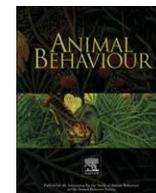




Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Bears 'count' too: quantity estimation and comparison in black bears, *Ursus americanus*

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ARTICLE INFO

Article history:

Received 10 March 2012

Initial acceptance 23 April 2012

Final acceptance 27 April 2012

Available online xxx

MS. number: A12-00195R

Keywords:

area

bear

number

quantity estimation

ratio

Ursus americanus

Studies of bear cognition are notably missing from the comparative record despite bears' large relative brain size and interesting status as generalist carnivores facing complex foraging challenges, but lacking complex social structures. We investigated the numerical abilities of three American black bears, *Ursus Americanus*, by presenting discrimination tasks on a touch-screen computer. One bear chose the larger of two arrays of dot stimuli, while two bears chose the smaller array of dots. On some trials, the relative number of dots was congruent with the relative total area of the two arrays. On other trials, number of dots was incongruent with area. All of the bears were above chance on trials of both types with static dots. Despite encountering greater difficulty with dots that moved within the arrays, one bear was able to discriminate numerically larger arrays of moving dots, and a subset of moving dots from within the larger array, even when area and number were incongruent. Thus, although the bears used area as a cue to guide their responses, they were also able to use number as a cue. The pattern of performance was similar to that found previously with monkeys, and suggests that bears may also show other forms of sophisticated quantitative abilities.

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Given that bears have the largest relative brain size of any carnivore (Gittleman 1986) even in comparison to other social species such as canines, about which there is a recent explosion of research (Miklósi et al. 2004; Hare 2007; Kubinyi et al. 2007), it is surprising that there are few published reports of their cognitive abilities. Other than reports on visual and spatial abilities (Bacon & Burghardt 1976; Tarou 2003; Kelling et al. 2006; Dungl et al. 2008; Perdue et al. 2011) and tool use (Bentley-Condit & Smith 2010; Deecke 2012) nothing is known of their cognitive traits in comparison to social species such as corvids (Emery & Clayton 2004; Seed et al. 2009), other large-brained mammals, such as primates (Tomasello & Call 1997; Rosati et al. 2010), and other carnivores, such as canines (Miklósi et al. 2004; Hare 2007; Kubinyi et al. 2007). This is a serious shortcoming in comparative psychology, and remedying this shortcoming could allow for better tests of the social intelligence (Jolly 1966; Humphrey 1976) and foraging hypotheses (Milton 1981, 1988). For instance, demonstrating that a nonsocial mammal that faces significant foraging challenges exhibits the same sorts of cognitive abilities as more social species within the same order may

indicate that adaptive problems faced in the physical environment, such as with foraging, is a better predictor of these kinds of cognitive traits, than is social living.

There are many examples of nonsocial animals that face significant foraging problems and demonstrate impressive cognitive skills, such as tool use and observational learning. For example, octopi and cuttlefish have the capacity to make conditional discriminations (Hvovrecny et al. 2007; Ikeda 2009). However, although these species also exhibit problem-solving behaviour similar to that of several vertebrate species, their strategies sometimes demonstrate fixed behavioural patterns, rather than significant behavioural flexibility (Fiorito et al. 1998; but also see Mather 2006). Interestingly, Mather (2006) assumed behavioural flexibility in part based on flexible prey choice, and this idea suggests that bears make an interesting test case for assessing such flexibility because bears show flexibility in their diet (Gittleman 1986). Comparisons of closely related species, such as bears, to other carnivores that vary in their sociality and feeding regime, would be vastly informative with regard to hypotheses about the relative importance of sociality versus foraging demands. Unfortunately, the data with regard to cognitive abilities in carnivores, particularly in ursines and felines, is still too scarce to allow for many direct comparisons.

Clearly, however, it is useful, not only to make comparisons between species that are more closely related, as in the order Carnivora, but also to those species that are more distantly related,

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as with primates. Researchers can make inferences about when in a species' evolutionary history a trait may have been most likely to emerge by examining the presence or absence of such traits in species both closely and distantly related. Of course, such inferences must be made cautiously with consideration to the possibility of convergent evolutionary processes. One can look for convergence by examining differences in species' behavioural ecologies, such as arboreal versus terrestrial lifestyles, different mating strategies, home range size (Perdue et al. 2011) and distribution of food resources (Milton 1981). By doing so we can best determine which selective pressures are most likely to have given rise to different cognitive abilities, such as spatial memory (Tarou 2003; Perdue et al. 2011; Zamisch & Vonk, in press), concept formation (J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data) and social cognition (Hare et al. 2002; Miklósi et al. 2004).

One well-studied area in comparative cognition is quantity estimation by nonhumans. Many species are capable of relative numerosity judgments (gorillas, *Gorilla gorilla*: Anderson et al. 2005; chimpanzees, *Pan troglodytes*: Boysen & Berntson 1995; Boysen et al. 1999; Beran 2001; rhesus macaques, *Macaca mulatta*: Brannon & Terrace 2000; Brannon et al. 2006; Cantlon & Brannon 2006; Beran 2007, 2008; capuchins: Judge et al. 2005; Beran 2008; lemurs: Santos et al. 2005; squirrel monkeys: Thomas & Chase 1980; dolphins: Jaakkola et al. 2005; Kilian et al. 2003; elephants: B. M. Perdue, C. F. Talbot, A. Stone & M. J. Beran, unpublished data; birds: Roberts & Mitchell 1994; Emmerton et al. 1997; Emmerton 1998; Pepperberg 2006; amphibians: Uller et al. 2003; fish: Agrillo et al. 2009; Gomez-Laplaza & Gerlai 2011). That is, they are able to choose among sets of items on the basis of the quantities or even numbers of items in those sets.

