



Understanding of object properties by sloth bears, *Melursus ursinus ursinus*

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Recent studies have shown that several species within the Carnivore order show impressive cognitive skills. However, bears, especially sloth bears, have received little attention with regard to their cognitive abilities. Here we presented seven sloth bears with three tasks to test their object permanence, short-term memory and ability to use acoustic cues to infer food location. In the object permanence test, subjects saw an object disappear in one of the three holes of a tree trunk. Bears retrieved the food in the correct hole significantly above chance, suggesting that they have some basic understanding that objects continue to exist even when they are not visible. To study sloth bears' short-term memory, we used different time delays (30 s, 60 s, 2 min) between the object's disappearance and the subject's retrieval. Bears performed at chance levels in all conditions. In the acoustic cues test, the experimenter shook one of two identical opaque containers, only one of which had been baited: when the baited container was shaken, this made a noise and thus revealed the presence of food inside; when the unbaited container was shaken, there was no noise, revealing by exclusion the presence of food in the other container. In both cases, bears selected the baited container significantly above chance. As sloth bears are a mainly insectivorous solitary species, good performance in the object permanence and acoustic cue tests suggests that their cognitive skills may be the result of foraging challenges rather than social ones. Failure in the short-term memory test, instead, may suggest that memory for short-term punctual events has little evolutionary significance for bears, although further studies are needed to draw definitive conclusions. © 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Studies of animal cognition are not equally distributed across taxa. Although studying cognition in some species may be especially rewarding if one seeks to investigate the evolutionary origins of human cognition (see e.g. Nielsen & Haun, 2015), the inclusion of diverse taxa is essential to understand how cognitive skills are distributed across species. This also helps to better contrast the different evolutionary hypotheses trying to explain such a distribution. Accordingly, there has been growing interest in the study of cognition in other taxa.

The Carnivore order, for instance, includes several species which are good candidates for having complex cognitive skills, having undergone a domestication process, showing a high degree of

dietary complexity or living in complex societies, all factors that have been linked to an enhancement of cognitive skills (see Barton & Dunbar, 1997; Barton, 2012; Dunbar, 1998; Hare, Brown, Williamson, & Tomasello, 2002; Milton, 1981). Dogs, *Canis familiaris*, for example, show complex cognitive skills across different domains, from discrimination learning and object permanence to spatial cognition and memory (Bensky, Gosling, & Sinn, 2013). In the social domain, dogs' cognitive skills appear to be especially enhanced (Bensky et al., 2013), although it is still debated whether this results from the domestication process (see Hare & Tomasello, 2005; Hare et al., 2002; Wynne, 2016). Enhanced cognitive skills have also been shown in other carnivore species that have not been domesticated, such as spotted hyaenas, *Crocuta crocuta*. Spotted hyaenas live in complex societies and accordingly show complex cognitive skills (see Aureli et al., 2008), including the ability to recognize individual conspecifics across multiple sensory modalities and recognize third-party kin and rank relationships among

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clan mates (Holekamp & Engh, 2002; see Vonk & Leete, 2017). Hyaenas can successfully solve novel foraging problems (Benson-Amram & Holekamp, 2012), and further assess whether their group outnumbers intruders based on the number of intruders' calls (Benson-Amram, Heinen, Dryer, & Holekamp, 2011), similarly to lions (McComb, Packer, & Pusey, 1994).

In contrast to these species, bears have not been domesticated and show very limited social interactions. However, they have large brains, and most species also have a generalist and highly seasonal diet (but see e.g. giant pandas, *Ailuropoda melanoleuca*, and polar bears, *Ursus maritimus*, for exceptions; Barton & Dunbar, 1997; Gittleman, 1986). This suggests that their cognitive skills may also be enhanced, possibly due to foraging rather than social challenges. Many bear species have unfortunately long been kept as pets by humans, used in circuses and for human entertainment (Burghardt, 1992; Hediger, 1964). Although these practices are ethically unacceptable, they suggest that these species may have good learning skills as well as the ability to adapt their responses (see e.g. Bacon & Burghardt, 1976). In terms of learning, black bears, *Ursus americanus*, may socially learn their foraging behaviour (Mazur & Seher, 2008) and can learn abstract concepts (Vonc, Jett, & Mosteller, 2012), although evidence on the acquisition of social concepts is more equivocal (Vonc & Johnson-Ulrich, 2014). Bears also demonstrate long-term memory of the concepts acquired, retaining them after several months (giant pandas: Dungl, Schratte, & Huber, 2008; black bears: Vonk et al., 2012).

