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Carnivore Concepts: Categorization in Carnivores "Bears" Further Study

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Although categorization abilities may serve as the foundation for most other complex cognitive processes, this topic has been relatively understudied in the order Carnivora compared to the extensive work on, for example, nonhuman primates. However, there is a growing number of studies examining the abilities of bears, felines, and canines to discriminate among stimuli that could represent conceptual categories. Thus far, results suggest that carnivores show comparable abilities to, for example: form natural categories, discriminate quantities, recognize cues of human emotion, and to discriminate kin. There is little existing work exploring concepts of sameness and relational reasoning in carnivores, and work on social concepts, such as representations of mental states, exist only in canines. Future studies are necessary to better understand the mechanisms underlying carnivores' categorization abilities and conceptual representations. Furthermore, future work should focus on differences in conceptual ability as a function of social lifestyle and dietary preferences within carnivores. Such studies will be helpful in understanding the evolutionary pressures responsible for conceptual processes in a variety of species, including humans.

Although comparative psychology has witnessed a recent explosion of research into canine cognition, other carnivore species have received much less attention. Recently, however, researchers have acknowledged that the study of carnivore cognition is important to the extent that it can inform hypotheses about the evolution of cognitive traits in species that vary in both sociality and dietary challenges. These factors have been deemed critical in hypotheses proposed to explain the evolution of advanced cognition. The Social Intelligence Hypothesis (Humphrey, 1976; Jolly, 1966) and the Technical Intelligence Hypothesis (Byrne, 1997), although not mutually exclusive, have been presented as competing ideas regarding the selective forces driving cognitive traits. The Social Intelligence Hypothesis emphasizes the challenges inflicted by maintaining cohesive social groups and tracking complex social relationships. The Technical Intelligence hypothesis focuses on the demands incurred by foraging over a large territory, tracking patchy food sources, and feeding on foods requiring extraction. More recently, the Cognitive Buffer Hypothesis (Sol, 2009), more generally emphasized the need for animals to adapt to fluctuating environments. However, formal tests of these ideas have often been limited to particular classes of animals, such as nonhuman primates (Byrne & Whiten, 1988) or birds (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Szekely, Liker, & Lefebvre, 2007). Carnivores, although they vary in all of the critical facets, have not been explored until recently with regard to these broad questions.

Benson-Amram and colleagues (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016) have conducted a large scale test of problem-solving, brain-size, and sociality in 39 carnivore species and found that brain size, but not social complexity, predicted success. These authors argued that the data supported the Cognitive Buffer hypothesis and emphasized the importance of behavioral innovation (Holekamp, Dantzer, Stricker, Yoshida, & Benson-Amram, 2015). However, the large scale study involved only a single problem-solving task, an extractive foraging task (Vonk, 2016). Thus, the study, the first of its kind regarding its comparative scope, opened the door for many potential follow-up programs of research to contrast different types of cognitive skills across a large number of species. This large-scale project nicely complements several (mostly) recent studies on bear cognition (Bacon, 1980; Bacon & Burghardt, 1976a, 1976b, 1983; Burghardt,

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1975, 1992; Dungl, Schratter, & Huber, 2008; Johnson-Ulrich et al., 2016; Keen et al., 2014; Perdue, 2016; Perdue, Snyder, Pratte, Marr, & Maple, 2009; Perdue, Synder, Zhihe, Marr, & Maple, 2011; Vonk & Beran, 2012; Vonk, Jett, & Mosteller, 2012; Vonk & Johnson-Ulrich, 2014; Vonk et al., 2015; Waroff, Fanucchi, Robbins & Nelson, 2017; West, Jett, Beckman, & Vonk, 2010; Zamisch & Vonk, 2012), and feline cognition (Bánszegi, Urrutia, Szenczi, & Hudson, 2016; Borrego & Dowling, 2016; Borrego & Gaines, 2016; Galvan & Vonk, 2016; Takagi et al., 2016.; for review see Vitale Shreve & Udell, 2015). Taken together, these studies will be critical in paving the way for future studies of carnivore cognition, as they represent an important shift away from focusing exclusively on canines.

In this review, we focus on studies of categorization and concept formation in the order Carnivora. Categorization is a fundamental cognitive building block, and whereas the ability to engage in this process should be widely shared in the animal kingdom, the extent to which concepts can be said to be abstract may be limited to species that evidence other forms of cognitive complexity. This complexity may arise as a result of facing challenges in the social or physical domain or both. Comparing the performance of various species on these tasks will be illuminating with regard to the influence of different selective pressures. By examining concepts across a variety of tasks and domains, we might determine which species excel in certain areas, or across areas, helping to support the idea of general intelligence (Burkart, Schubiger, & van Schaik, 2016) or modularity (Tooby & Cosmides, 1992), depending on the pattern of results. We will better be able to assess whether sociality confers benefits across all areas of cognition, or strictly within the social domain, and similarly whether foraging complexity confers benefits broadly or strictly with regard to physical cognition. We begin our view with a discussion of relatively simple categorical discriminations (e.g., those based on observable sensory or spatial cues) and work our way up to discussion of more cognitively complex conceptual discriminations, such as those involving abstract and relational concepts.

Basic Discriminatory Ability

Early assessments of animals' intellectual abilities involved the ability to engage in reversal learning (Hamilton & Brigman, 2015). With reversal learning tasks, animals learn a simple discrimination (e.g., choose the cup on the right) and, upon reaching a criterion level of performance, the contingencies are reversed such that they should now make the opposite choice (e.g., choose the cup on the left). Rapid acquisition of the novel contingency is a sign of learning flexibility. One of the early studies that compared a large number of carnivores on a spatial successive discrimination reversal found that only one species (cacomistle, *Bassariscus astutus*) performed comparably to previously tested black-faced capuchins (*Sapajus nigritus,* Gossette & Inman, 1966) with regard to a lower number of errors on reversal trials compared to the other carnivores tested; coati-mundis (*Nasua nasua*), kinkajous (*Potos flavu*s), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*; Gossette, Krause, & Speiss, 1968). Cacomistles are the smallest species within the *procyonidae* family, and it is possible that smaller species with larger relative brain size may show superior learning (Rensch, 1963). Shell and Riopelle (1958) tested four raccoons in a series of visual discrimination tasks involving reversals. Improvements over time (demonstration of learning sets) revealed that raccoons performed comparably to cats (Warren & Baron, 1956) but were inferior to monkeys (rhesus macaques, *Macaca mulatta*, Harlow, 1949; marmosets, *Callithrix*, Miles & Meyer, 1956; New World monkeys, *Platyrrhini*, Shell, 1955). However, with a larger sample of nine raccoons, Johnson and Michels (1958) found evidence for learning sets with regard to object size discrimination in raccoons that was superior to that of marmosets (Miles & Meyer, 1956) and cats (*Felis catus*, Warren & Baron, 1956), and approaching that of rhesus macaques (Harlow, 1949) and chimpanzees (*Pan troglodytes,* Hayes, Thompson, & Hayes, 1953). Furthermore, Warren and Warren (1959) found a raccoon to perform better than cats on a closed-field test involving reversals, but general task acquisition was comparable. However, at least one study demonstrated that cats performed better than monkeys on an ambivalent cue discrimination task where subjects were exposed to two different shapes (squares and rectangles) that varied in size (small, large) and also varied in terms of which cue (shape or size) was rewarded (Joshi & Warren, 1959). Doty, Jones, and Doty (1967) tested learning-set formation in mink, ferrets, skunks (*Mustelidae)*, and cats and found that all species showed learning but mink and ferrets showed the best interproblem learning – superior to that of some primates (e.g., marmosets). Skunks performed worse than ferrets but better than cats. Although the overall rate of learning was slower for mink compared to that previously found in rhesus macaques and chimpanzees, the curve of learning was similar. Overall, results suggest small differences between carnivore species, and generally lower performance on basic learning tasks compared to primates, but superior performance compared to rodents.

For example, raccoons have also been compared to rats and squirrels with regard to their discrimination performance. Both raccoons and squirrels (*Sciuridae*) can learn to use a single cue (e.g., sidedness, rotation, symmetry) to predict the location of food hidden under a food-well, but struggle when an additional cue is added (Hitchcock, Michels & Brown, 1963). Raccoons' performance showed more of a tendency to increase with the addition of a cue, compared to squirrels, but there were no significant species differences. Fields (1936) tested four raccoons in an apparatus with five choice points where raccoons were initially trained to approach a lit square. They were next trained to discriminate between geometric shapes (e.g., triangle versus square). Fields found the raccoons to perform better than rats (*Rattus*) previously tested in a similar paradigm (Fields, 1932). Raccoons showed varying success in performing discriminations based on the size or rotation of the geometric shapes, still outperforming rats.

There is relatively scant work on pinnipeds, although Schusterman (1966, 1967) tested Californian sea lions (*Zalophus californianus*) for reversal learning using size and shape as discriminative cues. In this study, the procedure was a bit more complex whereby the dimension signaling reward was gradually reversed, forcing attention shifts. Shifts did not always occur with the first trials, but occurred more gradually. Unfortunately, these particular tasks have not been presented to a wide number of species, limiting the basis for comparison. Results are also complicated by the tendency to compare overall error patterns across a number of tests, potentially masking species differences on individual trial types (Pollard, 1959, 1964). A general issue in comparative psychology is the tendency to focus on a single measure of performance, or the end result, rather than focusing on mechanisms used to solve tasks, which might more critically reveal species differences. Furthermore, species may be compared on a task involving a single modality without regard to species differences in proclivity to utilize particular sensory information.

