceptually from the features that support the potential for such an abstraction.

Category discrimination paradigms are ideal for studying the presence or absence of concepts of a particular nature, as well as concepts for which discriminations cannot be made by identifying key perceptual features that are shared between exemplars (Fize, Cauchoix, & Fabre-Thorpe, 2011; Roberts & Mazmanian, 1988; Vonk & MacDonald, 2002; 2004; Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). However, the use of pictorial stimuli makes it challenging to present images that depict such concepts without additionally providing perceptual-feature cues that could also be used to discriminate the stimuli in the absence of an abstracted rule or concept (cf. Vonk & Povinelli, 2012). Stimuli depicting a mother/offspring relationship must depict at least two members of the same species, with one individual being older, and probably larger than the other(s). Here, we set up a control task using one of the same perceptual cues (a larger and smaller item of the same type) but using images of foods, so that these images represented a similar perceptual cue but not the same social relationship, in order to identify which abstraction might underlie performance.

Based on the Social Intelligence Hypothesis, it is expected that social-living animals should be most likely to form concepts for social relationships (Humphrey, 1976; Jolly, 1966). However, researchers have not focused on falsifying the hypothesis that group living is critical to such social cognitive skills by testing species that do not live in social groups for the presence of similar concepts. Touch-screen technology is being implemented with a wider range of species in recent years, allowing researchers to carefully control the presentation of stimuli and available cues and to test for concepts extrapolated from pictorial stimuli in many previously unstudied taxonomic groups, such as carnivores. Based on this wealth of data, researchers can be confident that many species view the images as representative of real-life objects. Using such technology, Range, Aust, Steurer, and Huber (2008) demonstrated that dogs were able to form concrete-level concepts, such as "dogs" rather than "landscapes." Vonk, Jett, and Mosteller (2012) recently tested black bears on a series of natural category discrimination tasks that varied in level of abstraction and found that black bears could acquire concepts at each level of abstraction. Bears were of particular interest because they are large-brained carnivores that display varying degrees of foraging complexity (depending on the species) but are relatively much less social, compared with primates and other widely tested carnivores, such as canids and pinnipeds (Gittleman, 1986). Thus, they are unique in possessing one important attribute that is commonly associated with social intelligence (large brain size) in the absence of another (social lifestyle). In addition, a longer lifespan and weaning period also predict cognitive complexity (MacLean et al., 2012), as well as the relevance of the mother/offspring concept. In the previous studies, the bears showed transfer comparable to that shown by the great apes tested in the same tasks (Vonk, Jett, Mosteller, & Galvan, 2013; Vonk & MacDonald, 2002; 2004), suggesting that these tasks are appropriate given potential physiological differences, such as differences in visual ability between bears and primates. In addition, previous research has indicated that bears' vision is comparable with that of primates, especially with regard to form and color vision (Bacon & Burghardt, 1976; Burghardt, 1975; Dungl, Schratter, & Huber, 2008; Kelling et al., 2006), making them suitable subjects for visual concept discrimination studies. Perhaps equally importantly, the previous research calls into question the assumption that being adapted for social living is necessary for complex cognitive capacities, such as the capacity for

abstraction. However, those studies did not explicitly contrast acquisition or transfer of concepts of a social versus a nonsocial nature, which may be more dependent on the specializations adapted for a social lifestyle.

Because of the absence of truly comparative studies on this topic involving a broad range of species, it is unclear to what extent the formation of social concepts relies on specializations for social living. The present study compares the ability of two distantly related species to acquire a social concept of "mother/offspring": chimpanzees (*Pan troglodytes*), which live in complex social groups, and black bears (*Ursus americanus*), which lead relatively solitary lives.

In contrast to cognition of the more social carnivorescanines and pinnipeds-bear cognition is surprisingly understudied. Along with a single study reporting an observation of tool use in grizzly bears (Deecke, 2012), the only scientific reports of cognition in bears involve tests of physical cognition, such as the ability to learn spatial, visual, and quantity discriminations (Bacon & Burghardt, 1976; Dungl et al., 2008; Kelling et al., 2006; Perdue, Snyder, Pratte, Marr, & Maple, 2009; Perdue, Snyder, Zhihe, Marr, & Maple, 2011; Tarou, 2004; Vonk & Beran, 2012; Zamisch & Vonk, 2012). Because bears do not live in large social groups but face significant foraging challenges, one might predict sophisticated reasoning abilities in the physical, but not social domain. Primates, in contrast, live in complex social groups and, like humans, might be expected to excel at reasoning in the social domain. Chimpanzees should outperform species that have not faced complex social problems in their evolutionary history in aspects of social cognition that are relevant to their own ecology, such as identifying social relationships. Comparing the abilities of such distantly related and ecologically distinct species as bears and apes on such problems can help elucidate the contribution of group living and other factors to cognitive processes, such as social and physical reasoning.

The present study tested 3 black bears and 1 chimpanzee on identical two-alternative forced-choice tasks involving a social concept (mother/offspring relationship) and a nonsocial control (foods) for the first time. The subject's task was always to select the image that depicted a mother/offspring pair rather than an image that depicted other kinds of relationships (e.g., siblings, mated pairs, individuals, groups). The nonsocial task also involved choosing pairs or trios of items of the same variety in which one item was larger than the other(s)-such that the food photographs mimicked the social mother/ offspring images of various animals. The social concept task could be acquired either by representing an overarching concept for mother/offspring relationships or by using rules based on perceptual regularities such as "choose image that depicts larger and smaller individual that look similar." The latter rule could also be applied to the nonsocial discrimination (larger and smaller members of the same food category). The nonsocial problem could be solved only through the use of a perceptual rule. Use of the social concept should not facilitate transfer from the social to the nonsocial discrimination, whereas use of the perceptual rule should allow transfer between all discriminations. Thus, presenting such analogous tasks should tease apart two potential underlying representations that could contribute to above-chance performance on the social category discrimination.

Method

Subjects

One adult male chimpanzee, Joe, and 3 adult American black bears, Brutus, Dusty, and Bella, were tested. The chimpanzee was approximately 16 years of age when the experiments began. He had worked in entertainment as a juvenile, but had lived at the Mobile Zoo in Wilmer, AL, for many years before the onset of the research. Joe had already participated in several other experiments using the touch-screen computer, including a study of natural category discrimination (Vonk et al., 2013) and memory (Vonk & Mosteller, 2013). Joe had also been trained on match-to-sample tasks, including a test of relational reasoning (unpublished data). He had been participating in the research program for approximately 4 years when this study began. The bears had participated in a study of cognitive dissonance (West, Jett, Beckman, & Vonk, 2010) and spatial memory (Zamisch & Vonk, 2012), as well as a study of natural category discrimination (Vonk et al., 2012). The bears were also in training on a serial list task and a match-to-sample task. All subjects were trained on the twochoice discrimination procedure.

