Brain size predicts problem-solving ability in mammalian carnivores

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Despite considerable interest in the forces shaping the relationship between brain size and cognitive abilities, it remains controversial whether larger-brained animals are, indeed, better problem-solvers. Recently, several comparative studies have revealed correlations between brain size and traits thought to require advanced cognitive abilities, such as innovation, behavioral flexibility, invasion success, and self-control. However, the general assumption that animals with larger brains have superior cognitive abilities has been heavily criticized, primarily because of the lack of experimental support for it. Here, we designed an experiment to inquire whether specific neuroanatomical or socioecological measures predict success at solving a novel technical problem among species in the mammalian order Carnivora. We presented puzzle boxes, baited with food and scaled to accommodate body size, to members of 39 carnivore species from nine families housed in multiple North American zoos. We found that species with larger brains relative to their body mass were more successful at opening the boxes. In a subset of species, we also used virtual brain endocasts to measure volumes of four gross brain regions and show that some of these regions improve model prediction of success at opening the boxes when included with total brain size and body mass. Socioecological variables, including measures of social complexity and manual dexterity, failed to predict success at opening the boxes. Our results, thus, fail to support the social brain hypothesis but provide important empirical support for the relationship between relative brain size and the ability to solve this novel technical problem.

brain size | problem-solving | carnivore | social complexity | intelligence

Animals exhibit extreme variation in brain size, with the sperm whale's brain weighing up to 9 kg (1), whereas the brain of the desert ant weighs only 0.00028 g (2). Although body mass is the single best predictor of brain size (1, 3), some species have much larger brains than expected given their body size (e.g., humans and dusky dolphins), whereas other species have much smaller brains than expected (e.g., hippopotamus and blue whale) (1). Brain tissue is energetically costly (4–6), and therefore, large brains are presumed to have been favored by natural selection, because they confer advantages associated with enhanced cognition (3). However, despite great interest in the determinants of brain size, it remains controversial whether brain size truly reflects an animal's cognitive abilities (7–9).

Several studies have found an association between absolute or relative brain size and behaviors thought to be indicative of complex cognitive abilities. For example, brain size has been found to correlate with bower complexity in bower birds (10), success at building food caches among birds (11), numerical abilities in guppies (5), and two measures of self-control in a comparative study of 36 species of mammals and birds (12). Additionally, larger-brained bird species have been found to be more innovative, more successful when invading novel environments, and more flexible in their behavior (13–16). Although there is circumstantial evidence suggesting an association between problem-solving ability and brain size, experimental evidence is extremely rare. To experimentally assess the relationship between brain size and any cognitive ability across a number of species in a standardized way is challenging because of the unique adaptations each species has evolved for life in its particular environment (17). In this study, we investigate whether larger-brained animals do, indeed, exhibit enhanced problem-solving abilities by conducting a standardized experiment in which we present a novel problem-solving task to individuals from a large array of species within the mammalian order Carnivora.

Carnivores often engage in seemingly intelligent behaviors, such as the cooperative hunting of prey (18, 19). Nevertheless, with the exception of domestic dogs, carnivores have largely been ignored in the animal cognition literature (20). Mammalian carnivores comprise an excellent taxon in which to assess the relationship between brain size and problem-solving ability and test predictions of hypotheses forwarded to explain the evolution of large brains and superior cognitive abilities, because they exhibit great variation in their body size, their brain size relative to body size, their social structure, and their apparent need to use diverse behaviors to solve ecological problems. Although most carnivores are solitary, many species live in cohesive or fission–fusion social groups that closely resemble primate societies (21–23). Furthermore, experiments with both wild spotted hyenas (24) and wild meerkats (25) show that members of these species are able to solve novel problems, and in spotted hyenas, those individuals that exhibit the greatest behavioral diversity are the most successful problem-solvers (24).