In some cases, food items are the stimuli to be discriminated, and here it is natural for animals to 'go for more' if they can. For example, chimpanzees will select the greater number of food items (e.g. Beran & Beran 2004), and salamanders will move towards larger numbers of prey items (Uller et al. 2003). In other cases, however, nonedible items are presented for comparison. For example, fish (Agrillo et al. 2009; Gomez-Laplaza & Gerlai 2011) have been tested for their approach to a larger group of conspecifics. Sometimes, totally arbitrary stimuli are used, presumably because those stimuli release subjects from prepotent responding as would occur to food items or other naturalistic stimuli. For example, primate and bird species are presented with two arrays of dots on a touch-screen computer, with one array containing a greater number of dots (Emmerton 1998; Beran 2007, 2008) and are required to choose the larger array. Alternatively, they may be required to arrange dot stimuli in ascending or descending order (Brannon & Terrace 2000; Brannon et al. 2006; Cantlon & Brannon 2006). The use of arbitrary stimuli such as dots allows the researcher to control factors such as size of the stimuli and area covered by the stimuli in relation to the background. By controlling factors such as size, the researcher is able to calculate the ratio of area and number between arrays and assess which cues the animal is using to make the discrimination. However, only social species have been tested in paradigms carefully controlling factors such as dot size, ratio, area and movement of the stimuli (Brannon & Terrace 2000; Brannon et al. 2006; Cantlon & Brannon 2006; Beran 2008). Therefore, it may often be the case that these species can estimate the relative size or amount of some commodity but are not necessarily enumerating the specific items.

Some studies indicate that numerical estimation in nonhuman primate species may be more akin to magnitude estimation than true counting. The performance of both rhesus monkeys and capuchins declines with increased ratio between the quantity in two sets in tasks presenting two arrays of dots that vary in number, as predicted by Weber's law, which states that the size of a just noticeable difference in stimulus intensity is a constant proportion

of the original stimulus magnitude (Brannon & Terrace 2000; Brannon et al. 2006; Cantlon & Brannon 2006; Beran 2008). For instance, discriminating between arrays of three dots and six dots is easier than discriminating between arrays of three dots and four dots. As the ratios increase, the difference between the two arrays is smaller, making it more difficult to discriminate the arrays on a perceptual basis. However, studies also show that such tasks tap into numerical abilities as monkeys' performance remains high when the amount or area is not confounded with number, even when enumerating subsets within moving arrays (e.g. Beran 2008). Careful control of such nonnumerical factors can indicate whether species are capable of tracking and individuating items of a set, such as members of their group, and using number to do so versus some other stimulus property. Thus, there is reason to speculate that this skill might have emerged in particular in social species, such as primates, cetaceans and social birds such as corvids and parrots (Pepperberg 2006). However, it is possible that this is a more evolutionarily ancient capacity that serves as a foundation of numerical cognition and may be shared among other large-brained species that exhibit numerical abilities. One working hypothesis is that animals that forage over large home ranges must evolve the ability to discriminate quantities of items, such as foods, to assist them in choices regarding relative costs and benefits of travel time and energy payoffs. However, one possibility is that they are very good at assessing quantity or magnitude (approximate amount) for static items, but they do not need to assess numerosity (exact number of items), and, in particular, have not evolved the capacity for enumerating dynamic stimuli. We test this possibility for the first time.

Here, three American black bears chose larger or smaller arrays of static and moving dots, showing effects of ratio and area that made their performance quite comparable to that of better-studied social species. One bear was able to choose a smaller subset from within a larger array of moving dots, even when area was not confounded with number and only number operated as a valid cue to the correct choice. These results from a nonsocial, large-brained mammal on both static and moving arrays, controlling for area and number, indicate that group living is not a prerequisite for the capacity to make numerosity judgments and even to enumerate subsets of moving stimuli.

METHODS

Subjects

Three captive adult American black bear siblings (one female and two males) were tested. The bears had previously participated in studies of cognitive dissonance (West et al. 2010), spatial memory (Zamisch & Vonk, in press) and concept formation (J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data), although they had not previously been tested on tasks assessing quantity estimation or numerosity. The research took place in an off-exhibit area of the bears' enclosure at the Mobile Zoo in Wilmer, Alabama, U.S.A. Testing of subjects complied with the Institutional Animal Care and Use Committee of the University of Southern Mississippi (IACUC approval number 06091401). The experiments provided a form of enrichment for the subjects and did not present any risks or adverse effects. Housing and maintenance of the bears at the Mobile Zoo complied with regulations of the U.S. Department of Agriculture.

Materials

The experimental apparatus consisted of a durable Panasonic Toughbook laptop computer and a 19-inch, Vartech Armorall, Capacitive, touch-screen monitor welded to the front of a rolling

computer cart. Experiments were programmed using Visual Basic for Windows. Stimuli consisted of dots drawn inside of two outlined boxes (59.5×63.5 mm), which were centred to the left and right of centre screen. The dots within the boxes (hereafter arrays) ranged in number from 1 to 10, and in some conditions, varied by colour. Each had a randomly assigned diameter of 3–12 mm (Fig. 1). Correct responses were followed by a melodic tone and a blank screen paired with food reinforcement, which consisted of portions of the bears' regular zoo diet (fruits, vegetables) and special treats such as honey roasted peanuts, banana pellets, dried banana chips, yoghurt covered raisins and wafer cookies. Food was presented by hand by the experimenter. An incorrect response was followed by a buzz tone and a brief time-out with a blank screen.

