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Concept formation in American black bears, Ursus americanus

Jennifer Vonk^{a,*}, Stephanie E. Jett^b, Kelly W. Mosteller^c

^a Department of Psychology, Oakland University, Rochester, MI, U.S.A.

^b Department of Psychology, University of Southern Mississippi, Hattiesburg, MS, U.S.A.

^c Library & Information Resource Services, Spring Hill College, Mobile, AL, U.S.A.

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Keywords: black bear cognition concept formation level of abstraction Ursus americanus Despite their large relative brain size, bears have been neglected in studies of comparative cognition in comparison to their fellow carnivores, the social canines and pinnipeds. Here, three captive adult American black bears were presented with a series of natural concept discrimination tasks on a touchscreen computer, in which the discriminations varied in degree of abstraction. The more abstract discriminations could not be performed by attending to perceptual features of the stimuli alone. For instance, at the most abstract level, the bears were required to select images of animals rather than nonanimals, and exemplars within both categories were perceptually diverse. At least one bear performed at above-chance levels with transfer to novel images at each level of abstraction. The bear that began testing with the most abstract problems showed the best transfer on more abstract discriminations, suggesting that the usual practice of overtraining animals on perceptual discriminations may hinder their ability to acquire concepts at more abstract levels. The bears' performance suggests that a generalized diet may be more critical than group living with regard to the evolution of complex cognition in carnivores.

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Given the recent focus on cognitive abilities of social species such as corvids (Emery & Clayton 2004; Seed et al. 2009) and canines (Miklósi & Topál 2004; Hare 2007; Kubinyi et al. 2007), it is surprising that so little is known of the cognitive abilities of bears, with their large relative brain size, generalist diet and nonsocial lifestyle (Gittleman 1986). The only existing reports of their cognitive abilities examined their capacity to perform visual, spatial and numerical discriminations (Bacon & Burghardt 1976a, b, 1983; Tarou 2003; Dungl et al. 2008; Perdue et al. 2009, 2011; Vonk & Beran 2012). In contrast to other carnivores, such as canines and pinnipeds, black bears are less social and show much more flexibility in their diet and habitat. Focusing on carnivores alone, cognitive differences can be examined in a mammalian order containing species that are closely related phylogenetically but vary in terms of diet, physiological adaptations and social structure. Such studies will improve our understanding of the relative importance of these factors in promoting different cognitive and behavioural traits.

Both wild and domestic canines have recently been the focus of intense study (reviewed in: Miklósi & Topál 2004; Hare 2007; Kubinyi et al. 2007; Udell et al. 2012). Wild canines, living in packs,

E-mail address: jenvonk@gmail.com (J. Vonk).

generally show intense sociality, while domestic canines are socialized with human caregivers. Pinnipeds, which are now generally classified as carnivores, and are thought to have evolved from bearlike ancestors, have also been highly studied. For example, Abramson et al. (2011) found that sea lions. Otaria flavescens, appear to use a mechanism for estimating quantity similar to that of primates. Vonk & Beran (2012) recently came to the same conclusion in a rare study investigating quantity estimation in black bears. Over more than a decade of research, Schusterman and colleagues have discovered that California sea lions, Zalophus californianus, and other pinnipeds, such as the walrus, Odobenus rosmarus divergens, show advanced problem-solving and discrimination skills, comparable to those of primates (Reichmuth Kastak & Schusterman 2002; Schusterman et al. 2002, 2003; Schusterman & Reichmuth 2008). Some have argued that the social cognitive abilities of canines is superior to that of primates in some tasks (Hare & Tomasello 2005; Bräuer et al. 2006; Cools et al. 2008), although others have found primates to be superior in tests of physical cognition (Rooijakkers et al. 2009). Wobber & Hare (2009) suggested that social skills of domestic dogs, Canis familiaris, were specialized as a result of domestication, and that primates sometimes excelled where dogs did not. Primates live in complex social groups, but are also most closely related to humans. Although the social structure of pinnipeds is variable, many species live in large groups, unlike bears, which are generally solitary. The careful study of more distantly related species can help to tease apart the role of convergent and parallel evolution.





^{*} Correspondence: J. Vonk, Department of Psychology, Oakland University, 2200 N Squirrel Rd, Rochester, MI 48309, U.S.A.

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One might expect more social species to excel at tests of social cognition, whereas species that face significant foraging challenges might excel at tests of physical cognition. Thus, tests of bear cognition would allow for evaluation of social intelligence/Machiavellian contributions (Jolly 1966; Humphrey 1976) and foraging contributions (Milton 1981, 1988) to the development of cognitive specializations.

Within bears, black bears, along with brown bears, Ursus arctos, show a high degree of foraging flexibility, so they are classified as generalists. Other bears, such as polar bears, Ursus maritimus, eat meat almost exclusively, while the giant panda, Ailuropoda melanoleuca, is almost entirely herbivorous, making them specialists. Thus, further work will be necessary to test cognitive abilities within the Ursidae family, with special attention to diet, habitat and social structure as potential factors explaining species differences. If black bears perform comparably to large-brained, social-living animals on tests of cognitive ability, this result would support the importance of flexibility in diet and undermine the hypothesis that social living is a prerequisite for cognitive complexity, particularly in carnivores. Such a finding would also potentially call into question the hypothesis that canine performance in such tests is due to domestication (Hare et al. 2002; Kubinyi et al. 2007; Wobber & Hare 2009), as there may be other factors in the shared evolutionary history of carnivores leading to their large brain size and advanced problem-solving skills. Such factors might include the flexibility in feeding and habitat that is shown by black bears. Hypotheses about the impact of domestication may pertain more to aspects of social intelligence, such as the ability to read human social cues rather than to general intellectual ability (Hare & Tomasello 2005). Scheumann & Call (2004) have demonstrated successful use of human point cues by fur seals, Arctocephalus *pusillus*, to find hidden food, indicating that domestication is not necessary for social cognitive skills in carnivores. Rather, the captive environment may promote enhanced abilities to read human social cues, due to increased interactions with humans. A recent study finding that bats born in captivity, in contrast to wildcaught bats, were able to follow human point cues lends support to this hypothesis (Hall et al. 2011).

Of course the hypothesis that social living is not a prerequisite for 'intelligent' behaviour will come as no surprise to those familiar with research on cephalopods (Hvorecny et al. 2007), cleaner wrasses (Bshary & Grutter 2006; Salwiczek & Bshary 2011) and various other relatively solitary species that have demonstrated significant cognitive skill both in and out of the laboratory. However, the conceptual abilities of nonsocial and social carnivores have not been compared previously, despite the intriguing early work with bears (Burghardt 1975, 1992; Bacon & Burghardt 1976a, b, 1983; Bacon 1980). Concept formation paradigms are ideal for studying general intellectual function as discriminations can be presented along a continuum of abstraction where more abstract discriminations must be made on the basis of inferring a relationship among the exemplars beyond shared perceptual features (Roberts & Mazmanian 1988; Vonk & MacDonald 2002, 2004; Zentall et al. 2008; Fize et al. 2011). The few published empirical studies on bear cognition indicate that bears can perform conditional discriminations (Zakher 1974; Dungl et al. 2008), and that their colour vision (Bacon & Burghardt 1976b; Kelling et al. 2006) and ability to recognize form (Burghardt 1975) is comparable to that of primates, making them suitable subjects for visual concept discrimination studies. Furthermore, Range et al. (2008) successfully studied natural concept formation in a canine species using touchscreen computer methodology, paving the way for the use of this methodology in carnivores.