Joe was housed individually, although he had previously lived with another chimpanzee for a period of approximately 2 years as an adult (first with an adult female, and subsequently with another, younger male who was the son of the female). Thus, Joe had some limited experience with at least one mother/offspring pair, although his early history was unknown. The bears, who were siblings, were group-housed along with their mother and had lived as a family group since birth. At the time of the research they were approximately 9 years of age. The research took place in an off-exhibit area of the chimpanzee and bears' enclosures at the Mobile Zoo in Wilmer, AL. Testing of the animals complied with the institutional animal care and use review board at the University of Southern Mississippi, and the zoo was compliant with USDA regulations.

Materials

A durable Panasonic Toughbook laptop computer and 21-in. capacitive touch-screen monitor welded inside a hydraulic lift cart comprised the experimental apparatus for use with the chimpanzee. A 19-in.Vartech Armor touch capacitive touchscreen monitor welded to the front of a rolling computer cart was used, along with the Toughbook, for the bears. Experiments were programmed using RealBasic 2006 for Windows.

Stimuli consisted of two-dimensional photographs, approximately 400 × 600 megapixels, downloaded from the Internet, and edited using Adobe Photoshop CS2. The social task included four sets of 40 images: (1) chimpanzee mothers with offspring versus young and adult chimpanzees that appeared individually, in pairs or in groups, (2) mother bears with offspring versus young and older groups, pairs, and individual bears, (3) various primate mothers with offspring versus individuals, pairs, and groups of primates, and (4) various animal mothers with offspring versus individuals, pairs, and groups of animals. The species depicted in this final set of images were quite diverse and included reptiles and birds, as well as mammals. All social stimuli presented images of the face, including eyes. A list of all images used appears in the Appendix. A sample pair of images from each of the discriminations is presented in Fig. 1. Correct stimuli could not be determined on the basis of number of individuals depicted, because the mother/offspring images sometimes depicted multiple offspring and the nonmother images often depicted two or more individuals. Although it is the case that images of single animals were always incorrect, and such a condition may have aided in learning the task, single images were used less than half the time in each set, so, if used as a cue, would not have led to above-chance transfer.

Following the social tests, two social control tests were presented in order to test further generalization of the mother/ offspring concept. If the subjects had memorized which images were correct, they could succeed on a test that included previously reinforced images paired with previously nonreinforced images from all of the previous animal categories. However, if they did not acquire an overarching mother/ offspring concept, they should not show transfer to novel images of mother/offspring pairs from the same animal categories. These control tests used a subset of the same images used in the aforementioned four sets of mother/offspring images (familiar mixed test) and a set of 20 novel images of mother/offspring and 20 novel images of individuals, groups, and same-sized pairs of animals (novel mixed test). That is, these were images from the same categories as those previously presented, but the specific images themselves had not been presented to the subjects previously. For this second control test, the novel images also contained a mixture of different species, including some bears and primates.

During the nonsocial task, three sets of 40 images were used: (1) pairs of large and smaller fruits of the same kind versus singles, pairs, and groups of different fruits or the same fruits of identical sizes, (2) pairs of large and smaller vegetables and mushrooms of the same kind versus singles, pairs, and groups of different vegetables/mushrooms or same vegetables/mushrooms of identical sizes, and (3) pairs of large and smaller berries of the same kind versus singles, pairs, and groups of different berries or same berries of identical sizes. Two sample pairs of images from the berry category of nonsocial tasks appear in Fig. 2, along with a sample pair of fruit and vegetable stimuli.

An incorrect response was followed by an unpleasant buzzer tone and a brief time-out (750 msec) with a blank black screen. Correct responses were followed by a pleasant tone and a blank white screen and paired with food reinforcement, which consisted of portions of the animals' regular zoo diet (fruits, vegetables) and special treats such as honey-roasted peanuts, banana pellets, dried banana chips, yogurt- covered raisins, wafer cookies, and so on. Food was presented by hand.

Procedure

Subjects were tested in the indoor area of their home cages and could move freely in their home cages throughout testing sessions. Thus, participation was entirely voluntary. The computer cart was pushed up against the bars of the cage separating the human experimenter from the subjects, allowing the subjects access to the touch-screen monitor. The subjects had all been trained on a forced two-choice discrimination task in which they selected images of either supermodels (Joe, Dusty) or Planet of the Apes characters (Brutus, Bella), when paired with each other, until they reached a criterion of 80 % on four consecutive sessions without any guidance from the experimenter. Following training, they had participated in a natural category discrimination study using the same forced-choice two-alternative procedure (Vonk et al., 2012; 2013). During these discrimination tasks, all subjects had been presented with various images of bears, primates, and other animal species, some of which might have included images of mothers with their offspring. In the previous tasks they had been reinforced for selecting particular species, families, or orders of animals, but had not been trained to attend to the relationship between animals in the photos. All of the photos used in the present experiment were unfamiliar (had not been previously presented in the earlier experiments).

During testing, the experimenter was centered behind the computer cart observing the subjects' responses on the laptop monitor, which was positioned directly behind the touchscreen monitor and encased in a protective covering (for the chimpanzee). The experimenter did not provide any cues and could not see the subjects' faces, hands, or paws during the trial. The experimenter presented the subject with a food reward, as described above, immediately following a correct response, signaled by the tone, at a consistent location. Trials continued automatically until the end of a session.

All subjects were rewarded for selecting images belonging to the mother/offspring category and were not rewarded for









Chimpanzee Mother versus Chimpanzee Group



Primate Mother versus Primate Pair

Bear Mother versus Bear Juveniles





Animal Mother versus Animal Pair

Fig. 1 Examples of images from each social discrimination (mother/offspring), showing a pair of images from each set (chimpanzee, bear, primate, mixed animal). The correct stimulus is on the left

selecting images depicting other relationships. Each session involved 20 trials, such that there were 40 images used in each photo set for each discrimination: 20 S + and 20 S- images. Four sets of images were used in the social discrimination, along with two control sets, and three sets were used for the nonsocial discrimination. Thus, each subject participated in nine different discriminations. Care was taken to select images that were visually distinct within each of the category levels. Joe completed the social tasks in the following order: chimpanzee, bear, primate, and animal mothers; whereas the bears received the social sets in the following order: bear, chimpanzee, primate, and animal mothers. The idea was to begin each