Cats have been shown to learn discriminations involving brightness of stimuli much more quickly than they learn differences of patterns (Smith, 1935), although others have shown that they learn discriminations based on orientation and oblique angles within several days of training (Sutherland, 1963). Another study showed that cats learn pattern discriminations faster than object discriminations (Żernicki & Zabłocka, 1966). This study also demonstrated deleterious effects of visual deprivation and an impoverished environment. The nature of the stimulus presented and the training procedure can lead to significantly different conclusions regarding the species' aptitude for learning. Derdzinski and Warren (1969) showed that differential learning of pattern discrimination by cats might be due to disparities in complexity between stimuli. Cats have also been tested in auditory discrimination tasks, the results of which have suggested that they may have a slightly larger threshold for detecting change compared to humans (Rosenzweig, 1946). Presenting animals with the appropriate sensory stimuli according to their specialized sensory systems and physiology will be critical with any large-scale comparisons of species abilities.

Olfactory Discriminations

Some species may prioritize olfactory or tactile information over visual information when categorizing objects in their surroundings and this may be particularly true for carnivores. Previous work has shown that some carnivores, such as raccoons (Gregg, Jamison, Wilkie, & Radinsky, 1929) are color-blind, although they can learn reversal discriminations involving brightness (Michels, Fischer, & Johnson, 1960). Recently, we have tested striped skunks to assess their vision, and found it to be relatively poor compared to other carnivores (Johnson-Ulrich, Hoffmaster, Robeson, & Vonk, in press). Although most studies in carnivores have focused on visual discrimination, carnivores have also demonstrated the ability to learn olfactory discriminations. For example, coyotes (*Canis latrans*) learned to avoid food doses with lithium chloride after a single incident causing illness (Ellins & Martin, 1981). Recent work has presented seal (Laska, Lord, Selin, & Amundin, 2010; Laska, Svelander, & Amundin, 2008), feline (Mayes, Wilkinson, Pike, & Mills, 2015), and canine (Horowitz, Hecht, & Dedrick, 2013) species with olfactory discriminations. We will also return to the issue of olfaction as it aids in kin and conspecific recognition in a later section on carnivore concepts of kin relationships. Additionally, a number of studies have focused on direct application in terms of demonstrating that dogs can be used to detect explosives (e.g., Gazit & Terkel, 2003; Lazarowski et al., 2015) or disease (e.g., McCulloch et al., 2006; Willis et al., 2004). South African fur seals (*Arctocephalus pusillus)* were able to learn to select the odor of fish versus cloves and to generalize to the odor of squid versus pepper and myrtle (Laska et al., 2008). They were also able to learn to differentiate five odor classes (Laska et al., 2010), showing discrimination equivalent to that of humans, squirrel monkeys (*Saimiri sciureus*, Laska & Freyer, 1997), and honeybees (*Apis*, Laska, Galizia, Giurfa, & Menzel, 1999). Laska and colleagues suggested that sense of smell may be more important to seals than was previously believed.

In order to determine which type of cue might be prioritized by domestic cats, Mayes et al. (2015) contrasted the use of visual cues with olfactory cues in decision-making. Cats were first trained through positive reinforcement to make a discrimination between two visual-olfactory compounds. Once training was satisfied, a visual cue that signaled reinforcement was paired with an olfactory cue that signaled non-reinforcement, while an olfactory cue that signaled reinforcement was paired with a visual cue that signaled non-reinforcement, to create cue conflict compounds. Presented with a pair of these new compounds, most cats chose the compound with the previously reinforced visual cue rather than the compound with the previously reinforced olfactory cue, suggesting that visual information was prioritized over olfactory information. A follow-up odor only test was conducted to confirm that cats did have the ability to discriminate based on odor alone, emphasizing that, when presented with two viable cues, the cats preferentially attended to the visual over the olfactory cue. However, one cat consistently chose the conflict compound that contained the previously reinforced olfactory cue, suggesting individual differences – perhaps based on prior experience. Furthermore, the authors acknowledge that cue choice may be dependent on context, which would be highly adaptive, and thus, preferring visual cues in the context of this study does not mean that cats prioritize visual information in all contexts.

These studies involving olfactory discriminations have presented animals with relatively low-level discriminations that represent an animal's ability to distinguish between different perceptual features but do not necessarily constitute evidence for higher level, or more abstract, categories. Such evidence might be gained by showing that animals succeed in categorizing stimuli that belong to broad, abstract, overarching categories that contain exemplars that cannot be identified solely on the basis of directly observable features (Vonk & Povinelli, 2006). Researchers should determine animals' abilities to discriminate between more abstract categories, such as emotions, familiarity, or species identity, based on olfactory cues.

Natural Categories

Our own work involving natural concept discriminations involved presenting American black bears (*Ursus americanus,* Vonk et al., 2012; Vonk & Galvan, 2014) and great apes (chimpanzees, Vonk, Jett, Mosteller, & Galvan, 2013; gorilla, Vonk & MacDonald, 2002; orangutans, Vonk & MacDonald, 2004) with two alternative forced choice tests in which they discriminated between concrete, intermediate, and more abstract level categories. This work on levels of abstraction followed from earlier work conducted by Roberts and Mazmanian (1988), who found that pigeons (*Columba livia domestica*) and squirrel monkeys struggled to learn concepts at an intermediate level of abstraction when abstraction was defined on a continuum of inclusivity. That is, abstract concepts are defined as those at a superordinate level that contain several subcategories, and concrete level categories are those at the subordinate level that are more exclusive and contain exemplars that share many features in common. Intermediate level categories correspond to the basic level categories identified by Rosch and colleagues who demonstrated that basic level categories are usually first learned by human children, who only later learn subordinate and superordinate level categories (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). For example, when defining natural categories, the category "dog" may be deemed a basic or intermediate level category, while the various breeds of dogs are deemed concrete or subordinate level categories. Superordinate categories, such as carnivore, mammal, and animal may be considered increasingly abstract. Basic level categories contain intermediate levels of both within category and between category variance. Pigeons and squirrel monkeys were able to learn the abstract level discrimination of animal versus non-animal, despite encountering difficulty with the bird versus non-bird discrimination in Roberts and Mazmanian's study.

In our studies, subjects were presented with pairs of photographic stimuli presented on a touch-screen computer monitor and reinforced for selecting the stimulus that belonged to the arbitrarily determined "correct" category. At the most concrete level, subjects were rewarded for selecting images of members of their own species when presented alongside images of humans. These discriminations could be made by attending to one or few perceptual features, but may not have demonstrated representation of an overarching concept for the species depicted. For example, black bears may have learned to choose images where individuals depicted had long snouts and were covered in dark brown to blackish fur, and to avoid selecting photos where, for example, individuals stood on two legs, had lighter colored faces, and shorter noses. Of course, we varied photographs as much as possible to include humans with varying skin tones, and even some albino black bears (i.e., spirit bears) to try to induce use of a broader concept, but the fact remains that such concrete level discriminations can be made successfully through the use of independent, observable features.

However, bears were also successful at learning discriminations at more intermediate (e.g., basic) levels of categorization. That is, they also learned to select photographs of primates versus hoofstock and carnivores versus non-carnivores with an accuracy of 80% or higher, and they showed above chance levels of transfer when presented with novel sets of photographs depicting the same categories. Although orangutans (*Pongo abelii,* Vonk & MacDonald, 2004), like humans solved this intermediate level discrimination the most readily and with the most complete generalization, a gorilla (*Gorilla gorilla*, *gorilla,* Vonk & MacDonald, 2002), chimpanzees (Vonk et al., 2013), and black bears (Vonk et al., 2012) struggled with discriminations at this level. One bear in particular, though, outperformed all of the apes at the most abstract level discrimination of animal versus non-animal images, despite being presented with this discrimination prior to learning any of the ostensibly 'easier' discriminations. It is difficult to argue that animals are using features to generalize to novel images at this level because novel photo sets contained images of animals (e.g., blue whale, penguin) that shared few features with learned stimuli (e.g., horse, praying mantis). We argued that bears performed comparably to great apes when forming concepts at even fairly abstract levels. However, bears have not yet been tested on more abstract concepts such as sameness, relations, and concepts for unobservables, which would include concepts for things that cannot in principle take on physical form (Vonk & Povinelli, 2006). For example, concepts about freedom, thoughts, memories, religion, and so on would be considered unobservables, as would causal forces, such as gravity in the physical domain and mental states in the psychological domain.

Humans form concepts on the basis of extensive exposure to objects, learning labels through language, and being instructed explicitly what features are necessary and sufficient for category membership. It is yet unknown how other animals, in the absence of language and any other symbolic system, would be able to form categories that align with human identified taxonomic groupings. Furthermore, many of the captive animals tested for such categorization abilities would never have experienced the animals depicted in photographs in actuality, raising the question as to how such categories are formed. An interesting study by Rogers and colleagues (2014) found that black bears did not appear to recognize and respond to snakes using sight or smell; instead, they appeared to use movement to guide responding. Furthermore, the bears reacted more fearfully when presented with wild-caught garter snakes in areas where venomous snakes existed, but not in areas where venomous snakes have been long-absent, implicating the role of experience in categorization.

Vonk and Galvan (2014) attempted to analyze patterns of errors and correct responses in the bear and chimpanzee data on categorization with photographic stimuli but were unable to identify any features that were used consistently to control responding. Bears, a gorilla, and orangutans, appeared unlikely to rely on prior presentation or reinforcement history to inform their choices, whereas chimpanzees appeared most likely to select images of animals that had been presented previously, regardless of whether choices of these photographs had been reinforced. Thus, associationist accounts of learning based on reinforcement do not appear to adequately account for the performance of any of the species tested in our lab. Bears appeared more likely to avoid selecting less typical members of categories (e.g., insects among other animals), but the same was not true for our ape subjects. Possibly, bears are more likely to use typicality compared to features when making such discriminations. We are cautious in making strong statements about species differences given the very small samples in our studies, but we would encourage other researchers to extend these studies to further elucidate the strategies used in these tasks.