Range et al. (2008) demonstrated that dogs were able to form a concrete level category, one in which a large number of physical features were shared between exemplars within the category. Dogs were reinforced for selecting images of dogs rather than images of landscapes. They were not tested on more abstract level discriminations in which exemplars within categories may not share many perceptual features in common. For instance, Roberts & Mazmanian (1988) and Vonk & MacDonald (2002, 2004) varied abstraction in sets of natural stimuli such that sets of stimuli involved animals belonging to close taxonomic groups or superordinate (abstract) categories. Concrete categories included members of the same species, while intermediate categories included members of the same family or order, and the most abstract category included animals rather than nonanimals. Abstraction was defined based on the degree of perceptual dissimilarity between members of the same category. For instance, many animals share few features in common (e.g. worms, elephants, killer whales), whereas there is greater featural overlap between bird and primate categories (intermediate), and especially between gorilla and kingfisher categories (concrete). Roberts & Mazmanian (1988) found that pigeons and monkeys encountered the most difficulty with an intermediate level of abstraction, which roughly corresponds to the basic level categories that human children presumably acquire first (Rosch et al. 1976). That is, despite the prediction that animals would encounter the greatest difficulty at the most abstract level, both pigeons and squirrel monkeys could learn to categorize animals and nonanimals accurately at the most abstract level, but failed to acquire the bird versus nonbird discrimination at the intermediate level of discrimination even with additional training (Roberts & Mazmanian 1988). Although a gorilla, Gorilla gorilla gorilla, subject also encountered some difficulty with this level of abstraction (Vonk & MacDonald 2002), orang-utans, Pongo abelii, interestingly performed well with this task, acquiring the discrimination quickly and showing abovechance transfer immediately (Vonk & MacDonald 2004). However, too few individuals of each species have been tested on these tasks to begin to speculate about species differences. Members of both species of ape showed positive transfer to novel images on the most abstract problems. However, chimpanzees, Pan troglodytes, tested more recently showed no transfer on the more abstract problems (J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data).

Here, we presented three American black bears with several concept discrimination tasks that ranged along a continuum of abstraction. Whereas discriminations at the concrete level can be made on the basis of shared perceptual features, undermining the conclusion that transfer performance is indicative of true concept formation, the same argument cannot be levied at discriminations made at the more abstract level. If an organism shows transfer at the concrete level only, it is likely that it relies on perceptual similarity between novel exemplars and training exemplars, rather than knowledge of an overarching concept. However, if organisms show transfer to novel stimuli that share few features with training stimuli, as with the more abstract problems, there is good evidence for concept formation. The bears demonstrated concept formation even at the most abstract level, performing similarly to great apes tested in this paradigm in terms of transfer performance (Vonk & MacDonald 2002, 2004). Although Bacon (1980) and Burghardt (1975) explicitly compared the learning capacity of black bears to that of great apes almost four decades ago, researchers have failed to make explicit comparisons across identical tasks until now. These findings further challenge the idea that social living is the primary factor underlying the emergence of the capacity for abstraction (Jolly 1966; Humphrey 1976; Dunbar 2003). Large brain size may emerge as a result of a challenging physical environment and may lead to the ability for abstraction even for species that do not need to navigate complex social relationships on a daily basis.

Furthermore, our results suggest that, contrary to the typical strategy of over-training animals on perceptual categorization

tasks, presenting abstract discriminations before concrete U.S.A., which cons discriminations may facilitate conceptual learning. Here, the bear that began training with the most abstract problems outperformed spanned the front with a variable.

discriminations may facilitate conceptual learning. Here, the bear that began training with the most abstract problems outperformed the bears that began testing with more concrete or intermediate level discriminations. Although these conclusions are tentative, given the small sample size, they are consistent with evidence from previous work (Vonk 2002, 2003), in which apes performed at high levels on initial conceptual matching tasks in the absence of prior training on perceptual matching tasks.

METHODS

Subjects

Three captive adult American black bear siblings (one female and two males) were tested. The bears had participated in studies of cognitive dissonance (West et al. 2010) and spatial memory (Zamisch & Vonk, in press), but they had not previously been tested in a categorization task, or a study that involved making choices on a touchscreen computer. The research took place in an off-exhibit area of the bears' enclosure at the Mobile Zoo in Wilmer, AL, U.S.A., which consisted of two pens (3×2.4 m each) separated by heavy chain link fence, and a 1.2 m wide human access area that spanned the front of the two bear pens. Each pen had a doorway with a vertically sliding gate that allowed access to a pathway leading to the outdoor enclosure (Fig. 1). Testing of the animals complied with the Institutional Animal Care and Use Review Board of the University of Southern Mississippi (IACUC approval number 06091401), and the zoo was compliant with U.S. Department of Agriculture regulations. There were no expected adverse effects of the research. In fact, the study provided a form of enrichment for the bears and they participated voluntarily.

Materials

The experimental apparatus consisted of a durable Panasonic Toughbook Laptop Computer and a 19-inch Vartech Armorall Capacitative Touchscreen Monitor welded to the front of a rolling computer cart. Experiments were programmed using RealBasic 2006 for Windows. Stimuli consisted of two-dimensional photographs approximately 400×600 pixels downloaded from www. fotosearch.com and edited using Adobe Photoshop CS2.





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An incorrect response was followed by an unpleasant buzzer tone and a brief time-out 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 bears' regular zoo diet (fruits, vegetables) and special treats such as honey roasted peanuts, banana pellets, dried banana chips, yoghurt-covered raisins and wafer cookies. Food was presented by hand.

A description of the images used in each set of photographs is included in the Supplementary Material.

Procedure

Individual subjects were separated prior to testing but tested in the indoor area of their home cages. Subjects could move freely in their home cages throughout testing sessions. Thus, participation was entirely voluntary. The computer cart was pushed up against the interior mesh separating the human experimenter from the bear, allowing the bear access to the touchscreen monitor. One male, Brutus, had been trained to respond by touching the monitor with his nose, while the female, Bella, and the other male, Dusty, predominantly used their paws to touch the screen. The bears had been trained on a two-choice discrimination where they selected images of either supermodels or 'Planet of the Apes' characters until they reached a criterion of 80% correct on four consecutive trials without any guidance from the experimenter.

During testing, the experimenter was centred behind the computer cart observing the bears' responses on the laptop monitor, which was positioned directly behind the touchscreen monitor. The experimenter provided no cues and could not see the bear's face or paws during the trial. The experimenter presented the bear with a food reward, as described above, immediately following a correct response at a consistent location, which was signalled by the tone from the computer. Trials continued automatically until the end of a session. A record of the animals' responses was automatically stored by the computer in Excel format.