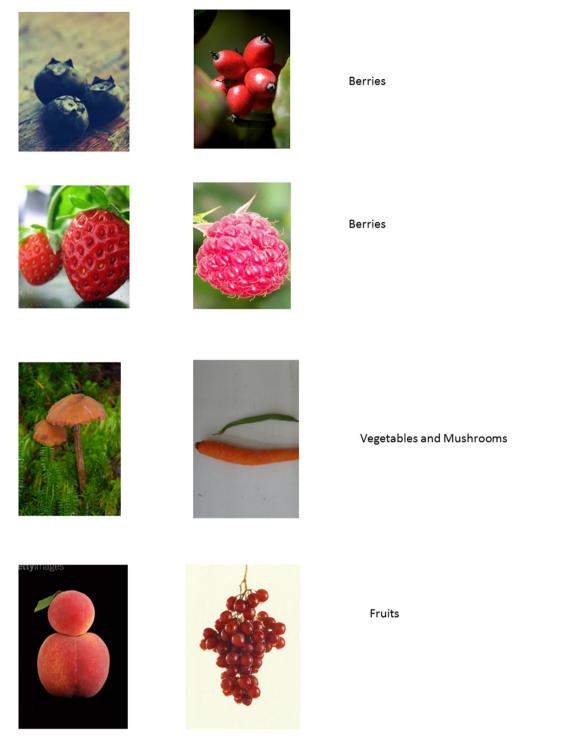


Fig. 2 Examples of images from each nonsocial discrimination showing a pair of images from each category (berries [2], vegetables, fruit). The correct stimulus is always pictured on the left

subject with a discrimination involving its own species or family, under the assumption that mother/offspring relationships in one's own family would be the most salient and easier to discriminate from other relationships. Then, increasingly abstract categories were presented as transfer tests of the general concept of mother/offspring. The category "primate" was more diverse than the categories of "chimpanzees" or "bears," given that it was a more inclusive category and contained more perceptually distinct exemplars. The animal category was even more inclusive and broad and contained even more perceptually distinct exemplars. Dusty, Brutus, and Joe completed all of the social sets, including controls, before moving on to the nonsocial sets. Bella received the nonsocial task first and completed all nonsocial sets before moving on to the social sets. This was done in order to compare acquisition of the discriminations if using the perceptual rule. It was assumed that if subjects learned the discrimination by virtue of the perceptual rule "choose larger and smaller member of the same type," they should be able to acquire the nonsocial discrimination and show transfer to the social discrimination.

Order of presentation of the nonsocial (food) stimuli was counterbalanced across subjects. The subjects received the food stimuli in the following orders: Brutus—berries, fruits, vegetables; Dusty—vegetables, berries, fruits; Bella—fruits, berries, vegetables; Joe—fruits, vegetables, berries. The level of inclusiveness of the food categories was relatively similar, so there was not a logical order to assign to all subjects.

The control tasks were presented following completion of the social tasks in order to determine whether the subjects' performance with previously seen images from all prior discriminations (familiar mixed) would be disrupted when they were presented as novel pairings in a new set, or whether they would continue to perform at high levels. Thus, two sets of stimuli were created. The S + set contained images that they had previously been reinforced for choosing, with several images randomly chosen from each set of photos. That is, the images included some bear mothers, some chimpanzee mothers, some primate mothers, and some other species from the previously learned mother/offspring sets. Likewise, the Sset contained images from the previous sets that had not been reinforced. If the subjects had simply memorized which photos had been correct or incorrect previously, or if they had acquired a concept for "mother/offspring" and used this concept to guide their choices in the task, they would be expected to do well at this task immediately, thus showing significant transfer. It would not be possible to distinguish between accounts of transfer that relied on acquisition of a concept or memorization of reinforcement histories with particular stimuli.

Therefore, as a further test of acquisition of a concept versus memorization of stimulus associations, we composed an additional set of images that contained novel images belonging to the same categories that had been previously reinforced (novel mixed). That is, novel images were selected to represent mother/offspring pairs and nonmother/offspring relationships. However, none of the images had been presented previously, so the animals had no reinforcement history with the specific photos used in this task. If the animals were using memory for specific images, rather than category membership, to dictate choices, they should perform randomly on first presentation of this set of images. However, if they had acquired the mother/offspring concept, they should perform above chance with these novel images. Thus, only abovechance performance on the first session of *both* familiar and novel mixed sets would indicate acquisition of the concept "mother/offspring." Alternatively, use of the rule "choose larger and smaller of same species" would also allow for significant transfer but should also allow continual transfer on the nonsocial task as well.

Side location of the correct stimulus was counterbalanced within testing sessions. Images were randomly paired and presented on each trial. No image was repeated within a session. Subjects were reinforced for every correct response. Intertrial intervals and number of sessions presented on a given day varied as a function of the subject's attention to the task. Intertrial intervals were typically less than a few seconds. If the animal was incorrect, the black screen that informed the experimenter of the response was presented briefly and then the next trial commenced immediately. If the subject was correct, the animal waited for the experimenter to offer a food reward before responding on the next trial. There was a period of 750 ms after the next trial was presented before a subject could make a response, to ensure that the subject did not simply initiate a response without viewing the images. Subjects were presented with four to 12 sessions on a given test day and tested 2 or 3 days a week over a period of several months. Subjects continued to work with a particular stimulus set until a criterion of an average of 80 % correct or more was achieved for four consecutive sessions, or 90 % or more was reached on two consecutive sessions. At that time, a stimulus set of novel photographs (transfer) depicting the same category discrimination was presented. At least two sessions of transfer images were always presented immediately following criterion on a previous set, on the same test day, such that there were no gaps in time between reaching criterion on one set and being presented with the relevant transfer images.

Bella began testing with the nonsocial discriminations, whereas all other subjects began testing with the social discriminations. The primary hypothesis was that animals might demonstrate transfer between the social tasks but that this transfer performance might be achieved using the rule "choose larger and smaller of same species," rather than through the acquisition of a social concept. Transfer between nonsocial tasks could be achieved only using the perceptual rule. Transfer from the nonsocial to the social task could be achieved by continuing to apply this rule, but transfer from social to nonsocial tasks should not happen if the animals were using only a social concept to guide responding. Thus, it was of primary importance to test the animals on the social task first. However, in order to assess the possibility that animals might show high levels of performance on the nonsocial task for reasons other than having acquired a rule during the social task, 1 subject was tested in the reverse order. Balancing task order was not expected to rule out order effects in such a small sample, but rather to provide a means to evaluate the possibility of an untrained mechanism for achieving above-chance

performance on the secondary task if significant "transfer" between tasks was achieved.