Other carnivores have also been tested for their ability to form natural categories. However, most of these studies have involved concrete level discriminations, such as distinguishing between photographs that contained images of dogs versus those that did not (e.g., landscape photos, Range, Aust, Steurer, & Huber, 2008), or categorizing dogs separately from other animals (Autier-Dérian, Deputte, Chalvet-Monfray, Coulon, Mounier, 2013). Racca and colleagues additionally demonstrated that dogs could distinguish between dog faces, human faces, and objects, using a preferential looking procedure. In this procedure viewing time of different stimuli is assessed with the expectation that animals look longer at novel or unfamiliar stimuli. These authors also tested the dogs for inversion effects, which are used to demonstrate the holistic nature of face processing, and the dogs ceased making reliable within-category discriminations with the inverted stimuli (Racca et al., 2010). This finding could be used to support the notion of face-superiority in visual processing; however, the dogs also showed an inversion effect with objects, which is atypical. The authors themselves identified some methodological issues that necessitate further testing before drawing conclusions with regard to how dogs perceive faces. Following from these results, another research team tracked the eye movements of dogs when presented with stimuli from four categories (dog faces, human faces, toys, alphabetic characters), and confirmed that dogs prefer to view conspecifics (Somppi, Törnqvist, Hänninen, Krause, & Vainio, 2012), reinforcing the conclusion that they do indeed discriminate among categories when presented with visual stimuli.

More in line with the original research on natural categorization reviewed by Herrnstein (1990), in which pigeons discriminated pictures containing humans from pictures not containing humans (among other things), Range and colleagues (2008) presented dogs with images containing dogs or the lack thereof. Once the dogs learned to choose dog over landscape photos presented on a computer touchscreen, they were tested for generalization to novel dogs superimposed on previously seen landscapes. This test allowed the researchers to differentiate between rule-based and featured-based categorization strategies. Although the dogs showed above chance transfer to the novel photos, generalization was not complete leaving open the possibility that successful performance represented alternative response strategies.

Autier-Dérian and colleagues' (2013) study demonstrated that dogs could additionally categorize various breeds of dogs as belonging to the same category. Domestic dogs are extremely diverse, and subjects were able to categorize images of dogs as dissimilar as poodles, German shepherds, and sheepdogs, for example, into the same category separately from non-dog images. Three thousand images were presented from each category, excluding wolves and foxes. Although the generalization was impressive in this study, the dogs' learning was carefully scaffolded with dogs first being trained to discriminate four major morphotypes (mastiff, hound, wolf, greyhound) from cows only. Categories became increasingly diverse once dogs mastered the more concrete level discriminations. Dogs also demonstrated reversal learning, which is presumably aided by the formation of general rule-based categories, rather than reliance on features and their association with reinforcement. The category of 'dog' would be seen as intermediate or basic in Rosch's terms (Rosch, 1978; Rosch & Mervis, 1975; Rosch et al., 1976). It will be interesting to determine whether dogs are capable of forming concepts at the most abstract level as well. To our knowledge, cats and other carnivores have yet to be tested in any such tasks.

Even if category-relevant features can be extracted by subjects, it does not mean that the subject recognizes the positive instances as representations of the real life objects depicted in photographs. Such an interpretation would be supported by the ability to see the equivalence of pictures and objects. We have tested for this capacity in a single American black bear (Johnson-Ulrich et al., 2016) and found good evidence that at least this bear perceives the correspondence between pictures and their referents, but it is still unclear the extent to which animals understand the representational nature of images.

Quantity Discriminations

As with discriminating natural categories, discriminating between objects that vary in mass or quantity may be relatively primordial and shared broadly in the animal kingdom because of the adaptive value of being able to discriminate larger and smaller amounts of food, prey, mating opportunities, and the like. Quantity discrimination is also one of the more heavily researched topics in comparative cognition; as such, there are data from several carnivore species, such as dogs (Ward & Smuts, 2007), cats (Bánszegi, et al., 2016; McComb, Packer, & Pusey, 1994; Pisa & Agrillo, 2009), raccoons (Davis, 1984) and bears (Vonk & Beran, 2012). Most of the work with carnivores has used actual food items as stimuli (Bánszegi et al., 2016; Ward & Smuts, 2007), although McComb et al. (1994) assessed the ability of lions (*Panthera leo*) to detect how many lions were vocalizing using auditory stimuli. Similarly, Benson-Amram, Heinen, Dryer and Holekamp (2011) showed that hyenas (*Crocuta crocuta*) responded with differential vigilance to playback recording of one, two, or three unfamiliar intruders, and adaptively approached more often when they outnumbered the number of callers. Davis (1984) trained a single raccoon to select cubes containing three food and non-food objects from cubes containing one or five objects. Our own study with black bears utilized a procedure commonly used with nonhuman primates (e.g., Beran, 2008) in which subjects are presented with arrays of black dots on a white background (usually a computer screen) and required to select the array containing the larger number of dots.

In our study, two of the three bears were trained to select the smaller number of dots (Vonk & Beran, 2012) from two arrays presented simultaneously on a touch-screen monitor. The third bear was trained to select the larger number of dots, which is more typical and reflects an apparently natural preference. Our results showed that bears, like nonhuman primates, showed effects of ratio consistent with the magnitude estimation model of quantity estimation. However, more interestingly, their performance was maintained at above chance levels even when number was in contrast with area of the dots on the screen (i.e., incongruent trials). The performance of the bear trained to choose the larger array did not differ between congruent and incongruent trials for the most complex, moving set of dots that contained a subset of differently colored dots. This result indicated that bears are capable of using number as a cue, even though they clearly depended quite heavily on area to spontaneously discriminate between larger and smaller sets. That they could do so even when presented with moving stimuli suggests that tracking individuals is possible for animals that did not evolve to live in large social groups and is, thus, not simply an adaptation to tracking group members. Future work should investigate differences in predator and prey species. For a prey species, a single predator is dangerous such that quantifying the size of a group may not be as critical as for a predator who must hunt where food is the most plentiful. Thus, we might expect predatory species to have superior quantification skills to non-predatory herbivores. Therefore, it would be interesting to compare results of obligate carnivores, such as polar bears (*Ursus maritimus*), to herbivores, such as Giant pandas (*Ailuropoda melanoleuca*).

Domestic dogs are also omnivorous and perform similarly to other species. Ward and Smuts (2007) presented domestic dogs with two different quantities of food in a forced two-choice task. Two ‘high performing’ dogs were then tested in additional conditions, in which some of the quantities were presented successively instead of simultaneously to determine if dogs potentially create a mental representation of quantity. When presented with two different food quantities simultaneously, dogs performed comparably to nonhuman primates, showing increased performance when the numerical distance between the two quantities increased as well as when the ratio between the two quantities decreased. Ratio effects generally indicate the use of a magnitude estimation mechanism (see Beran, 2008). Interestingly, both dogs were still significantly more likely to choose the larger quantity even when the quantities were not presented simultaneously. Furthermore, ratio and numerical distance were no longer significantly related to performance in the successive presentation condition. These results are not in line with the magnitude estimation model. Therefore, further research is needed to investigate the mechanisms underlying these findings. Ward and Smuts (2007, p. 79) recommend future studies in which quantity discrimination is studied and compared across breeds, to elucidate whether there is a relationship between quantity discrimination abilities and ‘ecological niche’, which they define as the selective breeding of dogs to fulfill particular roles in their relationships with humans. They predicted, as one example, that herding dogs may have superior quantification abilities compared to dogs bred solely for human companionship.

Along these lines, Baker, Shivik, and Jordan (2011) studied coyotes at the USDA National Wildlife Research Center to determine whether non-domesticated members of the *Canidae* family also demonstrated evidence of quantity discrimination. This facility houses over 100 coyotes in natural habitats that demonstrate behaviors very similar to behaviors documented for wild coyotes. The study used the same two alternative forced-choice procedure with food items as Ward and Smuts (2007), and the coyotes performed comparably to the domesticated dogs, with performance also increasing as numerical distance increased and ratios decreased. For comparison purposes, Baker, Morath, Rodzon and Jordan (2012) followed up with a study of domestic dogs. Although coyotes and dogs are closely related, it was surmised that the mechanisms underlying quantity discrimination in these species could differ, as they have experienced different selective and ecological pressures. However, the domestic dogs performed similarly to the previously tested coyotes, suggesting that domestication did not significantly alter the mechanism supporting quantity discrimination. Taken together, these findings support the idea that there may be a similar non-verbal quantitative ability across multiple species.

Recently, Petrazzini and Wynne (2015) expanded the food quantity discrimination test with domestic dogs by accounting for both number of food items and total quantity. In the congruent condition, total number of food items and total quantity of food co-varied, whereas, in the incongruent condition, the total number of food items was tested against total quantity of food. In both the congruent and incongruent conditions, dogs were statistically more likely to select the larger quantity of food, even though this sometimes meant selecting the smaller number of items. However, in this setup, one could argue that the largest item was always associated with the largest quantity group, making it unclear if the dogs were attending to that largest item or the overall quantity (which has been documented in domestic cats; Bánszegi et al., 2016). Therefore, a follow-up experiment was conducted, with two conditions. The first contained two sets of food with equal number of food items (4 x 4), but one set had the largest item while the other contained the largest overall quantity. The second equalized overall quantity between the two sets, but varied total number of food items (2 x 3) and the largest food item was in the larger number of items group. Results showed no significant difference in preference for the largest item when pitted against the largest quantity. Furthermore, when the overall quantity of food was the same, there was no significant preference for choosing the option with the larger item. Petrazzini and Wynne argued that, overall, dogs tend to use quantity over total number of items for spontaneous food selection. However, they argued that dogs may use multiple kinds of sensory information because when cues were limited to only quantity against largest food item or largest number of food items against largest food item (with quantity being equal), domestic dogs' performance decreased to near chance.