Recent studies have also addressed bears' cognitive skills other than learning. Black bears, for instance, show picture–object recognition (Johnson-Ulrich et al., 2016), may outperform gorillas, *Gorilla gorilla*, in discrimination learning tasks with the ambiguous cue paradigm (McGuire, Vonk & Johnson-Ulrich, 2017), and may partially use numbers to make numerosity judgements (Vonc & Beran, 2012). Bears also show evidence of tool use. In the wild, brown bears, *Ursus arctos*, use rocks as tools to relieve irritated skin or remove food remains from fur (Deecke, 2012), and in captivity they sometimes use objects to obtain out-of-reach food (Waroff, Fanucchi, Robbins, & Nelson, 2017). Bears are also proficient at solving novel foraging tasks. In a study comparing 39 carnivore species (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016), the best innovators were those species with larger brains relative to their body mass, including spectacled bears, *Tremarctos ornatus*, black bears, brown bears and polar bears, but not sun bears, *Helarctos malayanus*. Few studies have tested spatial memory in bears. Zarnisch and Vonk (2012) tested black bears foraging among baited and unbaited sites. The sites were then baited anew out of view of the bears, which were allowed to forage again after delays of 15 min to 4 h. The bears failed to locate the food in the baited sites, even when competition was increased, but their performance increased slightly when the same locations were repeatedly baited across several days. Although grizzly bears, *Ursus arctos horribilis*, also failed to locate food when tested with a similar procedure (Vonc et al., 2015), giant pandas appeared to be more successful in spatial memory tasks (Perdue, Snyder, Pratte, Marr, & Maple, 2009; Perdue, Snyder, Zhihe, Marr, & Maple, 2011).

Within the Carnivore order, nothing is yet known about a mostly nocturnal bear species native to India: the sloth bear (Brown, 1993; Yoganand, 2005). Adult sloth bears rarely interact with one another outside the mating season and, in contrast to some other bear species, do not congregate in feeding groups (Brown, 1993). Like some other bear species, however, they have a relatively complex diet (Brown, 1993), suggesting that foraging challenges, rather than social ones, may have been the driving force for the evolution of cognitive skills. We therefore selected some classic tasks to assess sloth bears' skills in the physical domain. First, we tested their object permanence (OP) skills; as they largely feed on termites and

honeybee colonies, which mostly consist of hidden prey, sloth bears should understand that food exists even when they cannot see it. Moreover, given that insects may remain out of view for long periods, bears could also have evolved the ability to maintain a short-term memory of food locations. Furthermore, acoustic cues may play an important role in this species: solitary individuals communicate with distant conspecifics through a large vocal repertoire (Brown, 1993), and relying on acoustic cues may be especially advantageous when foraging at night. Therefore, we tested whether bears could rely on acoustic cues to locate food, as other acoustic-dependent species (grey parrots, *Psittacus erithacus*: Schloegl, Schmidt, Boeckle, Weiss, & Kotrschal, 2012) and large-brained species do (dogs: Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; great apes: Call, 2004; capuchin monkeys, *Sapajus apella*: Paukner, Huntsberry, & Suomi, 2009; Sabbatini & Visalberghi, 2008; olive baboons, *Papio anubis*: Schmitt & Fischer, 2009). Finally, as sloth bears also communicate with conspecifics via olfactory cues (Laurie & Seidensticker, 1977), we included an olfactory control condition to exclude potential smell cues during testing.

METHODS

Subjects

We tested seven sloth bears of both sexes (four females, three males) and different ages (from 2 to 18 years; mean age \pm SE: 7 years and 4 months \pm 5 years and 8 months). One female (Heidirose) completely lost interest in the task after participating in 24 trials (of the 76 planned), so we included only these 24 trials in the analyses (which included all conditions). All bears are housed in the Leipzig Zoo, where they have access to several indoor and outdoor enclosures. Except for a mother and her cubs, bears are usually housed in individual enclosures. Although all bears receive different forms of enrichment, none of them had previous experience with cognitive tasks. During the task, individuals were never food deprived, and motivation to participate was ensured by using highly preferred food (i.e. cereals or fruit dipped in honey). The Leipzig Zoo controlled and approved the procedures.

Set-up

To increase the ecological validity of the task, we used a tree trunk to present food items to the bears (Fig. 1). The tree trunk was presented horizontally. It had three holes of approximately 20 \times 15 cm (one in the middle, one on the right and one on the left), which went all the way through the log, and which bears could access by extending their paw through the bars. In most conditions (see below), a small opaque curtain covered each of the three holes, so that food placed inside the holes could not be seen by bears, once the curtain was put back in place. The tree trunk could be moved closer to or further from the bear.