Predictions

Of course, the images provide additional cues that the subjects could use to acquire criterion levels of performance. They could elect not to choose images that included only a single item or individual and images that contained items that appeared to be of different kinds. However, in examining the list of images in the Appendix, one can see that using rules such as "don't choose single individual" or "don't choose images that include many of different kinds" would not facilitate performance on most trials within most sets of stimuli, and thus would not lead to above-chance performance. However, we analyzed performance as a function of the number of individuals depicted in the nonreinforced stimulus set as well.

Of course, an animal can also learn a discrimination by memorizing which stimuli are associated with reward. Such a process would allow one to acquire the discrimination but would not facilitate transfer to novel stimuli (with the exception of some transfer to similar stimuli) and would not result in a reduction of trials required to reach criterion across image sets. In order to demonstrate acquisition of the social concept, we predicted that the subjects should (1) demonstrate fewer trials to reach criterion with each subsequent photo set depicting the same discrimination of mother/offspring versus other relationships, (2) show transfer on each first session with novel mother/offspring images, (3) perform above chance on the novel mixed control test, and (4) not show transfer on the first nonsocial version of the task with food images. Above-chance transfer on the nonsocial task would not necessarily rule out use of a social concept on the social version of the task, but it would make it difficult to determine conclusively whether the subject was using only a perceptual rule ("choose image that depicts larger and smaller member of same type") or had also learned a social concept ("choose mother/offspring pair").

Analyses

At each level of discrimination, each subject's individual performance on only the very first session with novel photos was compared with chance (50 %) using binomial tests. These results appear in Table 1. Alpha was set to .05 for all statistical tests. The alpha level was not adjusted for multiple comparisons for several reasons. First, it was considered imperative to avoid the risk of falsely concluding that animals do not acquire concepts, when in fact they do (Type 2 error), relative to an error in which we attributed concept learning to an animal that did not really

acquire a concept. This was the case because there is little power to detect such effects in small sample sizes, and adopting a rigorous p value would substantially diminish our ability to detect any sign of concept learning in this difficult task (see also Crabbe, Wahlsten, & Dudek, 1999; Field & Armenakis, 1974; Nakagawa, 2004; Perneger, 1998). Nakagawa (2004) notes that there is a much greater probability of making a Type 2 versus a Type 1 statistical error in the field of animal behavior and behavioral ecology, as indicated by a meta-analysis on statistical power (Jennions & Møller, 2003). Perneger focuses on the fallacy in logic when applying corrections with the assumption that subjects are identical on all variables under consideration.

The number of sessions taken to reach criterion with each set of photos also appears in Table 1. If a subject has acquired a concept, one expects to see above-chance levels of performance at first or at least by second transfer (Sets 2 and 3) with each discrimination, whereas they should not be above chance on the first session with the training data (Set 1) because this finding would indicate a spontaneous, untrained preference for images belonging to that category and would not speak to acquisition of a learned category. In other words, the subjects should not know a priori, without feedback, which categories are "correct" without experience at the task, even if they are spontaneously able to discriminate the categories (Brown & Boysen, 2000; Murai et al., 2005). One should also see that the sessions required to reach criterion should decrease with each set of photos depicting the same category discrimination if the subject has indeed acquired the overarching concept being tested. Thus, examining both criterion performance against p values in binomial tests and the number of sessions required to reach criterion with each set of photos should jointly contribute to the conclusions as to whether individual subjects have indeed acquired concepts. Field and Armenakis (1974) showed that five significant effects at an alpha of .05, given 36 comparisons, yield only a .029 probability of obtaining a significant difference by chance. Thus, the risk of obtaining these results by chance alone is not substantial. Lastly, significance was primarily obtained when presenting stimuli for which the animals had already learned the reward contingencies (the familiar mixed control task), which seems less likely to be the result of chance.

Repeated-measures analyses of variance (ANOVAs) were conducted on both first-session performance and sessions to criterion, with set (1-3) and type (social, nonsocial) as factors. Because the nonsocial task contained only three sets, data from the fourth set of the social discrimination were omitted, so that we could conduct a nested repeated-measures ANOVA.

Table 1 The percentage of correct responses on the first session of each
set of photos, arranged by discrimination task, for each subject, along
with p values given by binomial tests comparing performance (number of

trials correct out of 20) with chance (50 %), and number of sessions to reach criterion (abbreviated StC).

Task	Set	Joe			Brutus			Dusty			Bella		
		%	р	StC	%	р	StC	%	р	StC	%	р	StC
Social	1	70	.12	44	40	.50	51	45	.82	41	75	.04	39
	2	50	1.0	64	40	.50	84	40	.50	24	55	.82	39
	3	55	.82	36	55	.82	33	65	.26	54	55	.82	47
	4	65	.26	45	50	1.0	18	40	.50	32	65	.26	17
Familiar		90	.001	4	80	.01	4	55	.82	25	65	.26	21
Novel		75	.04	16	65	.26	12	55	.82	41	45	.82	29
Nonsocial	1	80	.01	15	35	.26	20	60	.50	84	60	.50	25
	2	65	.26	56	55	.82	20	50	1.0	37	40	.50	34
	3	45	.82	43	70	.12	17	65	.26	14	65	.26	80

Significant p values are bolded

In addition, we calculated the average performance of each subject when only a single animal appeared in the nonreinforced stimulus set, because the reinforced stimuli always necessarily contained at least two animals, and we wanted to examine whether number of animals depicted might provide a clue as to which items not to select. We compared this average performance to that on trials in which two or more animals were depicted, using Wilcoxon tests.

Results

Repeated-measures ANOVAs revealed no effects of set or type on either first-trial performance or sessions to criterion (all Fs < 1.0, all ps > .05). Although the lack of an effect may be due in part to the small sample size (N = 4) and lack of statistical power (observed power < .10), this conclusion is also consistent with the pattern of results shown in Table 1 and Figs. 3 and 4. Performance did not differ as a function of the type of task (social vs. nonsocial), and did not improve (or decline) in a linear fashion across the first three sets of stimuli. Set number did not interact with type of task. We did not correct for multiple comparisons, given that our analyses were already underpowered to detect significant effects.

Binomial tests on first-session performance for each subject for each task reveal above-chance performance on the familiar mixed control test for Joe and Brutus (ps = .001 and .01, respectively), and the novel mixed control task (p = .04) and first session of the nonsocial task (p = .01) for Joe alone. Both Joe and Brutus also met criterion within the minimum number of sessions on the familiar mixed control task. The data can be seen in Fig. 5. Although only Joe was above chance on the first session of the novel control task, Brutus reached criterion on this discrimination in fewer sessions (12

vs. 16). In addition, Bella was above chance on the first session of the social task (p = .04). Although Joe began the first set of the nonsocial discriminations and Bella began the first set of the social discriminations at above-chance levels, neither subject reached criterion immediately and neither showed continued transfer with subsequent sets of images/ discriminations.