Procedure

Individual subjects were separated prior to testing, but were tested in the indoor area of their home cages. Subjects could move freely in their home cages throughout testing sessions. Thus, participation was entirely voluntary. The computer cart was pushed up against the interior mesh separating the human experimenter from the bear, allowing the animal access to the touch-screen monitor. One of the males (Brutus) had been trained to respond by touching the monitor with his nose, while the female (Bella) and the other male (Dusty) predominantly used their paws to touch the screen. The experimenter observed the animal's responses on the laptop monitor, which was centred behind the computer cart directly behind the touch-screen monitor. The experimenter could not see the bear's face or paws during the trial and did not know the correct response until the program provided feedback, and thus, could provide no cues. The experimenter presented the bear with a food reward, as described above, immediately following a correct response at a consistent location. Trials continued automatically until the end of a session.

Training

Bears were trained to discriminate between two arrays of dots, by choosing the array containing the larger (Brutus) or smaller (Dusty and Bella) number of dots. During training, the bears received 8–10 sessions per day, 3 days per week. The bears had previously been trained to perform two-choice discrimination tasks on a touch-screen computer (J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data). To train the bears to choose larger or smaller numerical arrays

of dots, they were first presented with 20-trial sessions in which they were required to choose accurately between arrays of one dot and arrays of three dots for five out of six consecutive trials within a session. If this criterion was not met, these were the only two arrays that were presented during the session. Once this criterion was met within a session, the bears were presented with arrays of two dots versus arrays of six dots until they performed that discrimination correctly for five out of six consecutive trials within a session. Thus, they could meet both criteria within a single 20-trial session if they were correct on five consecutive trials with each discrimination. It would thus take them a minimum of 10 trials to achieve this goal if they were correct on all 10 of these trials. Having passed both criteria, arrays of a varying and randomly determined number of dots between 1 and 10 were presented, where one set was always numerically larger than the other. These trials could occur within the same 20-trial session if the criterion was met on both simpler discriminations within the same session. When the bears reached this point, the start of each new session involved a new criterion for the warm-up discriminations (one versus three, and two versus six) so that instead of having to make five of six correct responses on these comparisons, the bears were required to meet a criterion of only two consecutive correct trials of one dot versus three dots, and two consecutive correct trials of two dots versus six dots on each session before the variable arrays began to appear. This procedure was implemented to remind the bears of the task at hand before moving on to the more difficult variable trials. The bears were required to reach a criterion of 80% correct (16/20 correct trials) on four consecutive 20-trial sessions that included both the warm-up trials and more difficult variable trials before moving to 100-trial sessions of variable dot arrays, which comprised the formal testing sessions.

Brutus was trained to choose the array containing more dots, whereas Dusty and Bella were trained to choose the array containing fewer dots. Because bears have never been tested for numerical abilities, we did not make assumptions a priori about the ease of performing these discriminations. Although prior research has indicated that choosing smaller sets is more difficult than choosing larger sets (Boysen & Berntson 1995), such studies have typically involved real food items. When abstract stimuli are used in paradigms where animals are trained to point to smaller arrays of real items, chimpanzees can overcome this bias (Boysen et al. 1999). Researchers have not explicitly compared the performance of nonhumans when choosing larger versus smaller arrays with static, abstract and nonecologically relevant stimuli. Thus, it was of interest to test the assumption that animals generally are predisposed to choose larger arrays, despite the small sample size.

Brutus was trained to initiate trials by touching a start button, but this procedure led to frustration behaviours for Dusty, so Dusty and Bella were trained without the start button, as this was more similar to prior testing for them (J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data). Given that Dusty experienced difficulty during the trials and showed an extreme side bias, after 25 sessions with one versus three dots, he was presented with a discrimination consisting of one dot versus eight dots until he acquired this discrimination (24 sessions). However, having acquired this discrimination, he was rapidly able to meet the criterion of five out of six correct trials with one dot versus three dots, and two dots versus six dots, and required only two such sessions before moving on to the formal testing phase.

Testing

Static sets

Because the bears had no experience with numerical stimuli, each bear began testing with static stimuli. On each trial, the bears

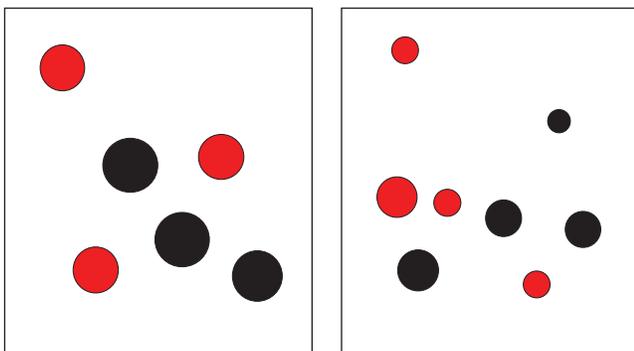


Figure 1. Example of a trial used to test numerical abilities of American black bears. For each trial, bears chose between two arrays (two outlined boxes with dots) on a computer screen. In this example, the array is incongruent because the array that has more dots has the smaller overall area of pixelated dots. This trial also shows how the arrays could be subdivided into subsets for which only black dots were relevant for comparing the two arrays.

were presented with two arrays of dots within a border, identical in size (Fig. 1), that ranged in number from 1 to 10 and that remained stationary on the screen throughout the trial. The dot arrays were randomly determined on each trial with the constraint that the two arrays could not contain equal numbers of dots. On some trials, the dot number was congruent with its overall amount of pixelated area (i.e. the array containing the larger number of dots was also larger in area). On other trials, the dot number was incongruent with its amount of pixelated area; that is, the array containing more dots contained a smaller area of pixelation. For Brutus, who was trained to choose the array with the larger number of dots, using either number or area as a cue would lead to high levels of performance on congruent trials, but using area as a cue would lead to lower levels of performance on incongruent trials. However, for the bears that were trained to choose the smaller number of dots, on incongruent trials, choosing the larger area would lead them to choose correctly, even though this would be in conflict with the rule that was being reinforced (i.e. choose smaller number). Of course, if they were operating on the basis of the rule that was being reinforced, but using area rather than number as a cue, they should have encountered greater difficulty on incongruent trials, where area and number were incongruent.