Recently, this approach was extended to a less social carnivore - the domestic cat (Bánszegi et al., 2016). Methods similar to Ward and Smuts (2007) and Baker et al. (2011) were used, in which arrays of two different numerical values of equal sized food pieces were presented. However, an additional condition was added where two single pieces of food of differing size (volume) were presented in four combinations, as it was argued, for a solitary obligate hunter, being able to assess size when determining the costs and benefits of a particular prey would be beneficial. In the first condition, domestic cats performed comparably to previous species studied, consistently selecting the larger number of food items when the ratio between the two quantities was small. When examining individual volume combinations, cats were significantly more likely to choose the array containing the larger item only in the middle ratio conditions of 4 versus 12 grams and 4 versus 16 grams, while not discriminating above chance with the largest difference of 4 versus 20 grams. The authors argued that there may be a motivational reason to choose the smaller size when the larger option is too large, such as the manageability of taking down prey of larger size or the desire to not leave any food uneaten. Thus, performance in this condition did not undermine results with the other discriminations. Again, it would be of interest to compare species that are obligate carnivores to those that are omnivorous to determine different preferences for larger single pieces and total arrays.

Cats have also been trained to choose between two and three dots (Pisa & Agrillo, 2009), but some have argued that trained, versus spontaneous, discriminations may be less informative in revealing the underlying strategies used by a species as a response to contingencies found in nature (Agrillo & Bisazza, 2014). That is, an animal's ability in a given context reflects the contingencies of the current task demands, and not necessarily innate abilities. With cats, the two methods have produced different findings; the cats in Bánszegi et al. (2016) could not discriminate between two and three balls of food. However, in general, using converging methods, it appears that carnivores share similar quantity estimation capacities with a broad range of species (see Agrillo & Bisazza, 2014 for review), and that the underlying mechanism may be some sort of magnitude estimation, at least for larger numbers. Horowitz et al. (2013), recognizing that most quantity discrimination tasks were based on visual cues, tested the ability of dogs to discriminate between quantities based on smell, but failed to find evidence that they could do so. However, other non-quantity discriminations may be tied with greater accuracy to olfactory differences. For instance, dogs may detect emotional states, such as fear, using pheromones and other chemical signals, but researchers are less adept at testing stimuli in non-visual domains given our own reliance on visual cues.

Emotions

As with discriminating quantities, discriminating between cues of various emotion states in conspecifics (or other species with which one interacts) could be highly adaptive. For example, an organism needs to detect when another is threatening versus friendly, angry versus peaceful, and so on. Few studies have examined how carnivores appreciate such signals of mental state in conspecifics (see also Pongrácz, Szabó, Kis, Péter, & Míklósi, 2014), but recent studies have indicated that domestic cats and dogs (described below) may perceive and distinguish among various human emotions. Of course, learning to respond differently to signals corresponding to different mood states does not constitute evidence for a concept of emotional states, but it does indicate that animals are able to attend to relevant features to make predictions of another's likely actions. Adjusting behavior to information indicating different categories of objects, events, or contexts constitutes the first step in categorical representation.

Dogs have been shown to alter their behavior based on the expressions displayed by human actors. For example, dogs displayed more avoidant behavior and less approach behavior to actors displaying anger, compared to actors displaying happiness (Deputte & Doll, 2011). Domestic dogs consistently and appropriately adjust their own behavior to human individuals behaving in friendly versus threatening manners (Vas, Topál, Gácsi, Miklósi, & Csányi, 2005; Vas, Topál, Győri, & Miklósi, 2008) – a pattern not revealed by even hand-reared wolves (*Canis lupus,* Gácsi, Vas, Topál, & Miklósi, 2013). Dogs are able to learn to associate happy, disgust, or fearful expressions with the location or absence of hidden food; however, they could not distinguish between neutral and happy faces (Buttelmann & Tomasello, 2013; Merola, Prato-Previde, Lazzaroni, & Marshall-Pescini, 2014). Using a different paradigm, researchers recently showed that dogs are capable of using the emotional expression on human faces as a discriminative cue (Muller, Schmitt, Barber & Huber, 2015). Dogs were trained to discriminate between happy and angry human faces when only part of the faces were shown (upper or lower halves). They then demonstrated significant transfer to probes that showed novel faces from the same part (upper or lower) or the opposite part to what was previously learned. These results, taken together, suggest that domestic dogs are capable of using the observable cues of emotion to predict different behaviors, but the nature of the underlying representation of emotion is still unknown. It will be important to assess the abilities of domestic cats to make similar discriminations to tease apart the role of domestication versus natural social structure. Of course such studies would need to acknowledge that the period of domestication for dogs has been much longer, and more intensive, with dogs being bred to interact with humans in particular ways, and cats, alternatively, being subjected to a more passive process of domestication (Driscoll et al., 2007; Driscoll, Clutton-Brock, Kitchener, & O'Brien, 2009).

Both domestic dogs and cats appear to attend to cues of owners' emotions in social referencing paradigms (Merola, Prato-Previde, & Marshall-Pescini, 2012; Merola, Lazzaroni, Marshall-Pescini, & Prato-Previde, 2015) and cats have also shown different patterns of behavior and approach depending on the emotion displayed by caregivers and strangers (Galvan & Vonk, 2016). In Merola et al. (2014) dogs were better able to distinguish the emotions displayed by their owners compared to strangers, and Galvan and Vonk (2016) also demonstrated that cats looked more to their caregivers than to strangers in a novel situation regardless of emotion displayed. This pattern might suggest that particular experiences must be present in order for cats and dogs to associate visual cues of emotions with expected outcomes. In both Merola and colleagues' (2015) and Galvan and Vonk's (2016) work, cats indicated subtler differences in behavior between conditions where humans displayed different emotions compared to dogs. It is recommended that researchers pay careful attention to behavioral cues, such as ear and body posture, vocalizations and so on, in addition to explicit choice, approach, and avoidance behaviors. It seems less likely that wild carnivores would be responsive to cues of human emotion, but future work should investigate understanding of their conspecifics' emotional states. As with most topics of research, wild and domestic dogs are studied much more frequently compared to other species.

Social Relationships

The recent proliferation of studies on canine cognition is undoubtedly due, at least in part, to proposed theoretical explanations of advanced cognition. The most discussed hypothesis, the Social Intelligence Hypothesis (Jolly, 1966; Humphrey, 1976) argues that evolving to life in large and complex social groups may have provided social animals with adaptations to help them recognize and track individual relationships and social cues, thus giving rise to cognitive traits such as imitation, transitive inference, reputation judgements, and theory of mind (i.e., the ability to attribute mental states to others). Although there is a large and growing body of empirical work studying theory of mind in non-humans, including canines, there is little work examining social cognition in less social carnivores, such as cats and bears. We will not review the research on theory of mind in canines in this paper as this work has received significant attention elsewhere (Hare, 2007; Hare & Tomasello, 2005; Miklósi & Topál, 2012).

Although one cannot dismiss the importance of testing less social animals for social concepts, it proves to be more challenging with animals that are typically not housed socially, and for whom doing so is unnatural. Many captive carnivores are singly-housed and it is difficult to impose careful control over studies of wild free-roaming animals, thus making it challenging to assess their understanding of others' relationships. Of course, researchers have also neglected to investigate such aspects of cognition in non-social animals presumably because of a pre-conceived notion that such experiments would fail, based on the Social Intelligence Hypothesis. However, to adequately test the hypothesis, it is absolutely critical to show that less social animals do not show the same capacity for advanced social cognition as their group-living peers. Testing less social species may also help to determine the role of brain size and dietary complexity in facilitating problem-solving and other advanced cognitive skills (see also Benson-Amram et al., 2016, whose large-scale study of several carnivore species failed to support the social complexity hypothesis but supported hypotheses concerning the importance of brain size). Thus, it is our hope that other researchers will extend such studies to less social species.

On that note, Borrego and colleagues have recently conducted a number of studies of problem-solving in various wild cat species (Borrego & Dowling, 2016; Borrego & Gaines, 2016). Borrego and Gaines found that social lions and spotted hyenas outperformed less social species such as leopards (*Panthera pardus*) and tigers (*Panthera tigris*), on an innovation task. However, given that hyenas are more distantly related from all of the cat species studied, and only hyenas and lion comprised the social group in this study, conclusions concerning the role of sociality should be made carefully. Some support is provided, however, by the finding that social carnivores outperform their non-social counterparts in cooperative tasks (N. Borrego, personal communication, June, 2014). If it is the case that group-living bolsters social cognition, social, but not relatively asocial, carnivores might be expected to represent concepts of social relationships, recognize kin, and so on. Although there are few studies of these types of concepts in carnivores, there are some studies examining kin recognition and concepts for other kinds of social relationships.

For example, we tested black bears and a single chimpanzee on a task where the goal was to select photos depicting the mother/offspring pair and not to select photos depicting other relationships (e.g., siblings, mated pairs, social groups; Vonk & Johnson-Ulrich, 2014). Importantly, both the correct and incorrect photos contained images of young animals and animals of mixed size. However, we also included control tests of food items that also varied in size and similarity in order to determine whether the social concept was learned more readily compared to a perceptual rule (i.e., choose image that depicts large and small object of same type) when applied to food items. Incomplete transfer was shown from the social to the non-social task and bears eventually responded above chance on transfer tests from mother/offspring photos depicting bears, to chimpanzees, to other primates, to various animals, which suggested that they may have extracted the relevant overarching concept. However, transfer between sets was incomplete and each set of photos required a significant number of trials to learn.

Moving forward, it will be important to test more explicit concepts of social knowledge and social status in animals that do interact with group-mates. Hyenas, a very social group, appear to track third party relationships in that adults support cubs in coalitions against other cubs, but are more likely to do so against low-born than high-born cubs (Engh, Esch, Smale, & Holekamp, 2000). Spotted hyenas also support dominant animals in disputes, even when they outrank both contestants, further supporting the idea that they recognize third party relationships (Engh, Siebert, Greenberg, & Holekamp, 2005). Furthermore, the original aggressor directed more aggression toward relatives of the opponent following conflict than during post-conflict control periods and to lower-ranking individuals that were unrelated to opponents. Other than in nonhuman primates, there have not been sufficient tests of understanding of third party relationships in nonhumans in order to make species comparisons.