This experiment followed the same two-choice discrimination procedure used by Vonk & MacDonald (2002, 2004). All subjects were rewarded for selecting images belonging to particular categories and were not rewarded for selecting images not belonging to those categories. The concrete level involved selecting photographs of conspecifics (black bears) while not selecting photographs of humans. To test whether the bears could learn another concrete level discrimination where they were not simply biased towards choosing members of their own species, they were also presented with a discrimination in which they were reinforced for selecting images of polar bears but not reinforced for selecting images of bears of any other species, including bears that both belonged to the previously reinforced categories and those that looked more similar to black bears (e.g. grizzly bears, sun bears, Ursus malayanus, spectacled bears, Tremarctos ornatus). This test constituted the concrete/intermediate level discrimination, as the unrewarded (S-) category was more diverse in terms of its exemplars than the rewarded (S+) category. As in the prior studies, at an intermediate/ abstract level of abstraction, animals were reinforced for selecting photographs of their own taxonomic groups (e.g. carnivores) but not for selecting photographs of animals from other taxonomic groups (a range of birds, reptiles, fish, insects, cetaceans, primates, rodents, etc.). To equate the level of abstraction of both the S+ and S- categories, the bears were also presented with an intermediate level discrimination between primates and hoofstock in which both S+ and S- categories were equally cohesive and intermediate in their level of abstraction. At the most abstract level, animals were rewarded for selecting photographs of animals versus nonanimals.

Figure 2 depicts examples of images used at each level of abstraction. As in previous studies (Roberts & Mazmanian 1988; Vonk & MacDonald 2002, 2004), abstraction was defined by the level of perceptual overlap between exemplars within a category, with more abstract categories containing exemplars with little perceptual overlap.

Each session involved 20 trials, such that there were 40 images used in each set of photographs for each discrimination; 20 S+ and 20 S- images. There were three sets of images used for each level of discrimination, except for the concrete/intermediate level, which involved four sets of images. Care was taken to select images that were visually distinct within each of the category levels. For example, the bear images included both young and old bears and close up and distant images, as well as images that showed only the faces of bears as well as the entire bodies. Within the carnivore images, there was a mixture of canines, felines, bears, hyaenas, and so forth, to create a diverse group of images and species within that category. The same



Black bear vs human

Mixed bear vs polar bear

Primate vs hoofstock

Carnivore vs noncarnivore

Animal vs nonanimal

Figure 2. Examples of stimuli presented during discrimination tasks.

was true for all other image sets. Some sets of photographs included groups or pairs of animals, rather than just individuals.

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. There was a time-out procedure for incorrect responses, with time-outs up to 5 s. Intertrial intervals (ITIs) and number of sessions presented on a given day varied as a function of the subject's attention to the task, but ITIs were typically less than a few seconds. If the bear 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 bear waited for the experimenter to offer a food reward before responding on the next trial. To ensure that the subject did not simply initiate a response without viewing the images, the subject had to wait 750 ms after presentation of the next trial images before it could respond. Subjects received 4-16 sessions on a given test day and were tested 2–3 days per week over a period of several years, with 1-year break between Brutus' testing sessions while the bears were moved to a novel enclosure. Brutus was working on the second set of animal/nonanimal images (abstract discrimination) during the time of the move. Subjects continued to work with a particular stimulus set until a criterion of 80% correct or more on a session was achieved for four consecutive sessions, or 90% correct or more was reached on two consecutive sessions. At that time, a novel stimulus set of all new photographs 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. When the bears completed the final set of images within a particular discrimination, they moved on to the next discrimination.

The bears were presented with the tasks in different orders in an attempt to control for (and test the influence of) order effects. Dusty began with the most abstract level discriminations and worked his way systematically to the most concrete level discriminations. Brutus was tested in the following order: concrete, concrete/intermediate, abstract, intermediate/abstract, intermediate. Bella was tested in the following order: intermediate/abstract, intermediate, concrete/intermediate, concrete, abstract. All of the bears received the same S+ and S- images within a set and the same order of stimulus sets within a discrimination except that, for the intermediate level discrimination, Brutus and Bella were reinforced for selecting images of primates and Dusty was reinforced for selecting images of hoofstock. The images within the control tests were adjusted accordingly.

The control tests were presented at the end of testing to determine whether the bears performed poorly on sets of images that contained a mixture of previously seen images from all prior discriminations (Mixed), or continued to perform at high levels. Thus, for each bear, 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 photographs at each level of discrimination. That is, the images included some black bears, some polar bears, some carnivores, either primates or hoofstock (depending on the subject) and some animals. The S- set contained images from the previous sets that had not been reinforced, such as humans, mixed bears, noncarnivores, primates or hoofstock and nonanimals. Because of the overlapping nature of the categories, some of the same species appeared in both S– and S+ sets, making it difficult to make the discrimination on the basis of categories. However, if the bears had simply memorized which photographs had been correct or incorrect previously, they would be expected to do well at this task initially. If the animals were using coherent categories, rather than memory for specific images to perform the tasks, one might expect a decrement in performance when the mixed images were first presented.

As a further test of this hypothesis, a set of images was also composed that contained novel images belonging to the same categories that had been previously reinforced (Random S+). That is, images were used that depicted animals from the same categories as those previously reinforced, that is, black bears, polar bears, carnivores, either primates or hoofstock (depending on the subject) and animals (for the S+ set), and the opposite categories included humans, mixed bears, hoofstock or carnivores and nonanimals (for the S- set). However, none of the images had been presented previously, so the animals had no reinforcement history with the specific photographs used in this task. If the bears use memory for specific images, rather than category membership, to dictate choices, then they should have performed randomly on the first presentation of this set of images. As with the mixed test, because of the overlapping categories, members of the same category could be included in both S+ and S- sets. For example, primates could belong to both the S+ an S- set because primates belonged to both the primate category and the noncarnivore category. Some species could belong to an S- category but be included as S+ because they were animals. Therefore, even if the bears memorized which categories, rather than which images, were 'correct', it would be difficult for them to perform above chance on this discrimination initially.

RESULTS

We examined the data at the individual level, given the individual differences in performance that we observed, which may have been partially a function of the different test orders. At each level of discrimination, each bear's individual performance on only the very first session (20 trials) with novel photographs was compared to chance using two-tailed binomial tests. In addition, we calculated the number of sessions taken to reach criterion with each set of photographs (Table 1).

If the animal has acquired a concept, one expects to see abovechance levels of performance at first, second and third transfer (sets 2, 3 and 4) 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 prior preference for images belonging to that category and would not speak to acquisition of a learned category. In other words, the bears should not know a priori, without feedback, which categories are 'correct' without experience at the task, even if they come to the table with the ability to discriminate the categories. One should also see that the sessions required to reach criterion should decrease with each set of photographs depicting the same category discrimination, if the subject has indeed acquired the concept being tested.