On some trials, there existed a quantitative cue as to the incorrect stimulus. It was always the case that stimuli depicting a single individual were incorrect. Therefore, if two or more individuals were depicted in the nonreinforced stimulus, the trial should be more difficult than when only a single individual was depicted, if animals relied on the availability of this quantitative cue. We therefore conducted Wilcoxon tests comparing performance on trials in which the nonreinforced stimulus contained only a single animal with those trials in which the nonreinforced stimulus contained two or more animals. These tests revealed no significant differences across all photo sets, although the difference between performance with and without the availability of the cue in the primate mother/nonmother discrimination approached significance. However, the effect was in the opposite direction from what we would predict based on the quantitative cue. That is, subjects performed more accurately when two or more individuals were depicted in the nonreinforced stimulus, just as in the reinforced stimulus (Z= -1.83, p = .07). This was also the case with the familiar mixed test stimuli (Z = -1.83, p = .07). Although admittedly, with 4 subjects, these tests were underpowered, one can see by examining Table 2 that performance was not consistently better when the nonreinforced stimulus contained one animal. A closer examination indicates that Bella may have used the availability of such a cue to inform performance on the first social set (bears) and Joe may have done so on the first two sets (chimpanzees, bears), but no subject appeared to use such

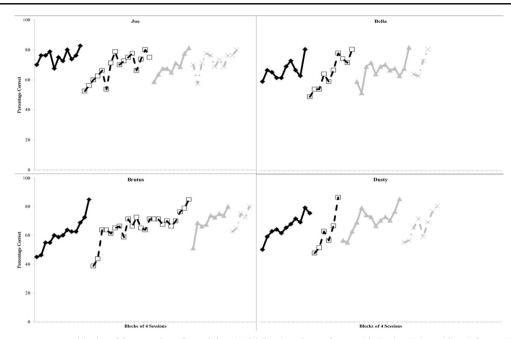


Fig. 3 Percentage correct across blocks of four sessions for training (solid lines) and transfer sets (dashed and dotted lines) for social discriminations. Each subject's performance is plotted separately

a cue subsequently. This result suggests that this was not a variable used by the subjects to perform accurately in this task across transfer sets. However, it is possible that Bella used this cue to allow her to perform above chance on the first session of the social task—a level of performance that she did not maintain once she apparently ceased to use this cue.

Discussion

The lack of consistent transfer (above-chance performance with novel images) and lack of overall decline in number of sessions to reach criterion across image sets suggest that these subjects, the bears in particular, were unable to abstract a social concept when discriminating photos of mother/

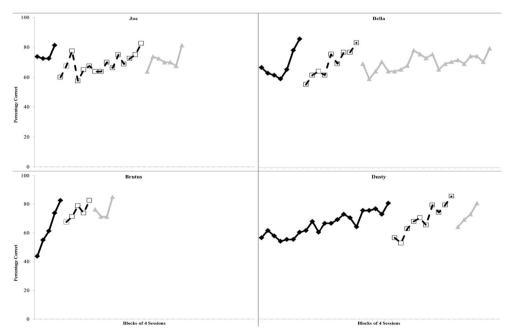


Fig. 4 Percentage correct across blocks of four sessions for training (solid lines) and transfer sets (dashed and dotted lines) for nonsocial discriminations. Each subject's performance is plotted separately

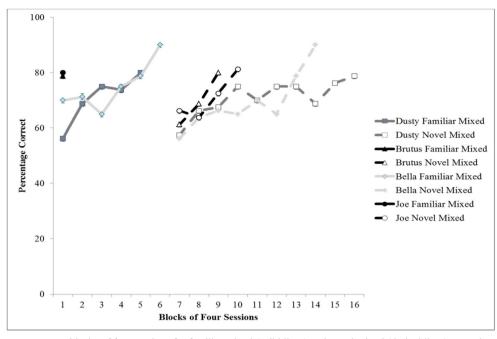


Fig. 5 Percentage correct across blocks of four sessions for familiar mixed (solid lines) and novel mixed (dashed lines) control tests

offspring from photos of other social relationships. It cannot be concluded that this species lacks the capacity to reason about social relationships, however, given that only a single relationship and a very small number of subjects were tested in the present study. In addition, although the bears were housed in a family group, limited experience with other bears may have had an impact on their ability to reason about social relationships. Furthermore, a potential confound that limits our ability to directly compare the performance of the bears with that of the chimpanzee is that the chimpanzee's first social test was composed of images of only his own species, whereas the bears' first social test was composed of images of various bear species. However, we find it unlikely that the bears would be rendered unable to abstract the concept of mother/offspring when this relationship was the only differentiating constant across all trials within the set of bear photos, simply because some of the bears were of closely related but not the exact same species as the subjects. Furthermore, the bears had previously demonstrated the capacity to categorize various bear species together (Vonk et al., 2012).

The chimpanzee showed transfer on the familiar mixed control and, more critically, on the novel mixed control task, indicating that he may have eventually acquired a more general social concept. The fact that he also showed transfer on the very first nonsocial discrimination might have suggested that he was instead using a perceptual rule, such as "choose larger and smaller pairs of similar objects." However, he did not continue to apply this rule on subsequent transfer tests with nonsocial stimuli, and the notion that chimpanzees might be capable of abstracting a social relationship concept would be consistent with previous findings that other apes (1 gorilla and 4 orangutans) were able to match stimuli according to social relationships and transferred learning of a mother/ offspring concept to novel stimuli (Vonk, 2002). However, given the other possible explanations for the results of those apes as well, this is a topic that begs further study.

Although most of the apes performed well in Vonk's (2002) task, it is possible that their performance revealed preferences for images depicting young animals, or involved a comparison of the number of individuals depicted in the images. An additional study demonstrated that 1 orangutan could attend to information about quantity of individuals in similar stimuli (Vonk, 2014). The orangutan and gorillas were also presented with a task involving matching physical activities, such as playing, eating, sleeping and grooming. The apes performed comparably on the social and nonsocial versions of this task (Vonk, 2002). They could have used cues such as the presence of food, and position of the eyes (closed vs. open) to help them match stimuli in this task as well. The present study improved on the previous work by attempting to tease apart the use of an overarching concept from the use of one possible perceptual cue.