Kin recognition is perhaps the most widely studied social concept, and again, the bulk of the data involves canine species. At least one study with harbor seals (*Phoca vitulina*), however, showed that seal mothers responded more strongly to play-back calls from their own pup, compared to calls from a nonfilial pup of similar age (Sauvé, Beauplet, Hammill, & Charrier, 2015). This was especially the case for mothers at a farther distance from the pup. Spotted hyena mothers react more vigorously to calls of their own pups, and more so to young pups than older pups, suggesting that hyena calls contain information about both identity and age (Holekamp et al., 1999). In this study, kin listened more to playbacks compared to non-kin, also supporting the presence of kin recognition by vocal means in hyenas. It is likely that many colony-living species recognize their offspring from other juveniles to avoid investment of effort and resources that would not result in increases in reproductive fitness. It is less clear whether other species must recognize related individuals.

Hepper (1994) originally showed that domestic dog mothers recognized their pups and vice versa, but it was unclear whether the mechanism was phenotype matching or familiarity. There is some recent evidence that, in hyenas, odor profiles from pasting differ between social groups, thus supporting the idea that hyenas can differentiate individuals or at least group members based on olfactory information (Theis, Schmidt, & Holekamp, 2012; Theis et al., 2013). Raccoons also appear to discriminate between the scent of individual conspecifics using a habituation-discrimination paradigm (Kent & Tang-Martinez, 2014). However, they showed an increase in investigating novel stimuli paired with familiarized stimuli when presented with urine, but not fecal samples. This finding supports the idea that information is contained in some, but not all, olfactory stimuli. Furthermore, the raccoons may have habituated to information about reproductive status, age, or other characteristics, not necessarily allowing them to identify specific individuals. Mongooses have also been shown to differentiate individual odors based on carboxylic acid profiles in anal pockets, but can also discriminate synthetic odors made from acids (Gorman, 1976), supporting the notion that such discriminations reflect perceptual acuity, rather than conceptual representations.

Hamilton and Vonk (2015) extended Hepper's study to show that, in the absence of familiarity, young male and female dogs differentiated between the scent of their sire and unrelated control dogs. The pattern of behavior demonstrated by males and females differed, indicating that it is critical for future research to consider sex differences. Males spent more time exploring the scent of non-kin males, whereas females showed a non-significant trend toward preferring the scent of their sires. It is possible that observed sex differences reflect the fact that our female subjects were not in estrous whereas male dogs may have been sexually receptive and viewed non-kin adult males as competitors. Others have also observed sex differences in response to olfactory stimuli (Drea, Vignieri, Kim, Weldele, & Glickman, 2002).

Hamilton and Vonk (2015) also tested whether young dogs recognized their siblings, with which there was some familiarity, and again found significant sex differences. Hepper (1994) concluded that dogs did not recognize siblings, but did not evaluate sex differences. Our results revealed that males, but not females, significantly preferred the scents of female non-kin to female sibling scents. This preference was not revealed when male subjects were presented with scents of male siblings and controls, supporting the idea that kin recognition may assist in maintaining optimal outbreeding. Although the dogs were able to discriminate the scents of kin and non-kin, behavioral responses alone do not indicate the presence of a more abstract concept of kinship. One would need to show generalization across modalities or other types of stimuli based on the overarching notion of relatedness.

Whether carnivores represent a concept for familiar and unfamiliar individuals is an open question. As reviewed above, in studies of discriminating human emotions, both domestic cats (Galvan & Vonk, 2016) and dogs (Merola et al., 2014) appear to respond differentially to familiar and unfamiliar humans. Cats have also been shown to respond more to their owner's versus a stranger's voice (Saito & Shinozuka, 2013), and to generally respond differently to familiar versus unfamiliar humans (Collard 1967; Casey & Bradshaw, 2008; Edwards, Heiblum, Tejeda, & Galindo, 2007). Jordan and Burghardt (1986) showed that the behavior of black bears shows habituation over time to the presence of familiar humans. Attard, Pitcher, Charrier, Ahonen and Harcourt (2010) found that male Australian sea lions (*Neophoca cinerea*) responded more strongly to calls from local versus foreign males, suggesting that they perceived local calls as more threatening. However, it is not clear whether these differences reflect a learned association or a more general concept of familiarity. Attard et al. (2010) found a significant difference in the acoustic qualities of local versus foreign male barks. Genets (*Genetta genetta l., Carnivora-Viverridae*) have also been shown to discriminate familiar versus unfamiliar members of the opposite sex on the basis of their scent-marks (Roeder, 1980), as have captive spotted hyenas (Drea et al., 2002) and feral ferrets, *Mustela furo L.* (Clapperton, Minot, & Crump,1988). Huber and colleagues tested dogs' ability to discriminate faces of two familiar humans, and then tested their generalization to stimuli that varied in the degree of information presented (Huber, Racca, Scaf, Virányi, & Range, 2013). For example, dogs were trained to discriminate actual human's heads but were tested with photographs of human's heads, and then photographs showing only the facial features, without the hairline or contour of the heads. The researchers found significant inter-individual variation in performance. Perhaps including auditory and olfactory cues would have aided in the dogs' discrimination performance. Overall, carnivores appear to respond to familiarity both in conspecifics and in other species with whom they interact.

Adachi and colleagues demonstrated cross-modal matching of dog owners' voices to their faces, which provided the first evidence that dogs do not merely associate auditory and visual stimuli, but instead form a representation of the owner's face when they hear the owner calling them (Adachi, Kuwahata, & Fujita, 2007). This was demonstrated by showing that the dogs looked longer when the face presented on an LCD monitor did not match the voice played back to them compared to when the face did match. Cuaya, Hernandez-Perez, and Concha (2016) have also recently shown that the temporal cortex shows significant activation when dogs are presented with human faces compared to common objects, suggesting that human faces are processed specially in dogs, as in humans. Dogs also showed activation in the caudate nucleus in response to the scent of a familiar human that was not present at the time of testing, suggesting that they discriminated the scent of a familiar human from others, and had positive associations with that scent (Berns, Brooks, & Spivak, 2015). Thus, at least domestic dogs may show recognition of individual humans, as well as conspecifics. It would be of interest to determine whether domestic cats show similar effects, but it is likely considerably more difficult to train cats to remain motionless in MRI scanners.

Dogs also appear to recognize individual conspecifics from the sound of their barks. Molnár and colleagues (Molnár, Pongrácz, Faragó, Dóka, & Miklósi, 2009) used a habituation/dishabituation paradigm to show that dogs discriminated between both context and individuals. Dogs oriented for a longer period of time to a sound that came from a novel context or dog compared to a sound from the same context or individual. This finding was obtained even when owners could not hear the playbacks, controlling for potential interference from human provided cues. Similar patterns for novel contexts have also been demonstrated when measuring heart rate rather than orientation (Maros et al., 2008). Thus domestic dogs likely discriminate between individuals of both their own and familiar species, such as humans, and may have a representation of individuals that goes beyond learned associations. Future work is needed to assess their understanding of relationships between individuals, however.

Relations

With regard to the concept of relations, the idea of sameness/difference and analogical reasoning is considered one of the most abstract concepts that can be tested in non-humans (along with concepts for unobservables, such as mental states; Vonk & Povinelli, 2006). There is evidence for concepts of sameness/difference in animals ranging from honeybees (Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001) and corvids (Smirnova, Zorina, Obozova, & Wasserman, 2014; although see Vonk, 2015) to non-human primates (Wasserman & Young, 2010). However, carnivores have not been extensively tested for such concepts. A single study indicates that dogs can transfer same/different concept learning to novel auditory tones (Pietrzykowska & Soltysik, 1975a). However, the same authors were unable to train the dogs to make same/different discriminations with photic stimuli (continuous and pulsing lights, Pietrzykowska & Soltysik, 1975b). We have attempted to train black bears in an identity match-to-sample task (a common method for assessing concepts of sameness) and have failed; however, we have also had difficulty training chimpanzees and gorillas to learn MTS tasks (unpublished data) so this failure isn't necessarily an indictment on the ability of bears to represent such concepts. As of yet, we do not have a strong hypothesis for why our subjects have failed to learn MTS tasks, when pigeons (Berryman, Cumming, & Nevim, 1963) and rats (Leising, Wolf, & Ruprecht, 2013) have been shown to perform these tasks consistently. It is possible that other species perform the task by viewing the array as configural, rather than as exemplifying sameness relationships (Katz, Bodily, & Wright, 2008; Wright, 1993). It is also possible that we have not presented a sufficient number of exemplars to strengthen the overall construct (Wright, Cook, Rivera, Sands, & Delius, 1988).

There are some relevant data on oddity learning in dogs. For example, oddity discriminations have been frequently used to assess cognitive impairment in dogs as a function of age (Zanghi, Araujo, & Milgram, 2015) and diet (Milgram et al., 2002) and biochemical treatments (Araujo, et al., 2011). Gadzichowski, Kapalka, and Pasnak (2016) recently demonstrated that a single malamute-husky mix was able to learn to select an odd object from three identical objects and generalized to novel problems at levels above chance. Researchers had previously found that hand-reared wolves outperformed Alaskan malamutes on a measure of oddity learning using the Wisconsin General Test Apparatus, which suggests that an oddity concept is not the product of domestication, but probably reflects wild dogs' hunting strategies (Frank, Frank, Hasselbach, & Littleton, 1989). That is, it might be advantageous to identify and select the weakest member of a rival pack or group of prey.

Furthermore, researchers have shown that dogs may learn labels for objects through a process known as fast-mapping (Kaminski, Call, & Fischer, 2004, but see Markman & Abelev, 2004), which involves reasoning by exclusion, which could be seen as a form of oddity learning. In Kaminski and colleagues' study, a border collie, Rico, inferred the names of novel objects, ostensibly through learning by exclusion – a similar process to that used by human children learning language.