Concrete Level: Bears versus Humans

There was considerable variance in how many sessions were required to acquire the concrete level of discrimination between black bears and humans (Table 1, Fig. 3). Binomial tests revealed that only Brutus showed positive transfer on the first, but not the second, set of transfer photographs. However, both Dusty and Bella responded at 70% correct on the first transfer test. Therefore, all three bears performed well on this task.

Concrete/Intermediate Level: Polar Bears versus Mixed Bears

The bears encountered greater difficulty in selecting images of polar bears over a mixture of other bear species. This was

 Table 1

 Percentage correct on the first session of each set of photographs, arranged by discrimination task, for each bear

Task	Brutus			Bella			Dusty			
		%	Р	Sessions	%	Р	Sessions	%	Р	Sessions
Concrete	1	60	0.50	39	65	0.26	22	40	0.50	12
	2	75	0.04	12	70	0.12	9	70	0.12	6
	3	60	0.50	12	65	0.26	27	70	0.12	6
C/Int	1	40	0.50	45	40	0.50	33	35	0.26	20
	2	50	1.0	24	55	0.82	8	65	0.26	13
	3	50	1.0	25	90	0.001	28	75	0. 04	9
	4	75	0.04	18	80	0.01	7	80	0.01	8
Int	1	55	0.82	35	70	0.12	21	20	0.01	28
	2	65	0.26	26	75	0.04	15	70	0.12	6
	3	80	0.01	4	75	0.04	15	75	0.04	14
Int/A	1	40	0.50	18	50	1.0	30	70	0.12	28
	2	80	0.01	10	70	0.12	38	85	0.003	9
	3	60	0.50	27	75	0.04	49	65	0.26	62
Abstract	1	50	1.0	35	40	0.50	22	70	0.12	12
	2	45	0.82	61	65	0.26	36	65	0.26	23
	3	55	0.82	17	80	0.01	27	90	0.001	10
Mixed		65	0.26	21	75	0.04	3	95	<0.001	2
Random		60	0.50	42	40	0.50	36	70	0.12	45

C: concrete; Int: intermediate; A: abstract. *P* values are given for binomial tests comparing performance (number of trials correct out of 20, first session only) to chance (50%) and number of sessions to reach criterion. Significant values are shown in bold.

understandable given that the S– category at the concrete/intermediate level was visually more disparate than the S– category at the concrete level. Bella and Dusty were tested on this level before the most concrete level, but for Brutus, this may have been difficult because the S– category was more similar to the S+ category he had previously encountered. That is, the 'mixed bear' category included images of other dark brown and black coloured bears, similar in colour to the black bear exemplars, while the 'polar bears' differed in colour from the previously reinforced exemplars. However, by the third transfer session, all three bears immediately chose images of the polar bears at above-chance levels (Fig. 4). The first photograph set appeared to be quite difficult as it contained a high proportion of polar bears that were quite distant, so a fourth set was created. Brutus was initially tested on the three other sets, then transferred back to the initial set that presented him with so much difficulty. He then scored 90% correct, demonstrating that he had now acquired the correct concept of polar bear (or learned which features were relevant). Brutus' performance was above chance on only the final transfer set, while Dusty and Bella were above chance with the final two sets of transfer.

Intermediate Level: Hoofstock versus Primates

Brutus and Bella performed much better on the second transfer session relative to the first (Fig. 5). Given the perceptual variability between exemplars within both the S+ and S- sets, it is impressive that the bears performed well on this discrimination. Brutus' performance was above chance with the second transfer set, while Dusty and Bella were above chance with the final transfer sets. Bella transferred above chance on both transfer sets. Dusty was also above chance with the very first session of the first set as well. Although this pattern might reflect a prior bias for choosing hoofstock, the number of sessions required to reach criterion on the training photographs argues against this conclusion.

Intermediate/Abstract Level: Carnivores versus Noncarnivores

Performance on the intermediate/abstract discrimination was variable (Fig. 6). Dusty did well on the first transfer test (80% correct). However, he performed worse on the second transfer set (62.5% correct). Brutus also performed better with the first set of transfer photographs, while Bella improved across sets. Brutus and Dusty showed positive transfer with the first transfer set, but not with the second, while Bella was above chance with the second transfer set. This was expected to be a difficult discrimination given that both S+ and S- sets included exemplars that were perceptually variable, with the S- set containing an even greater degree of variability between exemplars within the set, as it represented the absence of a coherent category. This difficulty was demonstrated by the finding that sessions to criterion did not diminish with subsequent sets, as they did in the more concrete level discriminations.



Figure 3. Percentage correct averaged across four session blocks by subject, grouped by training set (solid lines), transfer 1 and transfer 2 (dotted lines), for the concrete level of discrimination between black bears and humans.

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Figure 4. Percentage correct averaged across four session blocks by subject, grouped by training set (solid lines), transfer 1, 2 and 3 (dashed lines), for the concrete/intermediate level of discrimination between polar bears and mixed bears.

Abstract Level: Animals versus Nonanimals

Dusty scored 90% correct on his first session with the second transfer set, averaging 81.25% in the first block of four sessions. Dusty also required only 12 sessions to acquire the discrimination, even though he was presented with this, presumably, most difficult discrimination first (see Fig. 7). Bella averaged 73.75% on her first block of four sessions with the second transfer set. Both Bella and Dusty were above chance with the second transfer set, although Brutus was not above chance with either of the transfer sets. Brutus had more than a year-long interruption in testing with images on the first transfer set, which most likely affected his performance on

this discrimination. Table 2 indicates the time period of testing for all of the bears on all of the tasks.

Control Tests

Mixed

When presented with sets of images that were randomly chosen from the previous discriminations such that a set of 20 S_+ and 20 S_- images included images from the concrete, intermediate and abstract discriminations mixed together and randomly paired on each trial within a session, the bears responded as if the items belonged to a coherent set. That is, with the exception of Brutus,



Figure 5. Percentage correct averaged across four session blocks by subject, grouped by training set (solid lines), transfer 1 and transfer 2 (dashed lines), for the intermediate level of discrimination between hoofstock and primates.

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Figure 6. Percentage correct averaged across four session blocks by subject, grouped by training set (solid lines), transfer 1 and transfer 2 (dashed lines), for the intermediate/ abstract level of discrimination between carnivores and noncarnivores.

they immediately chose the S+ images at above-chance levels (Fig. 8). Both Dusty and Bella were above chance on the first session, while Brutus was not. These results can best be explained if the bears were memorizing the correctness or incorrectness of the individual images independent of their category membership and simply learning to select or not select images on the basis of prior reinforcement. Brutus's lower level of responding on the mixed control test can be explained by the fact that he received the control test 2 years and 2 months after beginning testing such that it may have been 2 years or more since he had been tested on some of the images included in this discrimination (see Table 2).