The bears received one to three 100-trial sessions two to three times per week over a period of 6 months. Brutus and Dusty were given 30 100-trial sessions in this static condition. Bella was given 20 100-trial sessions with static stimuli, as she was already performing at over 75% accuracy on both congruent and incongruent trials at this point.

Moving sets

The basic procedure for moving sets was the same as that for static sets, except that, in this experiment, the dots moved on the screen throughout the trial. Each dot was given a randomly selected trajectory and began to move around the screen within its perimeter area (i.e. the boxes that contained each array of dots within a delineated border) as soon as it appeared. The movement took place at one of four randomly selected speeds, and a dot moved in a straight line until it contacted one of the walls of the outline of the stimulus array, at which point it was redirected, as if it had been deflected. Thus, the movement appeared chaotic as dots passed through each other. All dots appeared at once and were moving simultaneously. Movement continued until the subject made a response by touching one of the arrays. Brutus and Dusty completed 30 100-trial sessions with moving stimuli. Bella completed 20 sessions, after which she was dropped from testing, given that she showed no signs of improvement with either congruent or incongruent sets.

Moving subsets

To test whether bears could individuate subsets of moving items, in this experiment the bears were required to enumerate only a subset of dots within each set of moving dots. Each array contained 1–12 dots with all dots moving at randomly determined speeds and directions as in the moving sets condition above. Each dot was randomly assigned a size and colour (black: target set; red: distracter set; see Fig. 1). Both black and red dots moved within the array. On the basis of previous work on colour discrimination in bears (Bacon & Burghardt 1976; Kelling et al. 2006), we thought that the bears should be able to discriminate easily between black and red dots. The target sets that were paired on each trial contained different numbers of dots. Once again, the target sets could be either congruent or incongruent in terms of their number and total area. Brutus completed 30 100-trial sessions and Dusty completed 20 100-trial sessions, after which testing was terminated, because Dusty showed no signs of improvement.

Analyses

Separate binary logistic regressions were conducted for each subject. Performance (correct/incorrect) was regressed on the predictors; difference in number (difference), ratio of number between arrays (ratio), ratio of area between arrays (area), congruence (congruent/incongruent) and the interaction of congruence with each of the other predictors. Prior to being entered into the regression, each continuous variable was standardized. The same analyses were performed for each discrimination (static sets, moving sets and moving with subsets). Alpha was set to 0.05 for all tests.

RESULTS AND DISCUSSION

Training

Brutus and Bella required 22 and 36 20-trial sessions, respectively, to complete training. Dusty persisted with a left-side bias and was moved to training with a discrimination of one dot versus eight dots, with 24 20-trial sessions consisting solely of this discrimination until he finally seemed to acquire this discrimination spontaneously. After this point, he rapidly reached criterion on one dot versus three dots and on two dots versus six dots after only two sessions, and proceeded to testing.

Testing

Static stimuli

If the bears could truly use number as a cue, we predicted little or no effect of congruence, although one might expect the congruent trials to be easier, because on these trials the bears could use both area and number as a cue to guide performance. For Bella and Dusty, we predicted that performance might be better on incongruent trials if they used the larger area to guide performance, although they were reinforced for choosing the smaller number. We also expected that the ratio would be negatively correlated with performance, given prior work with primates (Brannon & Terrace 2000; Brannon et al. 2006; Cantlon & Brannon 2006; Beran 2007, 2008). That is, as the ratio of difference between the arrays increases, performance should worsen.

Figure 2 depicts performance as a function of ratio between the areas in the arrays. Brutus performed better, on average, with congruent trials, as one might expect ($\beta = 0.35$, Wald = 3.74, $P = 0.05$, CI = 0.05–1.42). Area affected Bella's performance differently on congruent and incongruent trials. For Bella, there was a main effect of congruence ($\beta = 2.70$, Wald = 30.65, $P < 0.001$, CI = 0.03–0.18), and congruence interacted with area ($\beta = 2.95$, Wald = 75.77, $P < 0.001$, CI = 9.85–37.20). When separate logistic regressions were conducted for congruent and incongruent trials, area significantly predicted whether trials would be correct or not on both types of trials, but greater area led to worse performance on incongruent trials ($\beta = -1.13$, Wald = 17.62, $P < 0.001$, CI = 0.19–0.55) and better performance on congruent trials ($\beta = 1.83$, Wald = 77.60, $P < 0.001$, CI = 4.13–9.31). Dusty tended to perform better on incongruent trials, and when ratio was smaller, as with Bella, area affected Dusty's performance differently on incongruent and congruent trials. There was a main effect of congruence ($\beta = -1.42$, Wald = 52.50, $P < 0.001$, CI = 0.17–0.36) and ratio ($\beta = -0.65$, Wald = 9.45, $P = 0.002$, CI = 0.35–0.79), and congruence interacted with area ($\beta = 1.55$, Wald = 94.36, $P < 0.001$, CI = 3.45–6.44). When separate logistic regressions were conducted for congruent and incongruent trials, larger area led to worse performance on incongruent trials ($\beta = -0.44$, Wald = 12.65,