Here, we presented steel mesh puzzle boxes, scaled according to subject body size, to 140 individuals from 39 species in nine families of zoo-housed carnivores and evaluated whether individuals in each species successfully opened the boxes to obtain a food reward inside (Fig. 1A and Dataset S1). In addition to testing whether larger-brained carnivores are better at solving a novel technical problem, we inquired whether species that live in larger social groups exhibit enhanced problem-solving abilities compared with species that are solitary or live in smaller social groups. We also asked whether species exhibiting greater behavioral diversity are better at solving
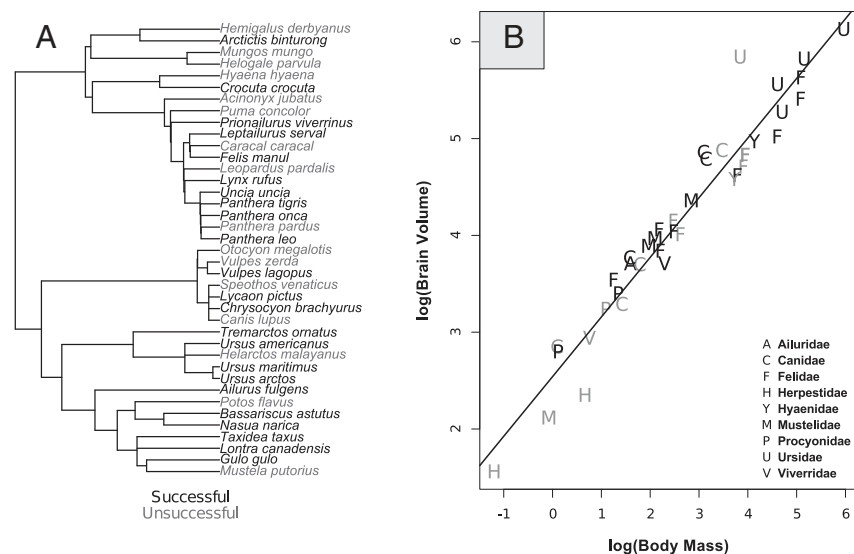
Fig. 1. (A) We tested the performance of zoo-housed individuals in 39 species from nine carnivore families by exposing them to our puzzle box problem, with the box scaled to accommodate body size. (B) The relationship between body mass (kilograms) and brain volume (milliliters) in 39 mammalian carnivore species. (A) Species in gray and (B) family names in gray represent species in which no tested subjects opened the box. Note that, in B, two species in the family Felidae (*Panthera pardus* and *Puma concolor*) have overlapping points.

problems than species exhibiting less behavioral diversity. Additionally, carnivores exhibit an impressive range of manual dexterity from the famously dexterous raccoons and coatis to the much less dexterous hyenas and cheetahs (26). Therefore, to ensure that our measure of problem-solving ability was not solely determined by manual dexterity and ensure that our problem-solving test was equivalently difficult across a range of species, we also examined the impact of manual dexterity on problem-solving success in this study.

Finally, the relative sizes of specific brain regions might be more strongly predictive of problem-solving ability than overall brain size relative to body size. Recently, Swanson et al. (27) used virtual brain endocasts to show that, although mammalian carnivore species with a higher degree of social complexity did not have larger total brain volumes relative to either body mass or skull size, they did have significantly larger cerebrum volumes relative to total brain volume. Therefore, we used deviance information criterion (DIC) model selection analysis to inquire whether any of four gross regional brain volumes (total cerebrum, posterior cerebrum, anterior cerebrum, and hindbrain) better predicted performance in our puzzle box trials than total brain size in a subset of 17 carnivore species for which these data were available from virtual brain endocasts (Dataset S1).

We retrieved data on brain size and the sizes of gross brain regions from published literature and used phylogenetic comparative statistics to assess relationships among these measures, social complexity, behavioral diversity, manual dexterity, and performance measures obtained during box trials. We used social group size as our proxy for social complexity, because in an earlier comparative study of mammalian carnivores, Swanson et al. (27) found that group size was just as effective of a proxy as the first axis from a principal component analysis of several different measures of social complexity in carnivores. We used an established measure of behavioral diversity, which we obtained by calculating the number of different behaviors exhibited by individuals from each species while interacting with the puzzle box (24, 28–30). To assess manual dexterity, we recorded occurrences of 20 types of forelimb movements following the work by Iwaniuk et al. (26). Finally, we used measures taken from virtual brains to analyze the effects of the size of specific gross brain regions on performance in puzzle box trials. These measures allowed us to inquire whether specific neuroanatomical or socioecological measures can help explain variation in problem-solving ability across species.