In addition, at the end of the mixed control test, we presented Brutus with the discriminations that he had learned earlier (one session with one set of photographs at each level of abstraction) as a further attempt to assess his memory for the prior tasks. We found that he was above chance on the concrete task, despite the long gap in testing (80% correct; binomial test: P < 0.01). He was not above chance on the concrete/intermediate task (65% correct; P = 0.13). He was above chance on both the intermediate and intermediate/abstract tasks (80% and 75% correct; P = 0.001 and 0.02, respectively), but not on the most abstract task, which he had never acquired (55% correct; P = 0.41). These findings suggest an



Figure 7. Percentage correct averaged across four session blocks by subject, grouped by training set (solid lines), transfer 1 and transfer 2 (dashed lines), for the abstract level of discrimination between animals and nonanimals.

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 Table 2

 Schedule of testing for each task for each subject throughout the experiment

Task	Set	Brutus		Bella		Dusty	
		Beginning	End	Beginning	End	Beginning	End
Concrete	1	12 Feb 2008	27 Feb 2008	21 Nov 2010	28 Nov 2010	4 Jun 2010	4 Jun 2010
	2	29 Feb	2 Mar	28 Nov	5 Dec	4 Jun 2010	9 Jun 2010
	3	2 Mar	9 Mar	5 Dec	15 Dec	9 Jun	9 Jun
C/Int	1	2008 4 Mar	2008 6 Apr	2010 24 Oct	2010 7 Nov	2010 12 May	2010 17 May
		2008 16 May	2008 16 May	2010	2010	2010	2010
	2	2008 8 Apr	2008 25 Apr	7 Nov	11 Nov	17 May	19 May
	3	2008 27 Apr	2008 6 May	2010 11 Nov	2010 19 Nov	2010 19 May	2010 2 Jun
	4	2008 6 May	2008 16 May	2010 19 Nov	2010 19 Nov	2010 2 Jun	2010 2 Jun
Int	1	2008 15 Feb	2008 26 Feb	2010 3 Oct	2010 10 Oct	2010 21 Apr	2010 7 May
	2	2010 26 Feb	2010 12 Mar	2010 10 Oct	2010	2010 7 May	2010 7 May
	2	2010	2010	2010	2010	2010	2010
	3	12 Mar 2010	12 Mar 2010	18 Oct 2010	24 Oct 2010	7 May 2010	10 May 2010
Int/A	1	11 Dec 2009	20 Jan 2010	10 Aug 2010	26 Aug 2010	5 Apr 2010	14 Apr 2010
	2	20 Jan 2010	22 Jan 2010	26 Aug 2010	9 Sep 2010	14 Apr 2010	16 Apr 2010
	3	22 Jan 2010	17 Feb 2010	9 Sep 2010	1 Oct 2010	16 Apr 2010	28 Apr 2010
Abstract	1	1 Apr	17 Apr	2 Jan 2 Jan	7 Jan	19 Mar	22 Mar
	2	17 Apr	18 May	7 Jan	2011 28 Jan	2010 22 Mar	2 Apr
		2008 16 Nov	2008 26 Nov	2011	2011	2010	2010
	3	2009 26 Nov	2009 11 Dec	28 Jan	9 Feb	2 Apr	5 Apr
Mixed		2009 5 Apr	2009 14 Apr	2011 13 Feb	2011 13 Feb	2010 11 Jun	2010 11 Jun
Random		2010 16 Apr 2010	2010 26 Apr 2010	2011 13 Feb 2011	2011 27 Mar 2011	2010 11 Jun 2010	2010 30 Jun 2010

C: concrete; Int: intermediate; A: abstract. *P* values are given for binomial tests comparing performance (number of trials correct out of 20, first session only) to chance (50%) and number of sessions to reach criterion. Significant values are shown in bold.



Figure 8. Sessions taken to reach criterion of 80% correct across four consecutive sessions or 90% correct across two consecutive sessions on the mixed and random control tests, by subject.

impressive long-term memory for stimuli and their reinforcement history, consistent with the findings from giant pandas that retained memory for simple visual discriminations 1 year after testing (Dungl et al. 2008), and with findings from pigeons that have been shown to remember the reinforcement history of hundreds of images after long retention intervals (Vaughan & Greene 1984; Cook et al. 2005).

Random

To confirm whether Bella and Dusty, at least, were relying on memory, to some degree, to solve the mixed control test, we presented the bears with a set of mixed but novel images (i.e. images that they had not seen before) that contained stimuli from each of the categories tested in the previous discriminations. This task should have been difficult, but not impossible, for the bears to perform by recalling the concepts that had been previously reinforced, but it would have been impossible for them to perform on the basis of memory for prior stimuli. Bella and Brutus were at chance levels initially with this task and required 28-45 sessions to reach criterion. Although Dusty's performance on the first session was at 70%, it was not above chance (P = 0.12), and his performance declined after the first session, Furthermore, he required 45 sessions to meet criterion on this task (Fig. 8). This result suggests that memory for particular images was a factor that contributed to performance on some of the other discriminations. However, the fact that the bears required more sessions to reach criterion on a random mix of images relative to sets of images that belonged to coherent categories is further evidence suggesting that they were indeed forming categories with the previously presented discriminations.

DISCUSSION

Like other species tested previously, bears appear to have the capacity to form general categories at even relatively abstract levels when there is not a significant overlap of perceptual features among members of a category. Although memory was clearly a factor and may have been used initially to reach criterion on the training sets, given that individuals did not always show clear transfer on the first opportunity to demonstrate it, it cannot be the sole explanation for the relatively high levels of performance in these tasks. It is clear that the bears eventually acquired concepts for the discriminations presented to them as they often achieved greater than 70% accuracy with completely novel images belonging to the same categories, sometimes with the first transfer set, but often with the second transfer set of images (see Table 1). It is unlikely that this performance was obtained through generalization of perceptual features from specific images that were reinforced from the training set of photographs on the more abstract category discriminations as the images used in each set were so unique. For instance, images used in the abstract category set 'animal' may have included a frog, turtle, parrot, whale, horse, siamang, Persian cat and wolf in training and then included a snake, salamander, owl, sea otter, cow, fox, panda and cockroach in the second set of (transfer) images (see Supplementary Material). This is also somewhat true for the intermediate level discriminations such as carnivore/noncarnivore, and there was also a high degree of transfer on this task. There were fewer images across photograph sets that were similar and that would have allowed transfer on the basis of perceptual features alone as the discriminations became more abstract. Even when the same species appeared in training and transfer sets, the individual pictures were unique in orientation, size of the animal, and so forth. However, if the bears generalized from photographs depicting the same or similar species as in previously learned sets, it may have contributed to transfer

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performance. The bears showed similar levels of acquisition and transfer across levels of abstraction.