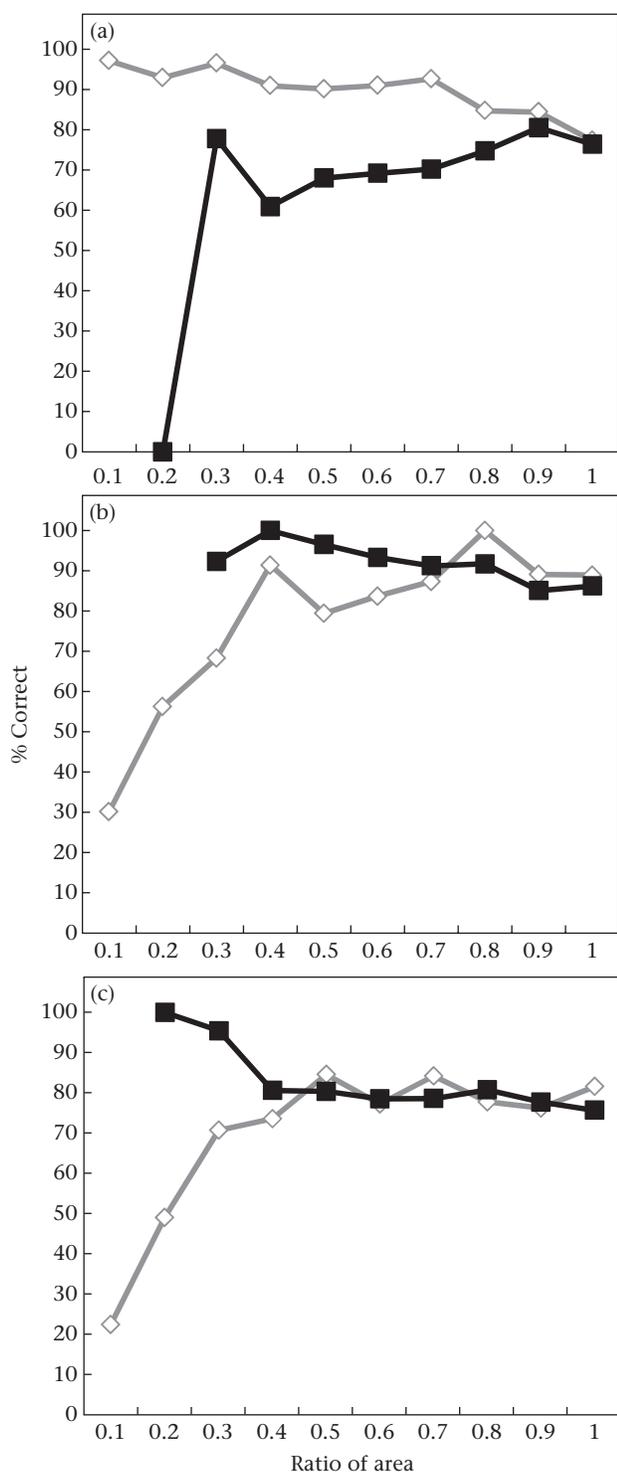


Figure 2. Percentage of bears' correct choices between two arrays with static stimuli as a function of the ratio between areas in congruent (open circles) and incongruent (solid squares) trials: (a) Brutus, whose correct choice was the larger ratio, and (b) Bella and (c) Dusty, whose correct choices were the smaller ratios.

$P < 0.001$, $CI = 0.5–0.82$) and better performance on congruent trials ($\beta = 1.11$, $Wald = 120.78$, $P < 0.001$, $CI = 2.49–3.70$).

Bella and Dusty's pattern of responding suggests that they were choosing based on larger area, which allowed them to perform better on incongruent trials when the smaller number of dots contained the larger area of pixelation. However, all three bears

reached above-chance levels of performance on both congruent and incongruent trials, so the use of area was not the whole story, and the bears often relied on number rather than area to make correct responses (binomial tests: all P s < 0.001). With these static data, only Dusty showed significant effects of ratio, which, according to Weber's law, indicates analogue magnitude estimation (see also Dehaene 1992; Feigenson et al. 2004; Beran 2008). Analogue magnitude estimation is thought to operate when individuals must represent large approximate quantities. Errors generally increase in proportion to the size of the set of items for which quantity is being estimated (Feigenson et al. 2004).

Moving stimuli

Once again, separate binary logistic regressions were conducted for each subject. Performance (correct/incorrect) was regressed on the predictors: difference in number (difference), ratio of number between arrays (ratio), ratio of area between arrays (area), congruence (congruent/incongruent) and the interaction of congruence with each of the other predictors. Here we expected the same effects as before; negative relationships between ratio and performance and perhaps effects of area on performance. We predicted that Brutus might perform slightly better on congruent trials, while the opposite would be true for Bella and Dusty, as choosing larger area and smaller number were in conflict on congruent trials.

As with static dot arrays, Brutus performed better on congruent trials when he could use both number and area as a cue, and, like primates tested previously, he performed better with smaller ratios between the arrays, main effect of congruence ($\beta = 0.63$, $Wald = 22.66$, $P < 0.001$, $CI = 1.45–2.44$) and ratio ($\beta = -0.44$, $Wald = 13.88$, $P < 0.001$, $CI = 0.51–0.81$), and an interaction of congruence with area ($\beta = -0.71$, $Wald = 25.48$, $P < 0.001$, $CI = 0.38–0.65$; Fig. 3). When separate logistic regressions were conducted for congruent and incongruent trials, larger area predicted better performance on incongruent trials ($\beta = 0.25$, $Wald = 6.68$, $P = 0.01$, $CI = 1.06–1.56$) and worse performance on congruent trials ($\beta = -0.45$, $Wald = 20.51$, $P < 0.001$, $CI = 0.52–0.77$). These results indicate that, with moving stimuli, Brutus relied more heavily on area as a cue. Also, ratio was significantly related to his performance, suggesting that he was using magnitude estimation to perform the task. Brutus showed the expected patterns in that he performed better with larger differences in number and smaller ratios between numbers. Figure 3 depicts performance as a function of the ratio between numbers of dots in the arrays.