Results

We tested one to nine individuals in each of 39 species (mean = 4.9 individuals; median = 5) (Table S1). Of 140 individuals tested, 49 individuals (35%) from 23 species succeeded at opening the puzzle box (Fig. 1A, Table S1, and Movie S1). The proportion of individuals within each species that succeeded at opening the box varied

considerably among families, with species in the families Ursidae (69.2% of trials), Procyonidae (53.8% of trials), and Mustelidae (47.1% of trials) being most successful at opening the puzzle box and those within the family Herpestidae (0%) being the least successful (Table S1). Total brain volume corrected for body mass varied among the species that we tested, with Canid and Ursid species having the largest brains for their body mass and Viverrid, Hyaenid, and Herpestid species having the smallest brains for their body mass (Fig. 1B and Table S1).

It appeared that the majority of subjects in our study actually gained an understanding of the puzzle and how to open it. If individuals were only using brute force to open the box or emitting exploratory behaviors without any understanding of how the puzzle works, then we should not have seen any evidence of learning the solution over time. To investigate whether the test subjects were actually learning the solution to the problem, we ran a non-phylogenetically corrected generalized linear mixed-effects model to examine how work time changed over successive trials for successful individuals. Work time significantly decreased as trial number increased ($F_{9,97} = 2.57; P = 0.01$), indicating that successful individuals improved their performance with experience.

The top model based on DIC model selection was one that contained brain volume, body mass, latency to approach the puzzle box, time spent trying to open the box, manual dexterity, behavioral diversity, and group size (Table 1). The only statistically indistinguishable model (i.e., ΔDIC < 2) did not include group size but was otherwise the same (Table 1). Individuals from carnivore species with both larger absolute brain volumes and larger brain volumes relative to their overall body mass were better than others at opening the puzzle box, but only relative brain volume was a statistically significant predictor [P value from Markov Chain Monte Carlo (pMCMC) = 0.013] (Figs. 2 and 3, Table 2, and Table S2). Our results were insensitive to variation in both the total number of individuals tested per species and the minimum number of trials conducted per individual. Specifically, we obtained the same qualitative results if we limited our analyses to only species in which at least three (398 trials on 112 individuals from 23 species) (Table S3) or four individuals (348 trials on 97 individuals from 18 species) (Table S4) were tested per species, and if we restricted our analyses only to individuals to which we administered at least three separate trials (total number of trials per individual was 3–10) (Table S5). Additionally, if we restricted our analyses only to trials 1–3 for individuals that were tested at least three times (388 trials on 39 species), we found that individuals from species with a larger brain volume for their body mass tended to be more likely to open the puzzle box (pMCMC = 0.052) (Table S6).

Individuals from species with large average group sizes, such as banded mongoose (average group size = 23.7 individuals), were

Table 1. Model comparisons using DIC model selection analysis to investigate the predictors of success in opening the puzzle box in 39 carnivore species

Fixed effects	λ-Posterior mode	λ-Mean (95% credible interval)	DIC	ΔDIC
BV + BM + L + WT + D + BD + GS	0.94	0.85 (0.49–0.99)	283.2	0
BV + BM + L + WT + D + BD	0.93	0.82 (0.33–0.99)	284.9	1.7
L + WT + D + BD + GS	0.95	0.87 (0.62–0.99)	286.4	3.2
L + WT + D + BD	0.96	0.85 (0.56–0.99)	288.5	5.3
WT + D + BD	0.93	0.84 (0.54–0.99)	288.5	5.3
BV + BM + L + GS	0.97	0.91 (0.76–0.99)	293.3	10.1
BV + BM + L	0.95	0.88 (0.65–0.99)	294.3	11.1
BV + BM + GS	0.98	0.91 (0.73–0.99)	294.5	11.3
L + GS	0.97	0.92 (0.78–0.99)	296.4	13.2
BV + BM	0.96	0.88 (0.65–0.99)	296.6	13.4
GS	0.97	0.91 (0.73–0.99)	298.1	14.9
Intercept	0.96	0.90 (0.71–0.99)	299.9	16.7