One finding that is striking is that some of the bears were able to learn the abstract discriminations in fewer sessions than they learned the more concrete level discriminations. This finding is important because abstract level discriminations cannot be made on the basis of attending to perceptual features such as body size, hair colour, or the presence of features like wings. This finding contrasts with that found in apes (gorillas and orang-utans: Vonk & MacDonald 2002, 2004; chimpanzees: J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data), but is somewhat consistent with the findings of Roberts & Mazmanian (1988), who found that pigeons and squirrel monkeys could eventually learn the most abstract discrimination but not an intermediate level discrimination. In addition, some of the bears learned rapidly and showed positive transfer with intermediate level discrimination, which were also learned rapidly by orang-utan subjects (Vonk & MacDonald 2004), but not by a gorilla (Vonk & MacDonald 2002). Intermediate-level concepts correspond to the basic-level concepts acquired first by young human children (Rosch et al. 1976). In showing that bears are able to form concepts that cannot be acquired solely on the basis of readily perceivable perceptual features, we have demonstrated the capacity for abstract representation, which has not previously been determined for this species, or for other species in this order.

Although the bears, on average, required more trials to reach criterion than did a gorilla and orang-utans tested previously (Vonk & MacDonald 2002, 2004), they acquired the discriminations more rapidly than chimpanzees tested on the exact same discriminations with the exact same procedure (J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data). While the bears on average required 22-33 sessions to reach criterion on the training sets across the different tasks, the chimpanzees required, on average, 35–75 sessions to reach the same criterion. While the orang-utans and the gorilla received 10 trials within a session (thus fewer sessions to criterion also means many fewer trials to criterion), the bears and chimpanzees received 20-trial sessions. Also of note is the fact that the orang-utans and the gorilla were required to meet a criterion of only two consecutive sessions at 80% (8/10 correct choices) before moving on to a novel set of images, while the bears and chimpanzees were required to meet a more stringent criterion of four consecutive sessions at 80% correct (16/20), or an average of 87.5% correct across four consecutive sessions, or 90% correct for two consecutive sessions. Had the less stringent criterion been adopted here as well, both bears and chimpanzees would have required fewer sessions to reach criterion. However, it is possible that differences in the procedures resulted in better opportunity to acquire and generalize the concepts being tested for the bears and chimpanzees. Indeed, changes from the original procedure were implemented in order to be more certain of concept acquisition prior to presenting transfer, and to increase the likelihood of forming a generalizable concept. All species were tested on a similar schedule receiving 4–16 sessions per day, 2 or 3 days per week over a period of several years. On the critical measure of concept transfer, the bears' performance once criteria had been established was comparable to that of the apes at each level of abstraction. Although there were differences in training that may have affected acquisition of the concepts between (1) the orangutans and the gorilla and (2) the bears and the chimpanzees, it is less likely that such differences affected generalization of the concepts. That these bears showed transfer comparable to apes tested previously (Vonk & MacDonald 2002, 2004; J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data) suggests that phylogenetic relatedness to humans and group living are not the only routes to the capacity for abstraction. Of course, other factors, such as physically challenging environments, most likely play a role in

complex cognition (Milton 1981, 1988; Emery & Clayton 2004), but few nonsocial species have been tested in comparable tasks to evaluate these hypotheses.

Although some might consider orang-utans to be a nonsocial species, it is widely believed that orang-utans, particularly adult males, live relatively solitary existences primarily as a function of the need for large territories, given patchily distributed resources (Galdikas 1985; Weiss et al. 2006). However, juveniles often form small groups for several years following their lengthy weaning period, and females form dominance hierarchies at feeding sites in the wild (Mitani et al. 1991; van Schaik 1999). Orang-utans, along with other primates, have evolved from group-living ancestors. Thus, it is not technically correct to assume that orang-utans are adapted to a nonsocial lifestyle (Singleton & van Schaik 2002). Their behaviour in captivity is also quite consistent with that of other primates that live in larger social groups in nature (Maple 1980). Thus, orang-utans should not be considered nonsocial, relative to bears. Furthermore, generous attention has been devoted to the cognitive abilities of carnivores in recent years, with competing hypotheses about sociality and domestication factoring into the evolution of their social cognitive skills (Miklósi & Topál 2004; Hare 2007; Kubinyi et al. 2007). Nonsocial carnivores, such as bears and large cats, have been severely understudied in comparison. This study is one of the first attempts to fill that gap.

In addition, the current findings hint at an important methodological insight. Traditionally, experimenters train nonhuman subjects to perform category and concept tasks by having them attend to stimuli in which perceptual similarities and differences are emphasized. For instance, before learning conceptual match-tosample tasks, animals are trained on identity matching, where they are required to match stimuli that are exactly the same as the sample. In one notable exception, orang-utans and one gorilla matched stimuli on the basis of first- and second-order relations when they had never been trained on identity matching, and these subjects performed at unusually high levels (Vonk 2003). In the current study, one of the bears (Dusty) was presented the most abstract discriminations first. This was the only subject who performed at 80% correct on transfer on this discrimination. This subject also performed well on the intermediate/abstract discrimination, which he received second, even though this was considered the next most difficult task, in terms of the breadth of stimuli within the categories. The bear that was trained first on the most concretelevel discriminations (Brutus) tended to have lower scores on many of the tasks. One might expect that presenting the most abstract category first would have presented problems as performance on the last task would be facilitated by practice or testing effects. However, this was not the case, as subjects did not tend to perform the best on the tasks that they were presented with last. If one reviews the number of sessions required to reach criterion on the training set at each level of abstraction with regards to order of testing, rather than abstraction, no clear patterns emerge. That is, order effects specifically, without regard to the nature of the task, do not account for performance, at least with regard to acquisition of criterion. One can see from Table 1 that Dusty required the same number of sessions to reach criterion on the first task he completed (abstract) as with the last set (concrete). Bella required as few sessions with her second task (intermediate) as she did with her last two tasks (concrete and abstract), and Brutus performed about the same on all tasks (first task: concrete; middle task: abstract; last task: intermediate). Therefore, one cannot conclude that the bears performed more poorly with later tasks because of proactive interference, or that they performed better with later tasks because of 'learning to learn'. The bears appeared to acquire discriminations at concrete, intermediate and abstract levels with equivalent amounts of exposure. Of course, with such a small sample size, the

conclusions we can draw from this study are tentative, but the results are intriguing and challenge us to reconsider a long history of experimental procedures. It is possible that by overtraining animals to attend to perceptual similarities (and reinforcing them for responding in this manner), we hinder them from seeing and responding to conceptual relationships between stimuli that do not share perceptual features in common.

An alternative is that the different results are due to individual differences, rather than to testing order. These alternative hypotheses are difficult to tease apart empirically. A larger sample size of subjects tested in a similar manner will be needed to distinguish between these possibilities. Although one might be tempted to conclude that Dusty's superior performance at the more abstract levels was due to superior ability rather than to test order, Dusty's performance was not superior to that of the other bears in all cognitive tests. For instance, Brutus outperformed both other bears in a test of quantity estimation (Vonk & Beran 2012), and Bella outperformed both male bears in tests of spatial memory (Zamisch & Vonk, in press). Of course it is possible that individuals vary in abilities across tasks, which is an interesting topic of study for future research (see also Vonk & Povinelli 2011). However, without more data on the performance of these and other bears, discussion of individual differences is somewhat subjective. Much further work is needed in the area of comparative psychology, as the topic of individual differences has been woefully neglected in comparative psychology until recently, despite its central importance in studies with small sample sizes (see also Vonk & Povinelli 2011) and in studies of behavioural ecology.