Overall, Bella performed very well on incongruent trials when she could choose larger area, but not on congruent trials when area conflicted with number. There was a significant main effect of congruence ($\beta = -1.15$, $Wald = 51.58$, $P < 0.001$, $CI = 0.23–0.43$) and significant interactions of congruence with each of the other predictors (numerical difference: $\beta = -0.55$, $Wald = 6.56$, $P = 0.01$, $CI = 0.38–0.89$; ratio: $\beta = -0.60$, $Wald = 9.98$, $P = 0.002$, $CI = 0.38–0.80$; area: $\beta = 0.79$, $Wald = 25.94$, $P < 0.001$, $CI = 1.63–3.00$). When separate logistic regressions were conducted for congruent and incongruent trials, larger area predicted poorer performance on incongruent trials ($\beta = -0.31$, $Wald = 6.66$, $P = 0.01$, $CI = 0.58–0.93$) and better performance on congruent trials ($\beta = 0.49$, $Wald = 23.29$, $P < 0.001$, $CI = 1.34–1.99$). A greater difference between number in the two arrays predicted better performance only on incongruent trials ($\beta = 0.47$, $Wald = 6.16$, $P = 0.01$, $CI = 1.10–2.32$). A greater ratio predicted worse performance only on congruent trials ($\beta = -0.45$, $Wald = 11.20$, $P = 0.001$, $CI = 0.49–0.83$).

Dusty generally performed better on incongruent trials, and his performance was affected differently by the numerical difference,

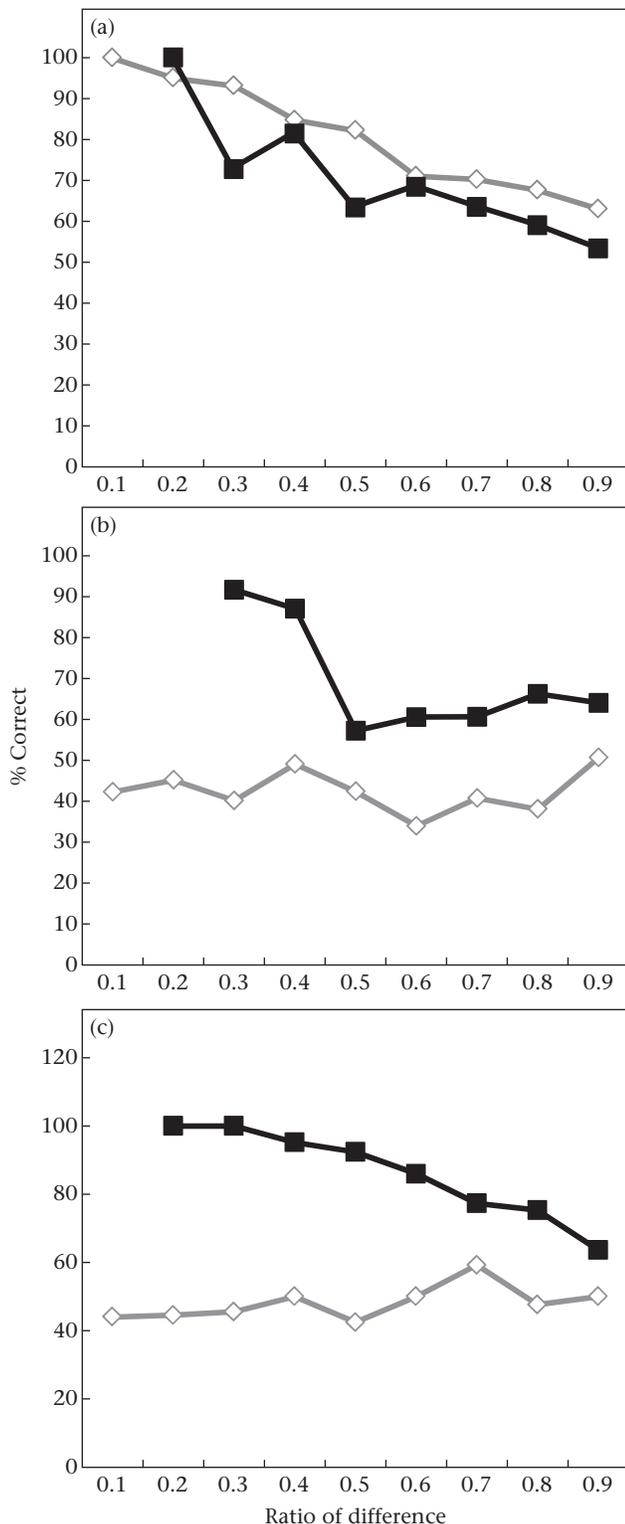


Figure 3. Percentage of bears' correct choices between moving stimuli as a function of the ratio between numbers in congruent (open circles) and incongruent (solid squares) trials: (a) Brutus, whose correct choice was the larger ratio, and (b) Bella and (c) Dusty, whose correct choices were the smaller ratios.