Conclusion

We have only touched on some of the findings related to concept representation in carnivores in this review, but we have highlighted the considerable overlap between the conceptual abilities of carnivores and other more highly tested species like nonhuman primates. We have tried to be inclusive in reviewing data from a wide range of carnivores, although data is admittedly sparse for the majority of species. What data do exist fails to suggest large cognitive differences within the order, Carnivora. In particular, our review suggests that even non-social carnivores share many of the cognitive abilities of their more social counterparts, indicating that the Social Intelligence Hypothesis cannot solely explain the evolution of sophisticated cognition (see also Benson-Amram et al., 2016; Holekamp et al., 2015). For example, even relatively asocial carnivores can form abstract natural categories, can discriminate quantities, and recognize familiar individuals of their own species as well as humans. They also appear to differentiate between human emotional states to some extent. Other areas of research are lacking, such as exploring whether carnivores have concepts for unobservables, and understand analogical relations. That is, do they perceive that the relationship between two or more items can be the same as the relationship between two or more different items? Given the few species studied, the small number of individuals of each species tested, and the limited topics that have been addressed, it is too early to conclude with any certainty as to whether foraging challenges supersede sociality in driving the evolution of conceptual reasoning. There are other areas of research with carnivores that we did not review, but we hope to have provided the reader with some indication that cognitive research with carnivores is important, and feasible, and that there are many remaining gaps in the literature just waiting for bright young scientists to fill them in. Studying carnivores in particular will allow researchers to better understand the relative contributions of dietary and social challenges to cognitive capacities.

References

Adachi, I., Kuwahata, H., & Fujita, K. (2007). Dogs recall their owner's face upon hearing the owner's voice. *Animal Cognition, 10*, 17–21.

Agrillo, C., & Bisazza, A. (2014). Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal Neuroscience Methods, 234*, 82–91.

Araujo, J. A., Greig, N. H., Ingram, D. K., Sandin, J., de Rivera, C., & Milgram, N. W. (2011). Cholinesterase inhibitors improve both memory and complex learning in aged beagle dogs. *Journal of Alzheimer's Disease, 26*, 143–155.

Attard, M. R. G., Pitcher, B. J., Charrier, I., Ahonen, H., & Harcourt, R. G. (2010). Vocal discrimination in mate guarding male Australian sea lions: Familiarity breeds contempt. *Ethology, 116*, 704–712.

Autier-Dérian, D., Deputte, B. L., Chalvet-Monfray, K., Coulon, M., & Mounier, L. (2013). Visual discrimination of species in dogs (*Canis familiaris*). *Animal Cognition, 16*, 637–51.

Bacon, E. S. (1980). Curiosity in the American black bear, *Ursus, 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.

Baker, J. M., Morath, J., Rodzon, K. S., & Jordan, K. E. (2012). A shared system of representation governing quantity discrimination in canids. *Frontiers in Psychology, 3*, 387.

Baker, J. M., Shivik, J., & Jordan, K. E. (2011). Tracking of food quantity by coyotes (*Canstis latrans*). *Behavioural Processes, 88*, 72–75.

Bánszegi, O., Urrutia, A., Szenczi, P., & Hudson, R. (2016). More or less: Spontaneous quantity discrimination in the domestic cat. *Animal Cognition, 19*, 879–888.

Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E. M., & Holekamp, K. E. (2016). Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Sciences of the United States of America, 113*, 2532–2537.

Benson-Amram, S., Heinen, V. K., Dryer, S. L., & Holekamp, K. E. (2011). Numerical assessment and individual call discrimination by wild spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour, 82*, 743–752.

Beran, M. J. (2008). Monkeys (*Macaca mulatta* and *Cebus apella*) track, enumerate, and compare multiple sets of moving items. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 63–74.

Berns, G. S., Brooks, A. M., & Spivak, M. (2015). Scent of the familiar: An fMRI study of canine brain responses to familiar and unfamiliar human and dog odors. *Behavioural Processes, 110*, 37–46.

Berryman, R., Cumming, W. W., & Nevim, J. A. (1963). Acquisition of delayed matching in the pigeon. *Journal of the Experimental Analysis of Behavior, 6*, 101–107.

Borrego, N., & Dowling, B. (2016). Lions (*Panthera leo*) solve, learn, and remember a novel resource acquisition problem. *Animal Cognition, 19*, 1019–1025.

Borrego, N., & Gaines, M. (2016). Social carnivores outperform asocial carnivores on an innovative problem. *Animal Behaviour, 114*, 21–26.

Burghardt, G. M. (1975). Behavioral research on common animals in small zoos. In Institute of Laboratory Animal Resources (Ed). *Research in Zoos and Aquariums: A Symposium held at the forty-ninth conference of the American Association of Zoological Parks and Aquariums* (pp. 103–133). Washington, D.C.: National Academy of Sciences.

Burghardt, G. M. (1992). Human–bear bonding in research on black bear behavior. In H. Davis & D. Balfour (Eds.): *The Inevitable Bond* (pp. 365–382). Cambridge, UK: Cambridge University Press.

Burkart, J. M., Schubiger, M. N., & van Schaik, C. P. (2016). The evolution of general intelligence. *Behavioral and Brain Sciences*, 1–65.

Buttelmann, D., & Tomasello, M. (2013). Can domestic dogs (*Canis familiaris*) use referential emotional expressions to locate hidden food? *Animal Cognition, 16*, 137–145.

Byrne, R. W. (1997). The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence? In A. Whiten, & R. W. Byrne (Eds.), *Machiavellian intelligence II: Extensions and evaluations* (pp. 289–311). New York, NY: Cambridge University Press.

Byrne, R. W., & Whiten, A. (Eds.). (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans.* New York, NY: Oxford University Press.

Casey, R. A. & Bradshaw J. W. S. (2008). The effects of additional socialization for kittens in a rescue centre on their behaviour and suitability as a pet. *Applied Animal Behaviour Science, 114*, 196–205.

Clapperton, B. K., Minot, E. O., & Crump, D. R. (1988). An olfactory recognition system in the ferret *Mustela furo L.* (carnivora: *Mustelidae*). *Animal Behaviour, 36*, 541–553.

Collard, R. R. (1967). Fear of strangers and play behavior in kittens with varied social experience. *Child Development, 38*, 877–891.

Cuaya, L. V., Hernández-Pérez, R., & Concha, L. (2016). Our faces in the dog's brain: Functional imaging reveals temporal cortex activation during perception of human faces. *PLoS ONE, 11*, e0149431. doi:10.1371/journal.pone.0149431

Davis, H. (1984). Discrimination of the number three by a raccoon (*Procyon lotor*). *Animal Learning & Behavior, 12*, 409–413.

Deputte, B. L., & Doll, A. (2011). Do dogs understand human facial expressions? *Journal of Veterinary Behavior: Clinical Applications and Research, 6*, 78–79.

Derdzinski, D., & Warren, J. M. (1969). Perimeter, complexity and form discrimination learning by cats. *Journal of Comparative and Physiological Psychology, 68*, 407–411.

Doty, B. A., Jones, C. N., & Doty, L. A. (1967). Learning-set formation by mink, ferrets, skunks, and cats. *Science, 155*, 1579–1580.

Drea, C. M., Vignieri, S. N., Kim, H. S., Weldele, M. L., & Glickman, S. E. (2002). Responses to olfactory stimuli in spotted hyenas (*Crocuta crocuta*): II. discrimination of conspecific scent. *Journal of Comparative Psychology, 116*, 342–349.

Driscoll, C., Clutton-Brock, J., Kitchener, A. C., & O'Brien, S. J. (2009). The taming of the cat. *Scientific American, 300*, 68–75.

Driscoll, C., Menotti-Ryamond, M., Roca, A. L., Hupe, K., Johnson, W. E., Geffen, E.,…Macdonald, D.W. (2007). The near eastern origin of cat domestication. *Science, 317*, 519–522.

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.

Edwards, C., Heiblum, M., Tejeda, A., & Galindo, F. (2007). Experimental evaluation of attachment behaviors in owned cats. *Journal of Veterinary Behavior: Clinical Applications and Research, 2*, 119–125.

Ellins, S. R., & Martin, G. C. (1981). Olfactory discrimination of lithium chloride by the coyote (*Canis latrans*). *Behavioral & Neural Biology, 31*, 214–224.

Engh, A., Esch, K., Smale, L., & Holekamp, K. (2000). Mechanisms of maternal rank 'inheritance' in spotted hyaena, *Crocuta crocuta*. *Animal Behavior, 60*, 323–332.

Engh, A. L., Siebert, E. R., Greenberg, D. A., & Holekamp, K. E. (2005). Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. *Animal Behaviour*, *69*, 209–217.

Fields, P. E. (1932). Studies in concept formation. II. The development of the concept of triangularity by the while rat. *Comparative Psychology Monographs, 42*, 1 – 70.

Fields, P. E. (1936). Studies in concept formation. IV. A comparison of white rats and raccoons with respect to their visual discrimination of certain geometrical figures. *Journal of Comparative Psychology, 21*, 341–355.

Frank, H., Frank, M. G., Hasselbach, L. M., & Littleton, D. M. (1989). Motivation and insight in wolf (*Canis lupus*) and Alaskan malamute (*Canis familiaris*): Visual discrimination learning. *Bulletin of the Psychonomic Society, 27*, 455–458.

Gadzichowski, K. M., Kapalka, K., & Pasnak, R. (2016). Response to stimulus relations by a dog (*Canis lupus familiaris*). *Learning & Behavior, 44*, 295–302.

Gácsi, M., Vas, J., Topál, J., & Miklósi, Á. (2013). Wolves do not join the dance: Sophisticated aggression control by adjusting to human social signals in dogs. *Applied Animal Behaviour Science, 145*, 109–122.

Galvan, M., & Vonk, J. (2016). Man's other best friend: Domestic cats (*F. silvestris catus*) and their understanding of human emotion cues. *Animal Cognition, 19*, 193–205.

Gazit, I., & Terkel, J. (2003). Domination of olfaction over vision in explosives detection by dogs. *Applied Animal Behavior Science, 82,* 65–73.

Giurfa, M., Zhang, S., Jenett, A., Menzel, R., & Srinivasan, M. V. (2001). The concepts of 'sameness' and 'difference' in an insect. *Nature, 410*, 930–933.