The current study also paves the way in demonstrating the utility of training bears to work on a touchscreen, which allows for the presentation of various tests such as match-to-sample tasks that are staple tasks in comparative psychology. Along with Vonk & Beran's (2012) study of quantitative ability, the current study provides the first demonstration of use of common techniques with previously neglected nonlaboratory species, to gain a fuller picture of the evolution of cognitive capabilities in both closely and distantly related species.

Conclusions

Based on the social intelligence/Machiavellian intelligence hypothesis (Jolly 1966; Humphrey 1976; Dunbar 2003), one would predict less cognitive complexity for species that did not evolve with sociality as a selective pressure. Although there is experimental evidence for complex cognition in various nonsocial species from various taxa, few such species have been tested in analogous paradigms alongside more social species. Here, black bears were tested in a paradigm that has been used to test the degree of abstraction in concept formation in three great ape species (chimpanzees: J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data; gorilla and orang-utans: Vonk & MacDonald 2002, 2004) and found to show similar levels of transfer. This is the first demonstration of concept formation at concrete, intermediate and abstract levels in a previously untested species, American black bears. Furthermore, more generally, there is a long-standing tradition in comparative psychology when training animals on concept or categorization tasks to first train them to attend to perceptual details. While preliminary, based on small sample sizes, the current findings hint that researchers should review standard practices for training on such tasks.

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Supplementary Material

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References

- Abramson, J. Z., Hernández-Lloreda, V., Call, J. & Colmenares, F. 2011. Relative quantity judgments in South American sea lions (*Otaria flavescens*). Animal Cognition, 14, 695–706, http://dx.doi.org/10.1007/s10071-011-0404-7.
 Bacon, E. S. 1980. Curiosity in the American black bear. Ursu, 4, 153–157.
- Bacon, E. S. & Burghardt, G. M. 1976a. Ingestive behaviors of the American black bear. Ursus, 3, 13–25.
- Bacon, E. S. & Burghardt, G. M. 1976b. Learning and color discrimination in the American black bear. Ursus, 3, 27–36.
- Bacon, E. S. & Burghardt, G. M. 1983. Food preferences in the American black bear: an experimental approach. Ursus, 5, 102–105.
- 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*, **120**, 38–47, http://dx.doi.org/10.1037/0735-7036.120.1.38.
- Bshary, R. & Grutter, A. S. 2006. Image scoring and cooperation in a cleaner fish, mutualism. Nature, 441, 975–978, http://dx.doi.org/10.1038/nature04755.
- 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.
- Burghardt, G. M. 1992. Human-bear bonding in research on black bear behavior. In: The Inevitable Bond (Ed. by H. Davis & D. Balfour), pp. 365–382. Cambridge: Cambridge University Press.
- Cook, R. G., Levison, D. G., Gillett, S. R. & Blaisdell, A. P. 2005. Capacity and limits of associative memory in pigeons. Psychonomic Bulletin & Review, 12, 350–358.
- Cools, A. K. A., Van Hout, A. J.-M. & Nelissen, M. H. J. 2008. Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanisms in dos rival those of higher primates? *Ethology*, **114**, 53–63, http:// dx.doi.org/10.1111/j.1439-0310.2007.01443.x.
- Emery, N. J. & Clayton, N. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, **306**, 1903–1907.
- Dunbar, R. I. M. 2003. The social brain: mind, language and society in evolutionary perspective. Annual Review of Anthropology, 32, 163–181.
- 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, http://dx.doi.org/10.1037/0735-7036.122.4.335.
- Fize, D., Cauchoix, M. & Fabre-Thorpe, M. 2011. Humans and monkeys share visual representations. Proceedings of the National Academy of Sciences, U.S.A., 108, 7635–7640, http://dx.doi.org/10.1073/pnas.1016213108.
- Galdikas, B. M. F. 1985. Adult male sociality and reproductive tactics among orangutans at Tanjung Putting. *Folia Primatologica*, **45**, 9–24.
- Gittleman, J. L. 1986. Carnivore brain size, behavioral ecology, and phylogeny. Journal of Mammalogy, 67, 23–36.
- Hall, N. J., Udell, M. A. R., Dorey, N. R., Walsh, A. L. & Wynne, Clive D. L. 2011. Megachiropteran bats (*Pteropus*) utilize human referential stimuli to locate hidden food. *Journal of Comparative Psychology*, **125**, 341–346, http://dx.doi.org/ 10.1037/a0023680.
- Hare, B. 2007. From nonhuman to human mind: what changed and why? Current Directions in Psychological Science, 16, 60–64.
- Hare, B., Brown, M., Williamson, C. & Tomasello, M. 2002. The domestication of social cognition in dogs. *Science*, 298, 1634–1636.
- Hare, B. & Tomasello, M. 2005. Human-like social skills in dogs? Trends in Cognitive Sciences, 9, 439–444.
- Humphrey, N. K. 1976. The social function of intellect. In: In Growing Points in Ethology (Ed. by P. P. G. Bateson & R. A. Hinde), pp. 303–317. Cambridge: Cambridge University Press.
- Hvorecny, L. M., Grudowski, J. L., Blakeslee, C. J., Simmons, T. L., Roy, P. R., Brooks, J. A., Hanner, R. M., Beigel, M. E., Karson, M. A., Nicols, R. H., et al. 2007. Octopuses (Octopus bimaculoides) and cuttlefishes (Sepia pharaonis, S. officinalis) can conditionally discriminate. Animal Cognition, 10, 449–459, http://dx.doi.org/10.1007/s10071-007-0085-4.
- Jolly, A. 1966. Lemur social behaviour and primate intelligence. *Science*, **153**, 501–506. Kelling, A. S., Synder, R. J., Marr, M. J., Bloomsmith, M. A., Gardner, W. & Maple, T. L. 2006. Color vision in the panda (*Ailuropoda melanoleuca*). *Learning* & Behavior, **34**, 154–161.
- Kubinyi, E., Virányi, Z. & Miklósi, A. 2007. Comparative social cognition: from wolf and dog to humans. Comparative Cognition & Behavior Review, 2, 26–46.

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Maple, T. L. 1980. Orangutan Behavior. New York: Van Nostrand Reinhold.

Miklósi, A. & Topál, J. 2004. Review comparative social cognition: what can dogs teach us? Animal Behaviour, 67, 995–1004.