Habituation and Training

Subjects were first habituated to the set-up: for 2 days, the experimenter (E) positioned the tree trunk (with no curtains) in front of each subject, outside the cage but within its reach, so that subjects could insert their paws and freely explore the trunk for 30 min a day. After the 2 days, all bears had shown interest in the trunk (i.e. touching, moving or exploring the trunk and its holes), and could proceed to the training. During the training, the tree trunk had no curtains, so that food was visible inside the holes. E pulled the trunk closer and out of the bear's reach, visibly positioned the food in one of the three holes, and then pushed the

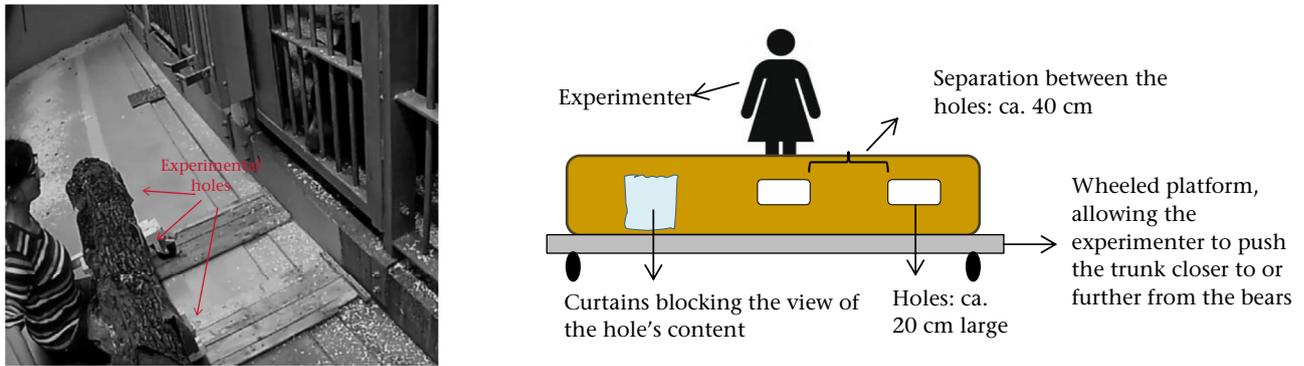


Figure 1. Experimental set-up from the experimenter's perspective (left) and from the bear's perspective (right).

trunk closer to the bear. The subject could retrieve the visible food by directly grabbing for it, or by extending the paw in the direction of one of the holes (so that E immediately delivered the chosen food), within 60 s. After four successful choices in five consecutive trials (which were completed within 5–20 trials, depending on the subject), curtains were placed in front of each hole and the empty tree trunk was pushed closer to the bear for 5 min, so that the subject could explore it. All subjects passed the training within one session. We then proceeded to the test phase, administering the following conditions in a pseudorandomized order across subjects through several sessions, counterbalancing the position of food across trials and conditions, and without locating food more than three consecutive times on the same side. In all the tests, bears were always given 60 s to make a choice. If they did not make a choice within this time (i.e. five trials), the experimenter coded the choice as being wrong and proceeded to the next trial.

Object Permanence Condition

We placed opaque curtains in front of the three holes. At the beginning of each trial, all curtains were opened, showing the empty holes to the bear. E was in the middle, pulled the tree trunk closer and out of the bear's reach, took a piece of food from behind the trunk with her right hand and kept it in the air to show it to the bear. When the bear was watching, E bent a little bit over the trunk and slowly placed the food in one of the holes, baiting the hole from the bear's side and closing the curtains (always starting from the left curtain, to control for stimulus enhancement), so that the holes were completely covered, and their contents could not be seen. Then E came back with her body in the middle and pushed the trunk closer to the bear, so that the subject could make a choice. After the choice, E moved the trunk out of the bear's reach, gave the food to the bear if it made a correct choice, and showed the bear the contents of each hole by opening the curtains. This condition tested whether bears understood that objects continue to exist when they are not visible (see [Cacchione & Rakoczy, 2017](#)). We administered 12 trials to each bear (i.e. four for each location).

Memory Conditions

We used the same procedure as in the Object permanence condition, but after baiting a hole and closing all curtains, we added a delay before allowing subjects to retrieve the food. The Memory condition tested whether bears remembered the location of hidden food after a short delay (see [Cacchione & Rakoczy, 2017](#)) of 30 s, 60 s or 2 min, administered in a counterbalanced order. We

administered a total of 36 trials to each bear (i.e. four for each location and condition).

Olfactory Control Condition

We used the same procedure as in the Object permanence condition, but the opaque curtains were always closed. E showed the food to the bear, as above, and when the bear was watching, E lowered it in the middle of the trunk and then simultaneously moved her hands laterally (briefly pausing in front of each hole), leaving the food in one of the three holes by baiting it from E's side and ensuring that no visible cue was provided to bears as to the position of the food. This condition controlled for the possibility that subjects could smell or see the food, or used cues given inadvertently by E to locate hidden food in the other conditions ([Albiach-Serrano et al., 2012](#); [Bräuer et al., 2006](#); see [Brown, 1993](#) for sloth bears' ability to locate food based on olfactory cues). We administered 12 trials to each bear (i.e. four for each location).