In the present study, it was possible to contrast the use of a physical rule in a social and nonsocial context with the use of an overarching concept for mother/offspring by examining the pattern of results from acquisition to possible transfer within and between discriminations. The data suggest that the subjects did not develop a perceptual rule of the type, "choose image that depicts large and small of same type," because they did not require fewer

Stimulus Set Number of Animals Depicted	Bears		Chimpanzees		Primates		Animals		Familiar Mixed		Novel Mixed	
	2+	1	2+	1	2+	1	2+	1	2+	1	2+	1
Bella	0.62 (0.12)	0.71 (0.16)	0.66 (0.15)	0.62 (0.17)	0.67 (0.10)	0.50(0.32)	0.71 (0.12)	0.71 (0.23)	0.72 (0.10)	0.71 (0.17)	0.70(0.13)	0.64 (0.15
Dusty	0.67 (0.16)	0.63 (0.14)	0.60 (0.17)	0.59 (0.19)	0.71 (0.10)	0.59 (0.32)	0.64 (0.12)	0.72 (0.20)	0.79 (0.10)	0.50 (0.25)	0.71 (0.11)	0.71 (0.13
Brutus	0.59 (0.17)	0.63 (0.15)	0.65 (0.13)	0.67 (0.16)	0.71 (0.10)	0.56(0.37)	0.71 (0.10)	0.65 (0.24)	0.80 (0)	0.75 (0.19)	0.66 (0.14)	0.74 (0.13
Joe	0.60 (0.14)	0.78 (0.14)	0.69 (0.12)	0.83 (0.12)	0.68 (0.12)	0.62 (0.32)	0.72 (0.10)	0.67 (0.25)	0.83 (0.09)	0.70 (0.12)	0.60 (0.14)	0.77 (0.15

 Table 2
 The proportions correct for trials on which the nonreinforced stimulus contained either a single individual or two or more individuals across each discrimination and for each subject. Standard deviations are shown in parentheses.

trials to reach criterion as they progressed through the discriminations (with the possible exception of Brutus), and they did not consistently generalize learning to novel sets of photos, or a novel discrimination even though use of such a rule would have supported such a generalization. Although Joe showed above-chance transfer on the first session with nonsocial stimuli, and Bella showed above-chance performance on her first session with social stimuli, neither subject maintained above-chance performance or reached criterion more quickly on these sets, making it difficult to conclude that they had learned an effective rule that generalized across sets. It is possible that the rule was more difficult to apply to some of the other sets of food images, given that such a rule is more esoteric than the overarching concept that could be applied to the animal images. Perhaps Joe used both a concept and a perceptual rule on the mother/offspring tasks, and when only the perceptual rule could be applied at transfer to the nonsocial problems, performance was affected. One possible rule considered here was to choose an image that contained a large and small image of the same type of object, but there may be other rules that allowed for the inconsistent transfer that was obtained here. Alternatively, the subjects appear to have relied to some degree on memory for particular images that were previously rewarded. They generally required fewer sessions to reach criterion on a task involving familiar images, although only 2 of the 4 subjects showed immediate transfer on the first session with this familiar mixed control task.

Of the bears, only Brutus performed above chance immediately with the mixed mother/offspring discrimination, but he did not generalize to novel images, suggesting that he used memory for previously reinforced images to dictate his choices, rather than an overarching concept. Brutus alone was also presented with three sessions of mixed familiar food images and performed at 90 % correct by the second session on this task as well, indicating that there was nothing special about his performance on the mixed social task. This finding of memory for previously presented stimuli would be consistent with Brutus's performance in previous natural category discrimination tasks (Vonk et al., 2012). In those tasks, Brutus demonstrated memory for images he had been trained to discriminate more than 2 years previously. However, it is notable that Brutus required fewer sessions than Joe to reach criterion on the novel mixed control task, perhaps suggesting that both subjects had discovered either a concept or rule that facilitated learning. In any case, Joe was able to initially perform well on transfer to the nonsocial tasks, whereas Brutus was not. Thus, attributing the use of a rule or concept to Joe but not to Brutus makes some sense.

Dusty did not demonstrate above-chance transfer on any of the discriminations, including the control tests, indicating that he did not use a relevant concept or rule to assist in the task. Although he and Bella obtained criterion with each set, indicating that they at least learned which stimuli were correct and/or incorrect, this memory was disrupted when the stimuli appeared in a mixed session representing the same concept. This is further evidence that they did not abstract a meaningful concept with which to organize their representations of the stimuli. Wright and colleagues (see Wright, 2013, for a summary) have cleverly demonstrated that some animals demonstrate evidence for concept learning only under very particular methodological constraints. For instance, pigeons may demonstrate acquisition of a concept only when they must select a sample image multiple times. They also show greater transfer when more exemplars are presented in training. It is possible that bears have social concepts but could not demonstrate the use of such a concept in our somewhat artificial laboratory task. However, it is important to note that all subjects were capable of demonstrating transfer, and thus acquisition of concepts, when concepts were of natural categories such as particular species or families of animals, rather than of social categories (Vonk et al., 2012, 2013). Taken together, these findings indicate that social relationship concepts are more difficult for both primates and carnivores

to acquire compared with natural categories that require categorizing species into family, order, and class categories. This finding is not surprising given that shared perceptual features can be used to categorize natural objects. It is possible that the subjects were unable to determine that offspring in the images belonged to the same species as the parents depicted.

This is the first test of categorization of images according to a social concept in a carnivore. It is also the first explicit comparison between the cognitive capacities of bears and chimpanzees. Bräuer, Kaminski, Riedel, Call, & Tomasello (2006) also tested the social and physical causal reasoning of carnivores and primates when they tested dogs and chimpanzees in an object-choice task. Given that dogs found food more easily with social cues, such as gaze and points, whereas chimpanzees found it easier to reason about physical cues, such as the sound of food rattling in a cup, researchers proposed that dogs are superior at reading human cues, perhaps because of their history of domestication (Hare, Brown, Williamson, & Tomasello, 2002; Hare et al., 2010). However, others have speculated that the social skills of dogs emerge within their ontological development, rather than their evolutionary history (Udell, Dorey, & Wynne, 2010). Such studies have sparked an ongoing debate as to the selective pressure responsible for the social cognitive skills of canines, and researchers have begun contrasting the abilities of wild and domestic canines (Udell, Dorey, & Wynne, 2008) and domestic dogs, with and without human contact or rearing (Dorey, Udell, & Wynne, 2010). Existing hypotheses center on the sociality of canines, either in their natural environments, living as pack animals, or as domestic species accustomed to following human commands. Bears present an interesting out-group test case because they are members of the same order, also have large brains, but do not live in large social groups, and are certainly not domesticated. Therefore, tests of bears allow us to disentangle the role of social lifestyle and large brain size, which are routinely confounded in studies of social species.