ratio and area depending on whether the trials were incongruent or congruent. There was a main effect of congruence ($\beta = -2.02$, Wald = 132.68, $P < 0.001$, CI = 0.09–0.19), and significant interactions of congruence with each of the other predictors (numerical

difference: $\beta = 0.89$, Wald = 13.28, $P < 0.001$, CI = 1.51–3.92; ratio: $\beta = 0.79$, Wald = 11.07, $P = 0.001$, CI = 1.38–3.51; area: $\beta = 2.38$, Wald = 193.26, $P < 0.001$, CI = 7.75–15.18). When separate logistic regressions were conducted for congruent and incongruent trials, greater area led to worse performance on incongruent trials ($\beta = -0.79$, Wald = 35.63, $P < 0.001$, CI = 0.35–0.59) and better performance on congruent trials ($\beta = 1.59$, Wald = 214.64, $P < 0.001$, CI = 3.97–6.08). A greater numerical difference tended to produce lower performance on incongruent trials ($\beta = -0.38$, Wald = 2.89, $P = 0.09$, CI = 0.44–1.06) and higher performance on congruent trials ($\beta = 0.51$, Wald = 26.06, $P < 0.001$, CI = 1.31–2.03). A greater ratio led to lower performance on both incongruent trials ($\beta = -1.31$, Wald = 42.66, $P < 0.001$, CI = 0.18–0.40) and congruent trials ($\beta = -0.52$, Wald = 16.13, $P < 0.001$, CI = 0.46–0.77), which was the expected result based on past research.

That Bella and Dusty continued to perform very well on incongruent trials but very poorly on congruent trials indicated that they were continuing to use area as a cue, which they could do more easily on trials when there was a larger numerical difference and a smaller ratio. However, if area was the only cue they were using, they should have been as far below chance on congruent trials as they were above chance on incongruent trials, and this was not the case. It may have been the case that they relied on area when it could be used as a cue, but attempted to use number to some degree on some other trials, although they failed to do so reliably. All bears showed the expected patterns of performing better with greater differences in numerical distance and smaller ratios between the stimuli.

Moving stimuli with subsets

Bella was discontinued in the experiment based on her overall low level of performance with moving stimuli and the need to continue testing her in other experiments. Once again, separate binary logistic regressions were conducted for both Brutus and Dusty. Performance (correct/incorrect) was regressed on the predictors: numerical difference in subsets, ratio of number between subsets in arrays, ratio of area between subsets in arrays, congruence and the interaction of congruence with each of the other predictors.

Brutus was able to enumerate a target set of moving stimuli accurately from among a larger set of moving stimuli, without relying exclusively on area as a cue. Regression analysis revealed a main effect of ratio ($\beta = -0.46$, Wald = 30.27, $P < 0.001$, CI = 0.54–0.75) but no interaction of congruence and numerical difference ($\beta = 0.34$, Wald = 3.52, $P = 0.06$, CI = 0.99–2.01). A greater numerical difference between arrays led to better performance on only the congruent trials ($\beta = 0.34$, Wald = 11.38, $P = 0.001$, CI = 1.15–1.70). The lack of a relationship on incongruent trials may have been an artefact of the anomalous poor performance with a difference of six dots between sets on incongruent trials where Brutus was incorrect on the single trial of this type. Importantly, there was no overall difference between Brutus's performance on congruent and incongruent trials in enumerating a subset among moving stimuli. Binomial tests revealed that Brutus was above chance on both congruent and incongruent trials (both P s < 0.001). In addition, although his performance showed the expected trends for difference and ratio, there was no effect of area.

Dusty continued to perform above chance only on incongruent trials (binomial test: $P < 0.001$; congruent trials: $P = 0.14$), suggesting that he continued to choose on the basis of area rather than number. Regression analysis supported this conclusion (congruence: $\beta = -2.11$, Wald = 110.52, $P < 0.001$, CI = 0.08–0.18; ratio: $\beta = -0.47$, Wald = 14.12, $P < 0.001$, CI = 0.49–0.80; congruence \times area: $\beta = 2.05$, Wald = 131.06, $P < 0.001$, CI = 5.48–11.07). When separate logistic regressions were conducted for congruent and incongruent

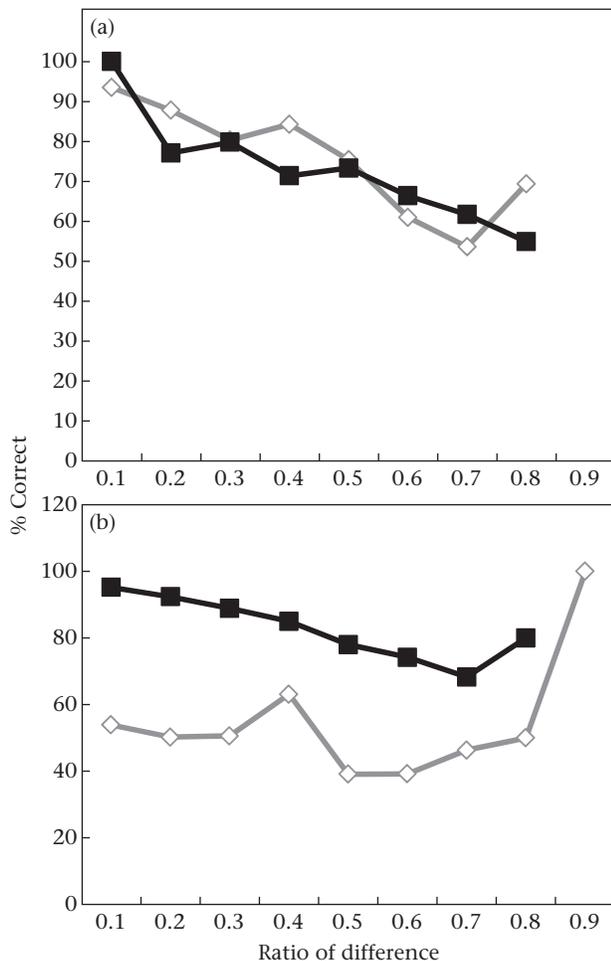


Figure 4. Percentage of bears' correct choices between subsets of moving stimuli as a function of the ratio between numbers in congruent (open circles) and incongruent (solid squares) trials: (a) Brutus, whose correct choice was the larger ratio, and (b) Dusty, whose correct choice was the smaller ratio.

trials, larger area predicted worse performance on incongruent trials ($\beta = -0.75$, Wald = 28.52, $P < 0.001$, CI = 0.36–0.62) and better performance on congruent trials ($\beta = 1.30$, Wald = 136.68, $P < 0.001$, CI = 2.96–4.58). Figure 4 depicts performance as a function of ratio between the number of dots in the arrays.