Shake Full Condition

E removed all curtains and pulled the tree trunk closer and out of the bear's reach. From behind the trunk, E took two identical paperboard containers, placed the food in one of the two out of the subject's view, raised both containers simultaneously above the corresponding lateral holes, and then shook the full container three times, to make the noise of the contents clearly audible. Then E simultaneously placed both containers in the corresponding lateral holes (baiting the hole from the bear's side when the bear was watching), came back with her body in the middle and then pushed the trunk closer to the bear, so that it could make a choice. As soon as the choice was made, the trunk was moved out of reach, the content of each container was shown to the bear and, for a correct choice, the food was given to the subject. This condition tested whether bears could use sound to locate hidden food (see [Call, 2004](#)). We administered eight trials to each bear (i.e. four for each location).

Shake Empty Condition

We used the same procedure as in the Shake full condition, but the empty container was shaken instead. This condition controlled for the possibility that subjects in the Shake full condition were relying on sound to make their choice, and not on stimulus enhancement, and further tested whether bears could infer by exclusion the location of food, from the lack of sound in the shaken container (see [Call, 2004](#)). Here, the bears had to first deduce that the absence of noise indicated an absence of food, and then had to

use this information to predict the presence of food in the other container (Schloegl et al., 2012). Shaking both empty and full containers in the same trials, instead, would not have allowed us to test inferential reasoning, but would have simply informed us about the bears' ability to follow acoustic cues to locate food. We administered eight trials to each bear (i.e. four for each location). Each subject received the first Shake trial after receiving at least 10 other trials, in which they associated testing with the presence of one food reward.

Statistical Analyses

We videorecorded 91% of the trials. A second observer later coded 25% of these trials for interobserver reliability, which was excellent (Cohen's $k = 0.91$, $N = 109$, $P < .001$; Gamer, Lemon, Fellows, & Singh, 2012). For each subject and trial, we coded whether subjects made the correct choice by choosing the location in which food had been hidden. Our dependent variable was each subject's mean percentage of correct choices. Given the limits of our data set, the use of a generalized linear mixed model was not advisable, as it led to a highly dispersed model, with convergence issues. We therefore ran nonparametric statistics in R 3.2.3 (R Core Team, 2016). Specifically, Wilcoxon exact tests (Hothorn & Hornik, 2017) were used to analyse whether the mean percentage of correct choices in each condition deviated from chance (i.e. 33% of choices in Object permanence, Memory and Olfactory control conditions; and 50% in Shake full and Shake empty conditions). We further used Wilcoxon exact tests to compare Object permanence and Memory conditions, to see whether conditions differed when increasing the delay. Finally, we repeated these analyses by including only the first two trials of each condition, to analyse bears' performance in the absence of learning effects. The alpha level was set at 0.05.

RESULTS

In the first two trials, performance was at chance level in the Olfactory control condition ($T = 6$, $N = 4$, $P = 0.188$). Performance was also at chance level in all the other conditions (Object permanence: $T = 23$, $N = 3$, $P = 0.188$; Memory 30 s: $T = 10$, $N = 5$, $P = 0.469$; Memory 60 s: $T = 13$, $N = 4$, $P = 0.859$; Memory 2 min: $T = 17$, $N = 3$, $P = 0.688$; Shake full: $T = 3$, $N = 2$, $P = 0.500$; Shake empty: $T = 12$, $N = 5$, $P = 0.375$).

As can be seen in Fig. 2, overall, subjects performed above chance level in the Object permanence condition ($T = 21$, $N = 6$, $P = 0.031$). In the Memory conditions, they performed at chance level (Memory 30 s: $T = 14$, $N = 5$, $P = 0.125$; Memory 60 s: $T = 6$, $N = 3$, $P = 0.250$; Memory 2 min: $T = 18$, $N = 6$, $P = 0.125$) and significantly worse than in the Object permanence condition (Memory 30 s: $T = 27$, $N = 6$, $P = 0.031$; Memory 60 s: $T = 21$, $N = 6$, $P = 0.031$; Memory 2 min: $T = 26.5$, $N = 6$, $P = 0.047$; Fig. 2). There was no difference in performance across the Memory conditions (Memory 30 s–60 s: $T = 4.5$, $N = 3$, $P = 0.750$; Memory 30 s–2 min: $T = 9.5$, $N = 2$, $P = 0.688$; Memory 60 s–2 min: $T = 7$, $N = 3$, $P > 0.999$). For interindividual variation, see Fig. 2. Subjects performed at chance level in the Olfactory control condition ($T = 0$, $N = 5$, $P = 0.063$; Fig. 2), indicating that subjects did not rely on smell when tested. Finally, subjects performed above chance in the Shake full ($T = 26.5$, $N = 7$, $P = 0.047$) and Shake empty conditions ($T = 21$, $N = 6$, $P = 0.031$; Fig. 2).