Model terms are behavioral diversity (BD), body mass (BM), brain volume (BV), dexterity (D), group size (GS), latency to approach puzzle box (L), and time spent working trying to open the puzzle box (WT).

no more successful at opening the puzzle box (pMCMC = 0.79) (Table 2) than individuals from solitary species, such as black bears (group size = 1) or wolverines (group size = 1). To further test whether social complexity affected carnivores' ability to open the puzzle box, we also compared success at opening the puzzle box between solitary species (group size = 1) and social species (group size > 1) where group size was a binary predictor. This comparison indicated that social species were no better at opening the puzzle box than solitary species (pMCMC = 0.99) (Table S7).

Surprisingly, individuals from species with larger body sizes were less successful than smaller-bodied species at opening the puzzle box (pMCMC = 0.036) (Table 2). Individuals that were more dexterous (pMCMC = 0.08) (Table 2) and those that spent more time attempting to open the puzzle box (pMCMC = 0.08) (Table 2) tended to be more successful, although neither of these were statistically significant. Individuals that more quickly approached the puzzle box (pMCMC = 0.57) (Table 2) or those that used a greater diversity of behaviors when interacting with the puzzle box (pMCMC = 0.39) (Table 2) were no more successful than others at opening the box. In nine of the puzzle box trials, individuals opened the box door but did not retrieve the food reward, which might reflect underlying differences in motivation. We included these trials in our main analyses (Table 2), but also, we ran our analyses without these nine trials and obtained the same qualitative results (Table S8).

In our brain region analyses, there was no obvious top model that best explained success at opening the puzzle box (Table 3). Models containing relative anterior cerebrum volume (anterior to the cruciate sulcus; ΔDIC = 0) and posterior cerebrum volume (posterior to the cruciate sulcus; ΔDIC = 0) were the two models with the lowest

DIC values (Table 3). However, models containing hindbrain volume (which includes both cerebellum and brainstem volumes; ΔDIC = 0.2) or total cerebrum volume (ΔDIC = 0.3) were not considerably worse. Notably, models containing body mass and total brain volume in addition to the volume of one of four specific brain regions all had lower DIC values than a model containing only body mass and total brain volume (ΔDIC ranged from 1.9 to 2.2) (Table 3). This result suggests that the addition of the volume of a brain region to the model improved its ability to predict performance in the puzzle box trials over a model containing only total brain volume (Table 3). In none of the models using the reduced dataset were the relative sizes of any specific brain region associated with success in opening the puzzle box (Table S9).

Discussion

The connection between brain size and cognitive abilities has been called into question by both a study pointing out the impressive cognitive abilities of small-brained species, such as bees and ants (7), and another study doubting that overall brain size is a valid proxy for cognitive ability (9). In the former case, Chittka and Niven (7) argue that larger brains are partially a consequence of the physical need for larger neurons in larger animals and partially caused by increased replication of neuronal circuits, which confers many advantages for larger-brained species, such as enhanced perceptual abilities and increased memory storage. Chittka and Niven (7) conclude that neither of these properties of larger brains necessarily enhance cognitive abilities. Interestingly, our results actually show that carnivore species with a larger average body mass performed worse than smaller-bodied species on the task that we presented to
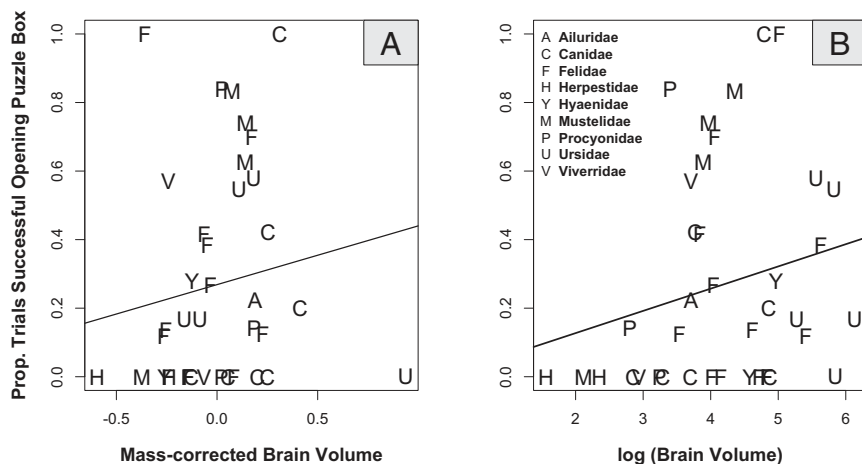