Conclusion

Many nonhuman species can discriminate smaller or larger amounts or even smaller or larger numbers of items when static stimuli are presented in the visual domain. Less evidence is available for moving stimuli, but some primates seem capable of discriminating these sets (e.g. Beran 2008). However, very few attempts have been made to assess the quantitative skill of carnivores, and there is no evidence as to whether bears can make these kinds of judgments. The present results suggest that they can, and at least one of the bears showed a pattern of results that matched nicely with that reported for nonhuman primates; namely, that it used the number of dots to control responding rather than some other stimulus property. But, despite showing proficiency in using number as a critical cue in making these discriminations and comparisons, other stimulus properties were highly salient for bears as well.

These results suggest that it is easier for bears to choose the larger amount rather than the smaller amount, even with two-

dimensional abstract stimuli, and even when they are reinforced for choosing the smaller amount. This is consistent with previous work with primates, which have difficulty inhibiting responses to select smaller amounts of food (Boysen & Berntson 1995; Boysen et al. 2001), although this bias can sometimes be overcome when abstract symbols replace the food items (Boysen et al. 1999; Shumaker et al. 2001). Our results also suggest that bears are naturally attracted to focus on choosing a larger number over a smaller one, even when number conflicts with area. One bear maintained that pattern even for the most difficult task, in which subsets of moving stimulus arrays had to be compared while the bear ignored the distractor's contribution to the overall number in that set. Thus, choosing a greater amount or a greater number of items when comparing two or more sets may be more intuitive than choosing a smaller amount or smaller number, even with arbitrary two-dimensional stimuli. This finding also matches that found with human children, who also prefer to 'go for more' (Estes 1976).

The bears seemingly found it easier to enumerate static rather than moving stimuli. This may not be surprising, given that they have not evolved to live in social groups and thus would not need to use number naturally to track individual members of a group, but rather to enumerate quantities of food items. Even live food items, such as fish, do not need to be individuated, and may be quantified by estimating size or area. In comparison, for social animals, such as primates, it may be important to track the presence of individual members of a moving group; thus, they may have evolved the ability to rely more heavily on number than on area when performing such tasks (see Beran 2008). Overall, however, bears showed similar trends to those found in primates previously tested in analogous tasks (Beran 2008), in that they were more likely to choose correctly on trials when the number-to-area ratio of dots in the two arrays was smaller. Thus, group living is not a necessary prerequisite for the capacity to enumerate static or moving stimuli, or subsets of moving stimuli. Perhaps the ability to enumerate stimuli has evolved to assist predators in discriminating among groups of prey that contain more vulnerable members, or more appetizing members. In this case, perhaps enumeration is an ability of predator species but not of prey species among nonsocial animals.

Our results are among the first to show that bears, an understudied species in comparative psychology and biology, may have evolved cognitive mechanisms equivalent to their distant primate relatives, at least within the quantitative domain. Only further research can determine where their capacities lie within the social-reasoning domain, and other areas of physical reasoning, such as causal reasoning, tool use, understanding of time and space, and categorization of natural stimuli. Such research will be critical for determining the necessary social and physical ecological factors for shaping an organism's cognitive development. Too often, researchers focus exclusively on species most closely related to humans, or those most amenable to testing, in examining particular cognitive traits or using standard methodology. Other species must be tested for comparative psychology to be truly comparative and for a fuller understanding of the evolution of cognition. More research with bears, along with other carnivores and nonprimate species, will provide exactly this result.

Demonstrating for the first time that important research questions can be addressed through the use of touch-screen technologies in this species is an important methodological advance. Bears are of particular interest because of their large brains, their relatively solitary lifestyles and flexible foraging patterns within the order Carnivora. Important comparisons to other species such as wild and domestic canines will have much to tell us about the evolution of social and physical reasoning. In conjunction with other work underway (J. Vonk, S. E. Jett & K. W. Mosteller, unpublished data), the present work suggests that bears are rapid

problem-solvers and are capable of abstract concept formation. These findings should help change the bias of researchers to focus on group living as the driving force for complex cognition. That touch screens can be used effectively with bears to test a wide range of cognitive abilities now provides the means to examine more closely their cognitive competence in comparison to other more widely studied species, such as primates, that have been performing computerized tasks for decades. It is exciting to consider that such divergent species can be tested in the same way to promote a fuller picture of comparative cognition and the diverse forces giving rise to both similar and distinct traits.

Acknowledgments

We are indebted to the Mobile Zoo, especially its director, John Hightower. Without his support and assistance, these experiments could not have been conducted. In addition, special thanks to Stephanie Jett for her assistance during data collection and Dr Joan Sinnott for her support. This research was supported by the Aubrey Keith Lucas and Ella Ginn Lucas Endowment for Faculty Excellence Awards (to J.V.), the National Science Foundation (grant number 0924811 to M.J.B.) and the National Institutes of Health (grant number 060563 to M.J.B.).

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