There has been a recent surge of interest in domains of reasoning with regard to social and nonsocial knowledge, but little empirical investigation of species differences in information processing or acquisition of concepts from different domains of knowledge. Tasks representing social and physical cognition in the same studies are rarely actually comparable because they often involve different cognitive demands and motor movements (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Herrmann, Hernández-Lloreda, Call, Hare, & Tomasello, 2010). Bräuer et al.'s (2006) study is unique in comparing the performance of animals of different species (dogs and chimpanzees) on parallel tests with cues that differed by virtue of their social or physical nature. There is a

paucity of research on the cognitive skills, social or physical, of relatively nonsocial carnivores, such as the large cats or bears. The present study adds to this limited knowledge by showing that bears encounter difficulty categorizing stimuli on the basis of social relationships. This is the first study of social cognition in bears, and directly compares their performance to that of a chimpanzee with a similar experimental history.

Although chimpanzees are much more widely studied, there are few studies of social concepts in chimpanzees. Previous studies have shown that chimpanzees may recognize relatedness among mothers and offspring (Parr & de Waal, 1999), which has been considered evidence for a social concept. However, this study focused on recognition of relatedness, which could be accomplished by matching physical features between related individuals, and did not test for an overarching concept of the relationship being tested. However, more recent studies have shown that apes (Vonk & Hamilton, 2014), macaques (Pokorny & de Waal, 2009), and even pigeons (Wilkinson et al., 2010) may have a concept for familiarity, both of conspecifics and objects. The results of these studies constitute solid evidence for the capacity for abstract social concepts in a variety of social species. However, no previous study has demonstrated the ability to reason about broad social relationship concepts in nonhumans. This study was the first to do so, and the results beg further study.

Conclusions

These findings add to the growing body of research that contrasts the cognitive abilities of our closest relativesthe great apes-with those of other, more distantly related species with unique ecologies. Although the bears reached criterion on these tasks after a similar number of sessions and showed similar capacity for memory of previously rewarded stimuli, they did not appear to acquire the social concept, whereas the chimpanzee may have demonstrated use of a social concept. The ability to extract information about social relationships from static stimuli may be the result of social complexity, given that chimpanzees live naturally in large, socially complex groups and that bears are relatively solitary animals. Testing other nonsocial and social species with a variety of behavioral ecologies and life histories will shed further light on both the abilities of other less-tested species, and the selective pressures giving rise to such abilities.

Author note We are indebted to the Mobile Zoo, especially its director, John Hightower. Without his support and assistance, these experiments could not have been conducted. We also give special thanks to Dr. Joan

Sinnott for her support and to Katherine Vowell and Stephanie E. Jett for their assistance during data collection. The research was supported by the Kenneth and Aubrey Lucas Fund from the University of Southern Mississippi.

References

- Bacon, E. S., & Burghardt, G. M. (1976). Learning and color discrimination in the American black bear. Ursus, 3, 27–36.
- Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology*, *106*, 38–47. doi:10. 1037/0735-7036.120.1.38
- Brown, D. A., & Boysen, S. T. (2000). Spontaneous discrimination of natural stimuli by chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology, 114, 392–400. doi:10.1037/0735-7036. 114.4.392
- Burghardt, G. M. (1975). Behavioral research on common animals in small zoos. In *Research in Zoos and Aquariums: A Symposium Held* at the Forty-ninth Conference of the American Association of Zoological Parks and Aquariums, Houston, Texas, October 6–11, 1973 (pp. 103–133). Washington, D.C: National Academy of Sciences.
- Crabbe, J. C., Wahlsten, D., & Dudek, B. C. (1999). Genetics of mouse behavior: Interactions with laboratory environment. *Science*, 284, 1670–1671.
- Dasser, V. (1988). A social concept in java monkeys. *Animal Behaviour*, 36, 225–230.
- Deecke, V. (2012). Tool-use in the brown bear (*Ursus arctos*). Animal Cognition, 15, 725–730. doi:10.1007/s10071-012-0475-0
- Dorey, N. R., Udell, M. A. R., & Wynne, C. D. L. (2010). When do domestic dogs, *canis familiaris*, start to understand human pointing? The role of ontogeny in the development of interspecies communication. *Animal Behaviour*, 79, 37–41. doi:10.1016/j.anbehav.2009. 09.032
- Dungl, E., Schratter, D., & Huber, L. (2008). Discrimination of face-like patterns in the giant panda (*Ailuropoda melanoleuca*). *Journal of Comparative Psychology*, 122, 335–343. doi:10.1037/0735-7036. 122.4.335
- Field, H. S., & Armenakis, A. A. (1974). On use of multiple tests of significance in psychological research. *Psychological Report*, 35, 427–431.
- Fize, D., Cauchoix, M., & Fabre-Thorpe, M. (2011). Humans and monkeys share visual representations. *Proceedings of the National Academy of Sciences of the USA, 108,* 7635–7640. doi:10.1073/ pnas.1016213108
- Gittleman, J. L. (1986). Carnivore brain size, behavioral ecology, and phylogeny. *Journal of Mammology*, *67*, 23–36.
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, 298, 1636– 1639.
- Hare, B., Rosati, A., Kaminski, J., Bräuer, J., Call, J., & Tomasello, M. (2010). The domestication hypothesis for dogs' skills with human communication: A response to Udell et al. (2008) and Wynne et al. (2008). *Animal Behaviour*, 79, e1–e6.
- Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, 317, 1360–1366.
- Herrmann, E., Hernández-Lloreda, M. V., Call, J., Hare, B., & Tomasello, M. (2010). The structure of individual differences in the cognitive abilities of children and chimpanzees. *Psychological Science*, *21*, 102–110. doi:10.1177/0956797609356511