Gorman, M. L. (1976). A mechanism for individual recognition by odour in *herpestes auropunctatus (carnivora: Viverridae*). *Animal Behaviour, 24*, 141–145.

Gossette, R. L., & Inman, N. (1966). Comparison of spatial successive discrimination reversal performances of two groups of New World monkeys. *Perceptual and Motor Skills, 23*, 169–170.

Gossette, R. L., Kraus, G., & Speiss, J. (1968). Comparison of successive discrimination reversal (SDR) performances of seven mammalian species on a spatial task. *Psychonomic Science, 12*, 193–194.

Gregg, F. M., Jamison, E., Wilkie, R., & Radinsky, T. (1929). Are dogs, cats, and raccoons color blind? *Journal of Comparative Psychology, 9*, 379–395.

Hamilton, D. A., & Brigman, J. L. (2015). Behavioral flexibility in rats and mice: Contributions of distinct frontocortical regions. *Genes, Brain & Behavior, 14*, 4–21.

Hamilton, J., & Vonk, J. (2015). Do dogs (*Canis lupus familiaris*) recognize kin? *Behavioural Processes, 119*, 123–134.

Hare, B. (2007). From nonhuman to human mind: What changed and why? *Current Directions in Psychological Science, 16*, 60–64.

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences, 9*, 439–444.

Harlow, H. F. (1949). The formation of learning sets. *Psychological Review, 56*, 51–65.

Hayes, K. J., Thompson, R., & Hayes, C. (1953). Discrimination learning set in chimpanzees. *Journal of Comparative and Physiological Psychology, 46*, 99–104.

Hepper, P. G. (1994). Long-term retention of kinship recognition established during infancy in the domestic dog. *Behavioural Processes, 33*, 3–14.

Herrnstein, R. J. (1990). Levels of stimulus control: A functional approach. *Cognition, 37*, 133–166.

Hitchcock, L. J., Michels, K. M., & Brown, D. R. (1963). Discrimination learning: Squirrels vs. raccoons. *Perceptual and Motor Skills, 16*, 405–414.

Holekamp, K. E., Boydston, E. E., Szykman, M., Graham, I., Nutt, K. J., Birch, S.,…Singh, M. (1999). Vocal recognition in the spotted hyaena and its possible implications regarding the evolution of intelligence. *Animal Behaviour, 58*, 383–395.

Holekamp, K. E., Dantzer, B., Stricker, G., Yoshida, K. C., & Benson-Amram, S. (2015). Brains, brawn and sociality: A hyaena's tale. *Animal Behaviour*, *103*, 237–48.

Horowitz, A., Hecht, J., & Dedrick, A. (2013) Smelling more or less: Investigating the olfactory experience of the domestic dog. *Learning and Motivation, 44*, 207–217.

Huber, L., Racca, A., Scaf, B., Virányi, Z., & Range, F. (2013). Discrimination of familiar human faces in dogs (*Canis familiaris*). *Learning and Motivation, 44*, 258–269.

Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson and R. A. Hinde (Eds.), *In Growing Points in Ethology* (pp. 303–317). Cambridge, UK: Cambridge University Press.

Jolly, A. (1966). Lemur social behaviour and primate intelligence. *Science, 153*, 501–506.

Johnson, J. I., Jr., & Michels, K. M. (1958). Learning sets and object-size effects on visual discrimination learning by raccoons. *Journal of Comparative and Physiological Psychology, 51*, 376–379.

Johnson-Ulrich, Z., Hoffmaster, E., Robeson, A., & Vonk, J. (in press). Visual acuity in the striped skunk (*Mephitis mephitis*). *Journal of Comparative Psychology*.

Johnson-Ulrich, Z., Vonk, J., Humbyrd, M., Crowley, M., Wojtkowsk, E., Yates, F., & Allard, S. (2016). Picture object recognition in an American black bear (*Ursus Americanus*). *Animal Cognition*, *19*, 1237–1242.

Jordan, R. H., & Burghardt, G. M. (1986). Employing an ethogram to detect reactivity of black bears (*Ursus americanus*) to the presence of humans. *Ethology, 73*, 89–115.

Joshi, B. L., & Warren, J. M. (1959). Discrimination of ambivalent cue stimuli by cats. *The Journal of Psychology: Interdisciplinary and Applied, 47*, 3–7.

Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: Evidence for "fast mapping". *Science, 304*, 1682–1683.

Katz, J. S., Bodily, K. D., & Wright, A. A. (2008). Learning strategies in matching to sample: If-then and configural learning by pigeons. *Behavioural Processes, 77*, 223–230.

Keen, H. A., Nelson, O. L., Robbins, C. T., Evans, M., Shepherdson, D. J., & Newberry, R. C. (2014). Validation of a novel cognitive bias task based on difference in quantity of reinforcement for assessing environmental enrichment. *Animal Cognition, 17*, 529–541.

Kent, L., & Tang-Martínez, Z. (2014). Evidence of individual odors and individual discrimination in the raccoon, *Procyon lotor*. *Journal of Mammalogy, 95*, 1254–1262.

Laska, M., & Freyer, D. (1997). Olfactory discrimination ability for aliphatic esters in squirrel monkeys and humans. *Chemical Senses, 22*, 457–465.

Laska, M., Galizia, C. G., Giurfa, M., & Menzel, R. (1999). Olfactory discrimination ability and odor structure-activity relationships in honey-bees. *Chemical Senses, 24*, 429–438.

Laska, M., Lord, E., Selin, S., & Amundin, M. (2010). Olfactory discrimination of aliphatic odorants in South African fur seals (*Arctocephalus pusillus*). *Journal of Comparative Psychology, 124*, 187–193.

Laska, M., Svelander, M., & Amundin, M. (2008). Successful acquisition of an olfactory discrimination paradigm by South African fur seals *Arctocephalus pusillus*. *Physiology & Behavior, 93*, 1033–1038.

Lazarowski, L., Foster, M. L., Gruen, M. E., Sherman, B. L., Fish, R. E., Milgram, N. W., & Dorman, D. C. (2015). Olfactory discrimination and generalization of ammonium nitrate and structurally related odorants in Labrador retrievers. *Animal Cognition, 18*, 1255–1265.

Leising, K. J., Wolf, J. E., & Ruprecht, C. M. (2013). Visual discrimination learning with an iPad-equipped apparatus. *Behavioural Processes, 93*, 140–147.

Markman, E. M., & Abelev, M. (2004). Word learning in dogs? *Trends in Cognitive Sciences, 8*, 479–481.

Maros, K., Pongrácz, P., Bárdos, G., Molnár, C., Faragó, T., & Miklósi, Á. (2008). Dogs can discriminate barks from different situations. *Applied Animal Behaviour Science, 114*, 159–167.

Mayes, E. E., Wilkinson, A., Pike, T. W., & Mills, D. S. (2015). Individual differences in visual and olfactory cue preference and use by cats (*Felis catus*). *Applied Animal Behaviour Science, 173*, 52–59.

McComb, K., Packer, C., & Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions*, Panthera leo*. *Animal Behaviour,47*, 379–387.

McCulloch, M., Jezierski, T., Broffman, M., Hubbard, A., Turner, K., & Janecki, T. (2006). Diagnostic accuracy of canine scent detection in early- and late-stage lung and breast cancers. *Integrative Cancer Therapies, 5*, 30–39.

Merola, I., Lazzaroni, M., Marshall-Pescini, S., & Prato-Previde, E. (2015). Social referencing and cat-human communication. *Animal Cognition,* 3*,* 639–648.

Merola, I., Prato-Previde, E., Lazzaroni, M., & Marshall-Pescini, S. (2014). Dogs' comprehension of referential emotional expressions: familiar people and familiar emotions are easier. *Animal Cognition, 17*, 373–385.

Merola, I., Prato-Previde, E., & Marshall-Pescini, S. (2012). Social referencing in dog-owner dyads? *Animal Cognition, 15*, 175–185.

Michels, K. M., Fischer, B. E., & Johnson, J. I. (1960). Raccoon performance on color discrimination problems. *Journal of Comparative and Physiological Psychology, 53*, 379–380.

Miklósi, A., & Topál, J. (2012). The evolution of canine cognition. In J. Vonk & T. K. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp.194–213). New York, NY: Oxford University Press.

Milgram, N. W., Zicker, S. C., Head, E., Muggenburg, B. A., Murphey, H., Ikeda-Douglas, C., & Cotman, C. W. (2002). Dietary enrichment counteracts age-associated cognitive dysfunction in canines. *Neurobiology of Aging, 23*, 737–745.

Molnár, C., Pongrácz, P., Faragó, T., Dóka, A., & Miklósi, Á. (2009). Dogs discriminate between barks: The effect of context and identity of the caller. *Behavioural Processes, 82*, 198–201.

Miles, R. C., & Meyer, D. R. (1956). Learning sets in marmosets. *Journal of Comparative and Physiological Psychology, 49*, 219–222.

Muller, C. A., Schmitt, K., Barber, A. L. A., & Huber, L. (2015). Dogs can discriminate emotional expressions of human faces. *Current Biology, 25*, 601–605.

Perdue, B. M. (2016). The effect of computerized testing on sun bear behavior and enrichment preferences. *Behavioural Sciences*, *6.* doi:10.3390/bs6040019

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.

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.

Petrazzini, M. E. M., & Wynne, C. D. L. (2015). What counts for dogs (*Canus lupus familiaris*) in a quantity discrimination task? *Behavioural Processes, 122*, 90 – 97.

Pietrzykowska, B., & Soltysik, S. (1975a). Transfer of the "same-different" differentiation task in dogs. *Acta Neurobiologiae Experimentalis, 35*, 39–50.

Pietrzykowska, B., & Soltysik, S. (1975b). A failure to train the "same-different" differentiation of photic stimuli in dogs. *Acta Neurobiologiae Experimentalis, 35*, 27–38.

Pisa, P. E., & Agrillo, C. (2009). Quantity discrimination in felines: a preliminary investigation of the domestic cat (*Felis silvestris catus). Journal of Ethology, 27*, 289–293.