Fig. 2. (A) Carnivore species with larger brain volumes for their body mass were better than others at opening the puzzle box. (B) There was no significant relationship between absolute brain volume and success at opening the puzzle box in carnivore species when body mass was excluded from the statistical model. Data presented represent the average proportion of puzzle box trials in which species were successful and are for presentation purposes only, whereas statistical results from our full model used for our inferences are shown in Table 2. Mass-corrected brain volume in A is from a general linear model and for presentation purposes only; statistical results from the full model are shown in Table 2.
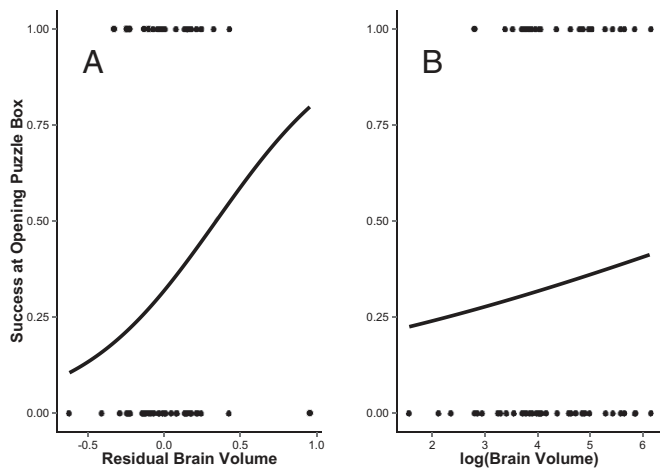
Fig. 3. (*A*) Individuals from carnivore species with larger brain volumes relative to their body mass were significantly better than others at opening the puzzle box (Table 2). (*B*) There was no significant relationship between absolute brain volume and success at opening the puzzle box in our individual-level analyses in which body mass was excluded (Table S2). Individuals with success equal to one opened the box, whereas those with success equal to zero did not. Mass-corrected brain volume in *A* is from a general linear model and for presentation purposes only; full statistical results are shown in Table 2 and Table S2. Regression lines represent predicted relationships from statistical models investigating the association between (*A*) brain volume relative to body mass or (*B*) log (brain volume) and success at opening the puzzle box.

them. Thus, it truly does seem that a larger brain size relative to body size is an important determinant of performance on this task, and it is not the case that larger animals are more successful simply because their brains are larger than those of smaller species.

Regarding whether overall brain size is a valid proxy for cognitive abilities, the use of whole-brain size as a predictor of cognitive complexity in comparative studies is questioned, because the brain has different functional areas, some of which are devoted to particular activities, such as motor control or sensory processing. Given this high degree of modularity in the brain, Healy and Rowe (8, 9) argue that overall brain size is unlikely to be a useful measure when examining how evolution has shaped the brains of different species to perform complex behaviors. Although the brain has functional modules, such as the hippocampus or the olfactory bulbs, which may be under specific selection pressures (31), these modules may also exhibit coordinated changes in size because of constraints on ways in which the brain can develop (32). In addition to functionally specialized modules, the brain also contains broad areas, such as the mammalian neocortex, that control multiple processes. Thus, there are reasons to believe that overall brain size may be an informative proxy for cognitive abilities, despite the modular nature of the brain.