- Humphrey, N. K. (1976). The social function of intellect. In P. Bateson & R. Hinde (Eds.), *Growing Points in Ethology* (pp. 303–317). Cambridge: Cambridge University Press.
- Jennions, M. D., & Møller, A. P. (2003). A survey of the statistical power of research in behavioral ecology and animal behavior. *Behavioral Ecology*, 14, 438–445.
- Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science*, 153, 501–506.
- Kelling, A. S., Snyder, R. J., Jackson, M., Marr, M. J., Bloomsmith, M. A., Gardner, W., & Maple, T. M. (2006). Color vision in the panda (*Ailuropoda melanoleuca*). *Learning & Behavior*, 34, 154–161. doi: 10.3758/BF03193191
- MacLean, E. L., Matthews, L. J., Hare, B. A., Nunn, C. L., Anderson, R. C., Aureli, F., & Wobber, V. (2012). How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition*, 15, 223– 238. doi:10.1007/s10071-011-0448-8
- Murai, C., Kosugi, D., Tomonaga, M., Tanaka, M., Matsuzawa, T., & Itakura, S. (2005). Can chimpanzee infants (*Pan troglodytes*) form categorical representations in the same manner as human infants (*Homo sapiens*)? *Developmental Science*, 8, 240–254.
- Nakagawa, S. (2004). A farewell to Bonferroni: The problems of low statistical power and publication bias. *Behavioral Ecology*, 15, 1044. doi:10.1093/beheco/arh107
- Parr, L. A., & de Waal, F. B. M. (1999). Visual kin recognition in chimpanzees. *Nature*, 399, 647–648. doi:10.1038/21345
- Perdue, B. M., Snyder, R. J., Pratte, J., Marr, M. J., & Maple, T. L. (2009). Spatial memory recall in the giant panda (*Ailuropoda melanoleuca*). *Journal of Comparative Psychology*, 123, 275–279. doi:10.1037/ a0016220
- Perdue, B. M., Snyder, R. J., Zhihe, Z., Marr, M. J., & Maple, T. (2011). Sex differences in spatial ability: A test of the range size hypothesis in the order Carnivora. *Biology Letters*, 7, 380–383. doi:10.1098/ rsbl.2010.1116
- Perneger, T. V. (1998). What's wrong with Bonferroni adjustments. British Medical Journal, 316, 1236–1238. doi:10.1136/bmj.316.7139.1236
- Pokorny, J. J., & de Waal, F. B. M. (2009). Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences of the USA, 106,* 21539–21543. doi:10.1073/ pnas.0912174106
- Range, F., Aust, U., Steurer, M., & Huber, L. (2008). Visual categorization of natural stimuli by domestic dogs (*Canis familiaris*). *Animal Cognition*, 11, 339–347.
- Roberts, W. A., & Mazmanian, D. S. (1988). Concept learning at different levels of abstraction by pigeons, monkeys, and people. *Journal of Experimental Psychology: Animal Behaviour Processes*, 14, 247– 260. doi:10.1037/0097-7403.14.3.247
- Seyfarth, R. M., Cheney, D. L., & Bergman, T. J. (2005). Primate social cognition and the origins of language. *Trends in Cognitive Sciences*, 9, 264–266. doi:10.1016/j.tics.2005.04.001
- Silk, J. B. (1999). Male bonnet macaques use information about thirdparty rank relationships to recruit allies. *Animal Behaviour*, 58, 45– 51. doi:10.1006/anbe.1999.1129
- Silk, J. B., Alberts, S. C., & Altmann, J. (2004). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour*, 67, 573–582. doi:10.1016/j.anbehav.2003.07.001
- Tanaka, M. (2001). Discrimination and categorization of photographs of natural objects by chimpanzees (*Pan troglodytes*). Animal Cognition, 4, 201–211. doi:10.1007/s100710100106
- Tarou, L. R. (2004). An examination of the role of associative learning and spatial memory in foraging of two species of bear (family: Ursidae) (Ailuropoda melanoleuca, Tremarctos ornatus), Dissertation Abstracts International: Section B. Sciences and Engineering, 64, 5260.
- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, 76, 1767–1773. doi:10.1016/j.anbehav.2008.07.028

- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). The performance of stray dogs (*Canis familiaris*) living in a shelter on humanguided object-choice tasks. *Animal Behaviour*, 79, 717–725. doi:10. 1016/j.anbehav.2009.12.027
- Vonk, J. (2002). Can orangutans (Pongo abelii) and gorillas (Gorilla gorilla gorilla) acquire concepts for social relationships? International Journal of Comparative Cognition, 15, 257–277.
- Vonk, J. (2014). Quantity matching by an orangutan (Pongo abelii). Animal Cognition, 17, 297–306. doi:10.1007/s10071-013-0662-7
- Vonk, J., & Beran, M. J. (2012). Bears "count" too: Quantity estimation and comparison in black bears (Ursus americanus). Animal Behaviour, 84, 231–238. doi:10.1016/j.anbehav.2012.05.001
- Vonk, J., & Hamilton, J. (2014). Orangutans (Pongo abelii) and a gorilla (Gorilla gorilla gorilla) match features in familiar and unfamiliar individuals. *Animal Cognition. Advance online publication.*. doi:10. 1007/s10071-014-0741-4
- Vonk, J., & MacDonald, S. E. (2002). Natural concept formation in a juvenile gorilla (*Gorilla gorilla gorilla*) at 3 levels of abstraction. *Journal of Experimental Analysis of Behaviour*, 78, 315–332. doi: 10.1901/jeab.2002.78-315
- Vonk, J., & MacDonald, S. E. (2004). Levels of abstraction in orangutan (*Pongo abelii*) categorization. *Journal of Comparative Psychology*, 118, 3–13.
- Vonk, J., & Mosteller, K. W. (2013). Perceptual versus conceptual memory processes in a chimpanzee (*Pan troglodytes*). In M. Howe, M. Toglia, H. Otgaar, & B. Schwartz (Eds.), *What Is Adaptive About Adaptive Memory*? (pp. 258–283). New York: Oxford University Press.

- Vonk, J., & Povinelli, D. J. (2012). Similarity and difference in the conceptual systems of primates: The unobservability hypothesis. In E. Wasserman & T. Zentall (Eds.), Oxford Handbook of Comparative Cognition (2nd ed.). New York: Oxford University Press.
- Vonk, J., Jett, S. E., & Mosteller, K. W. (2012). Concept formation in American black bears (Ursus americanus). Animal Behaviour, 84, 953–964. doi:10.1016/j.anbehav.2012.07.020
- Vonk, J., Jett, S. E., Mosteller, K. W., & Galvan, M. (2013). Natural category discrimination in chimpanzees (*Pan troglodytes*) at three levels of abstraction. *Learning & Behavior*, 41, 271–284. doi:10. 3758/s13420-013-0103-0
- West, S., Jett, S. E., Beckman, T., & Vonk, J. (2010). The phylogenetic roots of cognitive dissonance. *Journal of Comparative Psychology*, 124, 425–432. doi:10.1037/a0019932
- Wilkinson, A., Specht, H. L., & Huber, L. (2010). Pigeons can discriminate group mates from strangers using the concept of familiarity. *Animal Behaviour*, 80, 109–115. doi:10.1016/j.anbehav.2010.04. 006
- Wright, A. A. (2013). Functional relationships for investigating cognitive processes. *Behavioural Processes*, 93, 4–24. doi:10.1016/j.beproc. 2012.11.003
- Zamisch, V., & Vonk, J. (2012). Spatial memory in captive American black bears (Ursus americanus). *Journal of Comparative Psychology*, 126, 372–387. doi:10.1037/a0028081
- Zentall, T. R., Wasserman, E. A., Lazareva, O. F., Thompson, R. R., & Rattermann, M. (2008). Concept learning in animals. *Comparative Cognition and Behavior Reviews*, 3, 13–45. doi: 10.3819/ccbr.2008.30002