DISCUSSION

In our study, sloth bears' performance was better than chance level in the Object permanence, the Shake full and the Shake empty conditions. Importantly, bears did not rely on olfactory cues to locate hidden food, as they performed at chance level in the Olfactory control condition. In all Memory conditions, however, performance remained at chance level and worse than in the Object permanence condition.

Like other species (see Cacchione & Rakoczy, 2017 for a review), bears understand that objects continue to exist when they are not visible. Importantly, the procedure we used (closing the curtains by always following the same order) ensured that individuals relied on object permanence and not merely stimulus enhancement (i.e. select the last location touched by the experimenter) to locate food. However, their performance remained at chance level when a delay was introduced between baiting and retrieval. If there was a 30 s delay, bears failed to reliably locate the food they had seen disappear into one of the three holes. Incidentally, bears maintained continuous visual contact with the set-up more frequently during shorter trials (i.e. Object permanence, Olfactory control and Shake conditions) than during longer trials (i.e. Memory conditions). Therefore, it is possible that success in shorter trials was facilitated by the possibility to continuously focus their gaze on the set-up when trials were shorter. Our results are in contrast with what has been found in other species, which decrease their performance

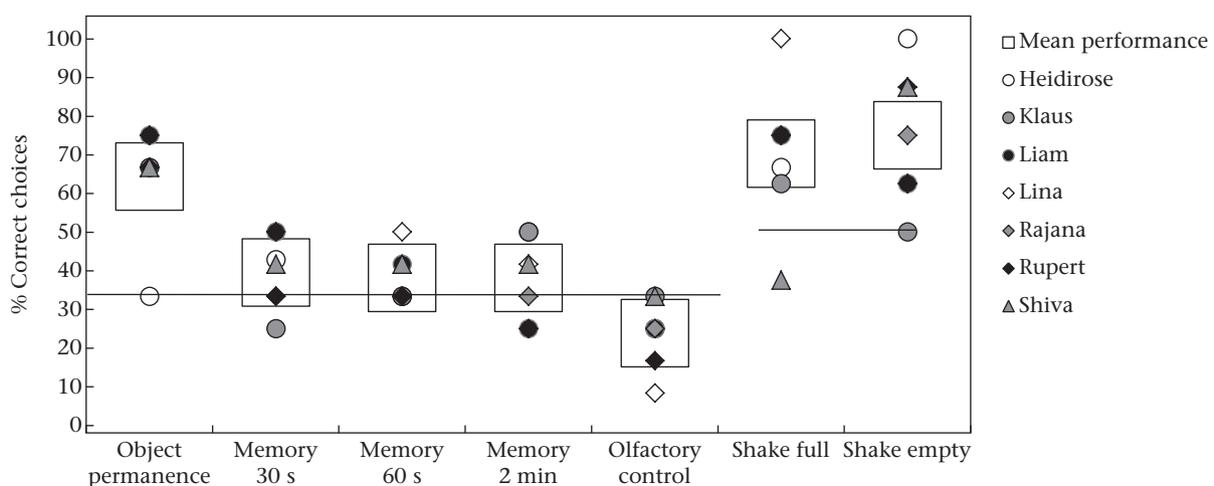


Figure 2. For each condition, mean percentage of correct choices for all the bears tested, and for each individual separately, across all trials. Horizontal lines represent chance levels.

but still manage to locate food after a comparable delay (e.g. chimpanzees, *Pan troglodytes*, bonobos, *Pan paniscus*, orang-utans, *Pongo abelii*: Barth & Call, 2006; Hribar & Call, 2011; capuchin monkeys, spider monkeys, *Ateles geoffroyi*, long-tailed macaques, *Macaca fascicularis*: Amici et al., 2010; dogs: Fiset et al., 2003; cats, *Felis catus*: Fiset & Doré, 2006). However, these results are in line with the only other study testing short-term memory in bears, which found that black bears fail to remember the location of hidden food after a 15 min delay (Zamisch & Vonk, 2012).