- Milton, K. 1981. Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist*, 83, 534–548.
- Milton, K. 1988. Foraging behaviour and the evolution of primate intelligence. In: Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans (Ed. by Richard W. Byrne & Andrew Whiten), pp. 285–305. New York: Clarendon.
- Mitani, J. C., Grether, G. F., Rodman, P. S. & Priatna, D. 1991. Associations among wild orang-utans: sociality, passive aggregations or chance? *Animal Behaviour*, 42, 33–46, http://dx.doi.org/10.1016/S0003-3472(05)80603-7.
- Perdue, B. M., Snyder, R. J., Pratte, J., Marr, M. & Maple, T. L. 2009. Spatial memory recall in the giant panda (*Ailuropoda melanoleuca*). Journal of Comparative Psychology, **123**, 275–279, http://dx.doi.org/10.1037/a0016220.
- Perdue, B. M., Synder, 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.
- Range, F., Aust, U., Steurer, M. & Huber, L. 2008. Visual categorization of natural stimuli by domestic dogs (*Canis familiaris*). Animal Cognition, 11, 339–347.
- Reichmuth Kastak, C. & Schusterman, R. J. 2002. Long-term memory for concepts in a California sea lion (Zalophus californianus). Animal Cognition, 5, 225–232, http://dx.doi.org/10.1007/s10071-002-0153-8.
- Roberts, W. A. & Mazmanian, D. S. 1988. Concept learning at different levels of abstraction by pigeons, monkeys, and people. *Journal of Experimental Psychology: Animal Behavior Processes*, 14, 247–260.
- Rooijakkers, E. F., Kaminski, J. & Call, J. 2009. Comparing dogs and great apes in their ability to visually track object transpositions. *Animal Cognition*, 12, 789–796, http://dx.doi.org/10.1007/s10071-009-0238-8.
- Rosch, E., Mervis, C. B., Gray, W. D., Johnson, D. M. & Boyes-Braem, P. 1976. Basic objects in natural categories. *Cognitive Psychology*, 8, 382–439.
- Salwiczek, L. H. & Bshary, R. 2011. Cleaner wrasses keep track of the 'when' and 'what' in a foraging task. *Ethology*, **117**, 939–948, http://dx.doi.org/10.1111/ j.1439-0310.2011.01959.x.
- van Schaik, C. P. 1999. The socioecology of fission-fusion sociality in orangutans. *Primates*, **40**, 69–86, http://dx.doi.org/10.1007/BF02557703.
- Scheumann, M. & Call, J. 2004. The use of experimenter-given cues by South African fur seals (*Arctocephalus pusillus*). *Animal Cognition*, 7, 224–230, http:// dx.doi.org/10.1007/s10071-004-0216-0.
- Schusterman, R. J. & Reichmuth, C. 2008. Novel sound production through contingency learning in the Pacific walrus (Odobenus rosmarus divergens). Animal Cognition, 11, 319–327, http://dx.doi.org/10.1007/s10071-007-0120-5.
- Schusterman, R. J., Kastak, C. R. & Kastak, D. 2002. The cognitive sea lion: meaning and memory in the laboratory and in nature. In: *The Cognitive Sea Lion: Meaning and Memory in the Laboratory and in Nature* (Ed. by M. Bekoff, C. Allen & G. M. Burghardt), pp. 217–228. Cambridge, Massachusetts: MIT Press.
- Schusterman, R. J., Kastak, C. R. & Kastak, D. 2003. Equivalence classification as an approach to social knowledge: from sea lions to simians. In: Equivalence Classification as an Approach to Social Knowledge: from Sea Lions to Simians (Ed. by

F. B. M. de Waal & P. L. Tyack), pp. 179–206. Cambridge, Massachusetts: Harvard University Press.

- Seed, A., Emery, N. & Clayton, N. 2009. Intelligence in corvids and apes: a case of convergent evolution? *Ethology*, **115**, 401–420.
- Singleton, I. & van Schaik, C. P. 2002. The social organisation of a population of Sumatran orang-utans. Folia Primatologica, 73, 1–20.
- Tarou, L. R. 2003. An examination of the role of associative learning and spatial memory in foraging of two species of bear (family: Ursidae) (Ailuropoda melanoleuca, Tremarctos ornatus). Ph.D. thesis, Georgia Institute of Technology, Atlanta.
- Udell, M. A. R., Dorey, N. R. & Wynne, C. D. L. 2012. Inter species social learning in dogs: the inextricable roles of phylogeny and ontogeny. In: *Comparative Cognition* (Ed. by T. Zentall & E. Wasserman), pp. 819–831. 2nd edn. New York: Oxford University Press.
- Vaughan, W. & Greene, S. L. 1984. Pigeon visual memory capacity. Journal of Experimental Psychology: Animal Behavior Processes, 10, 256–271, http:// dx.doi.org/10.1037/0097-7403.10.2.256.
- 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. 2003. Gorilla (Gorilla gorilla gorilla) and orangutan (Pongo abelii) understanding of first and second order relations. Animal Cognition, 6, 77–86.
- Vonk, J. & Beran, M. J. 2012. Bears 'count' too: quantity estimation and comparison in black bears (Ursus americanus). Animal Behaviour, 84, 231–238.
- in black bears (Ursus americanus). Animal Behaviour, 84, 231–238.
 Vonk, J. & MacDonald, S. E. 2002. Natural concept formation in a juvenile gorilla (Gorilla gorilla gorilla) at 3 levels of abstraction. Journal of the Experimental Analysis of Behaviour, 78, 315–332.
- Vonk, J. & MacDonald, S. E. 2004. Levels of abstraction in orangutan (Pongo abelii) categorization. Journal of Comparative Psychology, 118, 3–13.
- Vonk, J. & Povinelli, D. J. 2011. Individual differences in long-term cognitive testing in a group of captive chimpanzees. *International Journal of Comparative Psychology*, 24, 137–167.
- Weiss, A., King, J. E. & Perkins, L. 2006. Personality and subjective well-being in orangutans (Pongo pygmaeus and Pongo abelii). Journal of Personality and Social Psychology, 90, 501–511, http://dx.doi.org/10.1037/0022-3514.90.3.501.
- West, S., Jett, S. E., Beckman, T. & Vonk, J. 2010. The phylogenetic roots of cognitive dissonance. Journal of Comparative Psychology, 124, 425–432.
- Wobber, V. & Hare, B. 2009. Testing the social dog hypothesis: are dogs also more skilled than chimpanzees in non-communicative social tasks? *Behavioural Processes*, 81, 423–428, http://dx.doi.org/10.1016/j.beproc.2009.04.003.
- Zakher, I. 1974. Sravnitel'naia prochnost' uslovnykh refleksov na otnositel'nye i absoliutnye priznaki razdrazhitelei u medvedei. (Comparative stability of conditioned reflexes to relative and absolute stimulus cues in bears.). Zhurnal Vysshey Nervnoi Deyatel'nosti I P Pavlova, 24, 252–259.
- Zamisch, V. & Vonk, J. In press. Spatial memory in captive American black bears (Ursus americanus). Journal of Comparative Psychology.
- Zentall, T. R., Wasserman, E. A., Lazareva, O. F., Thompson, R. R. & Rattermann, M. 2008. Concept learning in animals. *Comparative Cognition & Behavior Review*, 313, 35–45, http://dx.doi.org/10.3819/ccbr.2008.30002.