Pollard, J. S. (1959). *A maze for comparative behaviour studies.* (Unpublished masters thesis). University of Canterbury, New Zealand.

Pollard, J. S. (1964). Interspecies differences in closed-field test performance. *Perceptual and Motor Skills, 18*, 403–404.

Pongrácz, P., Szabó, E., Kis, A., Péter,A., & Míklósi, A. (2014). More than noise? Field investigations of intraspecific acoustic communication in dogs (*Canis familiaris*). *Applied Animal Behaviour Science, 159*, 62–68.

Racca, A., Amadei, E., Ligout, S., Guo, K., Meints, K., & Mills, D. (2010). Discrimination of human and dog faces and inversion responses in domestic dogs (*Canis familiaris*). *Animal Cognition, 13*, 525–533.

Range, F., Aust, U., Steurer, M., & Huber, L. (2008). Visual categorization of natural stimuli by domestic dogs. *Animal Cognition, 11*, 339–347.

Rensch, B. (1963). The relation between the evolution of the central nervous functions and the body size of animals. In J. Huzley, A. C. Hardy, & E. Ford (Eds.), *Evolution as a process* (pp.?). New York, NY: Collier Books.

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.

Roeder, J. J. (1980). Marking behaviour and olfactory recognition in Genets (*Genetta genetta L., Carnivora-Viverridae*). *Behaviour, 72*, 200–210.

Rogers, L. L., Mansfield, S. A., Hornby, K., Hornby, S., Debruyn, T. D., Mize, M., Burghardt, G. M. (2014). Black bear reactions to venomous and non-venomous snakes in eastern North America. *Ethology, 120*, 641–651.

Rosch, E. (1978). Principles of categorization. Cambridge, MA: MIT Press.

Rosch, E., & Mervis, C. B. (1975). Family resemblances: Studies in the internal structure of categories. *Cognitive Psychology, 7*, 573–605.

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.

Rosenzweig, M. (1946). Discrimination of auditory intensities in the cat. *The American Journal of Psychology, 59*, 127–136.

Saito, A., & Shinozuka, K. (2013) Vocal recognition of owners by domestic cats (*Felis catus). Animal Cognition 16*, 685–690.

Sauvé, C. C., Beauplet, G., Hammill, M. O., & Charrier, I. (2015). Mother–pup vocal recognition in harbour seals: Influence of maternal behaviour, pup voice and habitat sound properties. *Animal Behaviour, 105*, 109–120.

Schusterman, R. J. (1966). Serial discrimination: Reversal learning with and without errors by the California sea lion. *Journal of the Experimental Analysis of Behavior, 9*, 593–600.

Schusterman, R. J. (1967). Attention shift and errorless reversal learning by the California sea lion. *Science, 156*, 833–835.

Shell, W. F. (1955, May). *Learning sets in platyrrhine monkeys*. Paper presented at the meeting of the Southeast Psychological Association, Atlanta.

Shell, W. F., & Riopelle, A. J. (1958). Multiple discrimination learning in raccoons. *Journal of Comparative and Physiological Psychology, 50*, 585–587.

Smirnova, A., Zorina, Z., Obozova, T., & Wasserman, E. (2014). Crows spontaneously exhibit analogical reasoning. *Current Biology, 25*, 256–260.

Smith, K. U. (1935). Apparatus for the study of sensory discrimination in mammals. *Science, 82*, 423–425.

Sol, D. (2009). The cognitive-buffer hypothesis for the evolution of large brains. In R. Dukas & R. M. Ratcliffe (Eds.), *Cognitive Ecology II* (pp. 111–136). Chicago, IL: University of Chicago Press.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences USA, 102*, 5460–5465.

Sol, D., Szekely, T., Liker, A. & Lefebvre, L. (2007) Big-brained birds survive better in nature. *Proceedings of the Royal Society B*, 274, 763–769.

Somppi, S., Törnqvist, H., Hänninen, L., Krause, C., & Vainio, O. (2012). Dogs do look at images: Eye tracking in canine cognition research. *Animal Cognition, 15*, 163–174.

Sutherland, N. S. (1963). Cat's ability to discriminate oblique rectangles. *Science, 139*, 209–210.

Takagi, S., Arahori, M., Chijiiwa, H., Tsuzuki, M., Hataji, Y., & Fujita, K. (2016). There's no ball without noise: Cats' prediction of an object from noise. *Animal Cognition, 19*, 1043–1047.

Theis, K. R., Schmidt, T. M., & Holekamp, K. E. (2012). Evidence for a bacterial mechanism for group-specific social odors among hyenas. *Scientific Reports, 2*, 615.

Theis, K. R., Venkataraman, A., Dycus, J. A., Koonter, K. D., Schmitt-Matzen, E. N., Wagner, A. P.,…Schmidt, T.M. (2013). Symbiotic bacteria appear to mediate hyena social odors. *Proceedings of the National Academy of Sciences, 110*, 19832–19837.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York, NY: Oxford University Press.

Vas, J., Topál, J., Gácsi, M., Miklósi, Á., & Csányi, V. (2005). A friend or an enemy? dogs' reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. *Applied Animal Behaviour Science, 94*, 99–115.

Vas, J., Topál, J., Győri, B., & Miklósi, Á. (2008). Consistency of dogs' reactions to threatening cues of an unfamiliar person. *Applied Animal Behaviour Science, 112*, 331–344.

Vitale Shreve, K. R., & Udell, M. A. R. (2015). What's inside your cat's head? A review of cat (*Felis silvestris catus*) cognition research past, present and future. *Animal Cognition, 18*, *1195–1206.*

Vonk, J. (2015). Corvid cognition: Something to crow about? *Current Biology, 25*, R69–R71.

Vonk, J. (2016). Bigger brains may make better problem-solving carnivores. *Learning and Behavior, 44*, 99–100.

Vonk, J., Allard, S., Torgerson-White, L., Bennett, C., Galvan, M., McGuire, M. M., Hamilton, J., Johnson-Ulrich, Z., & Lieb. J. (2015). Manipulating spatial and visual cues in a win-stay foraging task in captive grizzly bears (*Ursus arctos horribilus*). In E. A. Thayer (Ed.) *Spatial, Long-and Short-term Memory: Functions, Differences and Effects of Injury* (pp. 47–60). Hauppauge, NY: Nova Publishers.

Vonk, J., & Beran, M. J. (2012). Bears "count" too: Quantity estimation and comparison in black bears (*Ursus americanus*). *Animal Behaviour, 84*, 231–238.

Vonk, J., & Galvan, M. (2014). What do natural categorization studies tell us about apes and bears? *Animal Behavior & Cognition, 1*, 309–330.

Vonk, J., Jett, S. E., & Mosteller, K. W. (2012). Concept formation in American black bears, (*Ursus americanus). Animal Behaviour, 84*, 953–964.

Vonk, J., Jett, S. E., Mosteller, K. W., & Galvan, M. (2013). Natural category discrimination in chimpanzees (*Pan troglodytes*) at three levels of abstraction. *Learning and Behavior, 41*, 271–284.

Vonk, J., & Johnson-Ulrich, Z. (2014). Social and nonsocial category discriminations in a chimpanzee (*Pan troglodytes*) and American black bears (*Ursus americanus*). *Learning and Behavior, 42*, 231–245.

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. (2006). Similarity and difference in the conceptual systems of primates: The Unobservability hypothesis. In E.Wasserman & T. Zentall (Eds.), *Comparative Cognition: Experimental Explorations of Animal Intelligence*. (pp. 363–387). England: Oxford University Press.

Ward, R. E., & Smuts, B. B. (2007). Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Animal Cognition, 10*, 71–80.

Waroff, A. J., Fanucchi, L., Robbins, C. T., & Nelson, O. L. (2017). Tool use, problem-solving, and the display of stereotypic behaviors in the brown bear (*Ursus arctos*). *Journal of Veterinary Behavior, 17*, 62–68.

Warren, J. M., & Baron, A. (1956). The formation of learning sets by cats. *Journal of Comparative and Physiological Psychology, 49*, 227–231.

Warren, J. M., & Warren, H. B. (1959). Interspecies differences in learning by carnivores? *Perceptual and Motor Skills, 9*, 1–346.

Wasserman, E. A., & Young, M. E. (2010). Same–different discrimination: The keel and backbone of thought and reasoning. *Journal of Experimental Psychology: Animal Behavior Processes, 36*, 3–22.

West, S., Jett, S. E., Beckman, T., & Vonk, J. (2010). The phylogenetic roots of cognitive dissonance. *Journal of Comparative Psychology, 124*, 425–432.

Willis, C. M., Church, S. M., Guest, C. M., Cook, W. A., McCarthy, N., Bransbury, A. J.,…Church, J. C. (2004). Olfactory detection of bladder cancer by dogs: Proof of principle study. *British Medical Journal, 329*, 712 – 716.

Wright, A. A. (1993). When is a stimulus a pattern? In T. Zentall (Ed). *Animal cognition: A tribute to Donald A. Riley*. (pp. 35–41) Hillsdale, NJ: Lawrence Erlbaum Associates.

Wright, A. A., Cook, R. G., Rivera, J. J., Sands, S. F., & Delius, J. D. (1988). Concept learning by pigeons: Matching-to-sample with trial-unique video picture stimuli. *Animal Learning & Behavior, 16*, 436–444.

Zamisch, V., & Vonk, J. (2012). Spatial memory in captive American black bears (*Ursus americanus*). *Journal of Comparative Psychology, 126*, 372–387.

Zanghi, B. M., Araujo, J., & Milgram, N. W. (2015). Cognitive domains in the dog: Independence of working memory from object learning, selective attention, and motor learning. *Animal Cognition, 18*, 789–800.

Żernicki, B., & Zabłocka, T. (1996). Object discrimination learning and object—pattern discrimination transfer in visually deprived cats. *Behavioural Brain Research, 82*, 79–83.

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