Of course, this is not to say that bears have no short-term memory. With other experimental procedures, or in the wild, bears may show better memory. In the wild, for instance, the costs of a wrong choice are much higher than in captivity, and wild subjects may be more motivated to remember the location of food (see e.g. Vonk et al., 2015). However, it may also be that bears can better remember long-term, repeated events, rather than short-term punctual ones. Despite failing to locate food after a delay of 15 min, for instance, black bears learned to do so if they repeatedly experienced specific food locations over time (Zamisch & Vonk, 2012). Similarly, black bears and giant pandas can retain a memory of newly acquired concepts even after several months (Dungl et al., 2008; Vonk et al., 2012). Anecdotally, sloth bears have impressive long-term memory, recognizing vets after several months (zookeepers at the Leipzig zoo, personal communication). Therefore, it is possible that sloth bears may perform very differently in a long-term memory task, if stimuli were presented through other modalities (e.g. olfactory) or if negative stimuli (e.g. vets) rather than positive stimuli (e.g. food) were used.

In contrast, bears performed remarkably well in the Shake full and Shake empty conditions. Like great apes (Call, 2004), and in contrast to wild boars, *Sus scrofa scrofa*, and domestic pigs, *Sus scrofa domestica* (Albiach-Serrano et al., 2012), sloth bears reliably selected the container with a food reward, both when the baited and the unbaited containers were shaken. This shows that bears did not simply base their choice on stimulus enhancement, going for the shaken cup regardless of the sound made. Instead, bears could use auditory information as a cue to locate food (Shake full), and could further infer by exclusion that containers producing no sound also contained no food (Shake empty). Given that the bears we tested are captive and, thus, often exposed to human artefacts, it is unfortunately not possible to rule out that the bears did not have a causal understanding that food causes noise, but rather had simply learned to associate the noise with food throughout their lives. In this respect, testing wild bears would help to disentangle whether associative learning or causal inference helped bears to solve the task, and could provide more cues about the ecological relevance of this skill, which probably reflects natural foraging habits. In the wild, for instance, sloth bears often feed on honey (Brown, 1993). Not only are active honeybee hives usually surrounded by flying buzzing bees (so that sloth bears may simply associate acoustic cues with food), but they also produce sound when shaken (so that bears may appreciate the causal link between food and sound).

Overall, our findings suggest that bears' cognitive skills in the physical domain only partially reflect their large brains and relatively complex diet (Brown, 1993): although they showed object permanence, used cues to locate food and could infer the location of food by exclusion, they failed to remember hidden food after more than 30 s. It is possible that these differences in performance across tasks reflect more specific foraging challenges faced by bears during evolution. For instance, bears may need object permanence because they largely feed on continuously hiding termites and honeybees; they may need to keep long-term memories of the spatial location of their colonies, but may not specifically need

short-term memory to keep track of insects when they are out of view, as bears do not individually follow and eat single insects. However, it is also possible that some of the skills shown in bears are shared with other carnivores as a result of homology, instead of reflecting specific selective pressures experienced since bears diverged from the other taxa. Apart from object permanence tasks, which have been conducted across a variety of species and suggest that this is a rather common skill (within and outside the Carnivore order), the paucity of comparable data in the physical domain does not allow us to draw any definitive conclusion on the evolutionary origins of bears' cognitive skills.

Overall, our study confirms that bears are a promising candidate for research on comparative cognition. The exploration of different cognitive domains in this taxon may reveal interesting distributions of cognitive skills, which may, in turn, allow us better understanding of the evolutionary forces shaping cognition. The use of different experimental approaches and, ideally, the inclusion of wild individuals, will provide a unique opportunity to gain a better insight into the cognitive skills of these fascinating but still understudied species.

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References

- Albiach-Serrano, A., Bräuer, J., Cacchione, T., Zickert, N., Amici, F., Ujfalussy, D., et al. (2012). The effect of domestication and ontogeny in swine cognition (*Sus scrofa scrofa* and *S. s. domestica*). *Applied Animal Behaviour Science*, 141(1–2), 25–35. <https://doi.org/10.1016/j.applanim.2012.07.005>.
- Amici, F., Aureli, F., & Call, J. (2010). Monkeys and apes: Are their cognitive skills really so different? *American Journal of Physical Anthropology*, 143, 188–197.
- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., et al. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology*, 49(4), 627–654. <https://doi.org/10.1086/586708>.
- Bacon, E. S., & Burghardt, G. M. (1976). Learning and color discrimination in the American black bear. *International Conference on Bear Research & Management*, 3, 27–36. Retrieved from http://www.bearbiology.com/fileadmin/tpl/Downloads/URSUS/Vol_3/Bacon_Burghardt_B_Vol_3.pdf.
- Barth, J., & Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, and *Pongo pygmaeus*) and young children (*Homo sapiens*). *Journal of Experimental Psychology*, 32, 239–252.
- Barton, R. A. (2012). Embodied cognitive evolution and the cerebellum. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1599), 2097–2107. <https://doi.org/10.1098/rstb.2012.0112>.
- Barton, R. A., & Dunbar, R. I. M. (1997). Evolution of the social brain. In A. Whiten, & R. Byrne (Eds.), *Machiavellian intelligence* (pp. 240–263). Cambridge, U.K.: Cambridge University Press.
- Bensky, M. K., Gosling, S. D., & Sinn, D. L. (2013). The world from a Dog's point of view. In *Advances in the study of behavior* (Vol. 45, pp. 209–406). <https://doi.org/10.1016/B978-0-12-407186-5.00005-7>.
- 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(9), 2532–2537. <https://doi.org/10.1073/pnas.1505913113>.
- 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(4), 743–752. <https://doi.org/10.1016/j.anbehav.2011.07.004>.

- Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, 279(1744), 4087–4095. <https://doi.org/10.1098/rspb.2012.1450>.
- Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology*, 120(1), 38–47. <https://doi.org/10.1037/0735-7036.120.1.38>.
- Brown, G. (1993). *The great bear almanac*. New York, NY: Lyons & Burford Publishers.
- Burghardt, G. M. (1992). Human-bear bonding in research on black bear behavior. In H. Daid, & D. Balfour (Eds.), *The inevitable bond: Examining scientist-animal interactions* (pp. 365–382). Cambridge; New York, NY: Cambridge University Press.
- Cacchione, T., & Rakoczy, H. (2017). Comparative metaphysics: Thinking about objects in space and time. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. R. Zentall (Eds.), *APA Handbook of comparative psychology* (pp. 579–599). Washington, DC: American Psychological Association.
- Call, J. (2004). Inferences about the location of food in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *Journal of Comparative Psychology*, 118(2), 232–241. <https://doi.org/10.1037/0735-7036.118.2.232>.
- Deecke, V. B. (2012). Tool-use in the brown bear (*Ursus arctos*). *Animal Cognition*, 15(4), 725–730. <https://doi.org/10.1007/s10071-012-0475-0>.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, 178–190. [https://doi.org/10.1002/\(SICI\)1520-6505\(1998\)6:5<178::AID-EVAN5>3.3.CO;2-P](https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.3.CO;2-P).
- Dungl, E., Schratler, D., & Huber, L. (2008). Discrimination of face-like patterns in the giant panda (*Ailuropoda melanoleuca*). *Journal of Comparative Psychology*, 122(4), 335–343. <https://doi.org/10.1037/0735-7036.122.4.335>.
- Fiset, S., Beaulieu, C., & Landry, F. (2003). Duration of dogs' (*Canis familiaris*) working memory in search for disappearing objects. *Animal Cognition*, 6, 1–10.
- Fiset, S., & Doré, F. Y. (2006). Duration of cats' (*Felis catus*) working memory for disappearing objects. *Animal Cognition*, 9, 62–70.
- Gamer, M., Lemon, J., Fellows, I., & Singh, P. (2012). *Irr: Various coefficients of interrater reliability and agreement*. Retrieved from <https://cran.r-project.org/package=irr>.
- Gittleman, J. L. (1986). Carnivore brain size, behavioral ecology, and phylogeny. *Journal of Mammalogy*, 67(1), 23–36. <https://doi.org/10.1126/science.95.2469.427-b>.
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, 298(5598), 1634–1636. <https://doi.org/10.1126/science.1072702>.
- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, 9(9), 439–444. <https://doi.org/10.1016/j.tics.2005.07.003>.
- Hediger, H. (1964). *Wild animals in captivity*. New York, NY: Dover.
- Holekamp, K. E., & Engh, A. L. (2002). Field studies of social cognition in spotted hyenas. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 371–377). Oxford, U.K.: Oxford University Press.
- Hothorn, T., & Hornik, K. (2017). *Exact distributions for rank and permutation tests*. Retrieved from <https://cran.r-project.org/web/packages/exactRankTests/exactRankTests.pdf>.
- Hribar, A., & Call, J. (2011). Great apes use landmark cues over spatial relations to find hidden food. *Animal Cognition*, 14, 623–635.
- Johnson-Ulrich, Z., Vonk, J., Humbyrd, M., Crowley, M., Wojtkowski, E., Yates, F., et al. (2016). Picture object recognition in an American black bear (*Ursus americanus*). *Animal Cognition*, 19(6), 1237–1242. <https://doi.org/10.1007/s10071-016-1011-4>.
- Laurie, A., & Seidensticker, J. (1977). Behavioural ecology of the sloth bear (*Melursus ursinus*). *Journal of Zoology*, 182(2), 187–204. <https://doi.org/10.1111/j.1469-7998.1977.tb04155.x>.
- Mazur, R., & Seher, V. (2008). Socially learned foraging behaviour in wild black bears, *Ursus americanus*. *Animal Behaviour*, 75(4), 1503–1508. <https://doi.org/10.1016/j.anbehav.2007.10.027>.
- 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. <https://doi.org/10.1006/anbe.1994.1052>.
- McGuire, M. C., Vonk, J., & Johnson-Ulrich, Z. (2017). Ambiguous results when using the ambiguous-cue paradigm to assess learning and cognitive bias in gorillas and a black bear. *Behavioral Sciences*, 7, 51. <https://doi.org/10.3390/bs7030051>.
- Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist*, 83(3), 534–548. <https://doi.org/10.1525/aa.1981.83.3.02a00020>.
- Nielsen, M., & Haun, D. (2015). Why developmental psychology is incomplete without comparative and cross-cultural perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371. <https://doi.org/10.1098/rstb.2015.0071>.
- Paukner, A., Huntsberry, M. E., & Suomi, S. J. (2009). Tufted capuchin monkeys (*Cebus apella*) spontaneously use visual but not acoustic information to find hidden food items. *Journal of Comparative Psychology*, 123(1), 26–33. <https://doi.org/10.1037/a0013128>.
- Perdue, B. M., Snyder, R. J., Pratte, J., Marr, M. J., & Maple, T. L. (2009). Spatial memory recall in the giant panda (*Ailuropoda melanoleuca*). *Journal of Comparative Psychology*, 123(3), 275–279. <https://doi.org/10.1037/a0016220>.
- Perdue, B. M., Snyder, R. J., Zhihe, Z., Marr, M. J., & Maple, T. L. (2011). Sex differences in spatial ability: A test of the range size hypothesis in the order carnivora. *Biology Letters*, 7(3), 380–383. <https://doi.org/10.1098/rsbl.2010.1116>.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>.
- Sabbatini, G., & Visalberghi, E. (2008). Inferences about the location of food in capuchin monkeys (*Cebus apella*) in two sensory modalities. *Journal of Comparative Psychology*, 122(2), 156–166. <https://doi.org/10.1037/0735-7036.122.2.156>.
- Schloegl, C., Schmidt, J., Boeckle, M., Weiss, B. M., & Kotrschal, K. (2012). Grey parrots use inferential reasoning based on acoustic cues alone. *Proceedings of the Royal Society B: Biological Sciences*, 279(1745), 4135–4142. <https://doi.org/10.1098/rspb.2012.1292>.
- Schmitt, V., & Fischer, J. (2009). Inferential reasoning and modality dependent discrimination learning in olive baboons (*Papio hamadryas anubis*). *Journal of Comparative Psychology*, 123(3), 316–325. <https://doi.org/10.1037/a0016218>.
- Vonk, J., Allard, S., Torgerson-White, L., Bennett, C., Galvan, M., McGuire, M. M., et al. (2015). Manipulating spatial and visual cues in a win-stay foraging task in captive grizzly bears (*Ursus arctos horribilis*). In E. A. Thayer (Ed.), *Spatial memory: Long and short-term memory: Functions, differences and effects of injury* (pp. 47–60). Hauppauge, NY: Nova Science Publishers, Inc.
- Vonk, J., & Beran, M. J. (2012). Bears 'count' too: Quantity estimation and comparison in black bears, *Ursus americanus*. *Animal Behaviour*, 84(1), 231–238. <https://doi.org/10.1016/j.anbehav.2012.05.001>.
- Vonk, J., Jett, S. E., & Mosteller, K. W. (2012). Concept formation in American black bears, *Ursus americanus*. *Animal Behaviour*, 84(4), 953–964. <https://doi.org/10.1016/j.anbehav.2012.07.020>.
- Vonk, J., & Johnson-Ulrich, Z. (2014). Social and nonsocial category discriminations in a chimpanzee (*Pan troglodytes*) and American black bears (*Ursus americanus*). *Learning & Behavior*, 42(3), 231–245. <https://doi.org/10.3758/s13420-014-0141-2>.
- Vonk, J., & Leete, J. (2017). Carnivore concepts: Categorization in carnivores 'bears' further study. *International Journal of Comparative Psychology*, 30. <http://escholarship.org/uc/item/61363164>.
- 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: Clinical Applications and Research*, 17, 62–68. <https://doi.org/10.1016/j.jvbeh.2016.11.003>.
- Wynne, C. D. L. (2016). What is special about dog cognition? *Current Directions in Psychological Science*, 25(5), 345–350. <https://doi.org/10.1177/0963721-416657540>.
- Yoganand, K. (2005). *Behavioral ecology of sloth bear (Melursus ursinus) in Panna National Park, Central India* (Ph.D. thesis). Rajkot, India: Saurashtra University.
- Zamisch, V., & Vonk, J. (2012). Spatial memory in captive American black bears (*Ursus americanus*). *Journal of Comparative Psychology*, 126(4), 372–387. <https://doi.org/10.1037/a0028081>.