Here we examined relationships between relative brain size, size of specific brain regions, and problem-solving success. Although none of the regional brain volumes that we examined significantly predicted success on this task (Table S9), the addition of the volume of these brain regions improved the ability of our models to explain performance in the puzzle box task over a model containing only total brain volume (Table 3). We emphasize, however, that only 17 species were included in that analysis. Nevertheless, relative brain size was a significant predictor of problem-solving success across species, and this result was robust in all of our analyses. Thus, our data provide important support for the idea that relative brain size can be useful in examining evolutionary relationships between neuroanatomical and cognitive traits and corroborate results from artificial selection experiments showing that larger brain size is associated with enhanced problem solving (5). It will be important in future work to use more detailed noninvasive brain imaging methods rather than endocasts to evaluate whether hypothetically important brain areas, such as prefrontal and cingulate cortexes, contribute to the relationship between brain size and performance during problem solving.

Assessment of the ecological and neuroanatomical predictors of problem-solving ability has some important implications for hypotheses proposed to explain the adaptive value of large brains and sophisticated cognition. One such hypothesis that has garnered much support in primate studies is "the social brain hypothesis" (33, 34), which proposes that larger brains evolved to deal with challenges in the social domain. This hypothesis posits that selection favored those individuals best able to anticipate, respond to, and perhaps even manipulate the actions of conspecific group members. However, a major shortcoming of the social brain hypothesis (35, 36) is its apparent inability to explain the common observation that species with high sociocognitive abilities also excel in general intelligence (37, 38). There is, in fact, a long-standing debate as to whether animal behavior is mediated by cognitive specializations that have evolved to fulfill specific ecological functions or instead, domain-general mechanisms (38, 39). If selection for social agility has led to the evolution of domain-general cognitive abilities, then species living in social groups should solve technical problems better than solitary species. However, we found that carnivore species living in social groups performed no better on our novel technical problem than solitary species. Thus, whereas social complexity may select for enhanced ability to solve problems in the social domain (40), at least in carnivores, greater social complexity is not associated with enhanced ability to solve a novel technical problem.

Table 2. Results from Bayesian phylogenetic generalized linear mixed-effects models to investigate the predictors of success in opening the puzzle box in 39 mammalian carnivore species

	Effective sample size	Posterior mean (95% CI)	Posterior mode	pMCMC
Random effect				
Species	3,094	13.8 (0.0007–40.4)	4.3	—
Individual identification	2,791	21 (7.6–38.2)	16.1	—
Fixed effect				
Intercept*	3,284*	−36.5 (−60.7 to −16.1)*	−30.6*	0.0003*
Brain volume*	3,284*	8.5 (1.3–16.3)*	7.8*	0.013*
Body mass*	3,720*	−4.6 (−9.2 to −0.2)*	−4.9*	0.036*
Latency to approach	3,284	−0.12 (−0.5–0.3)	−0.1	0.57
Work time	2,493	0.34 (−0.04–0.7)	0.4	0.08
Behavioral diversity	3,018	1.7 (−1.9–6)	1.2	0.39
Dexterity	3,284	2.7 (−0.3–5.8)	2.2	0.08
Group size	3,284	−0.04 (−0.3–0.2)	−0.02	0.79

pMCMC is the Bayesian *P* value. Sample sizes are 495 trials on 140 individuals from 39 different species. 95% CI, 95% credible interval.
*Statistically significant.

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Table 3. Model comparisons using DIC model selection to investigate whether the volumes of specific brain regions better predicted success in opening the puzzle box than total brain volume in 17 mammalian carnivore species

Model name	Fixed effects	λ-Posterior mode	λ-Mean (95% CI)	DIC	ΔDIC
Anterior cerebrum	AC + BM + BV	0.006	0.42 (0.0003–0.99)	88.4	0
Posterior cerebrum	PC + BM + BV	0.004	0.37 (0.0002–0.98)	88.4	0
Brainstem/cerebellum	BS/CL + BM + BV	0.006	0.42 (0.004–0.99)	88.6	0.2
Cerebrum	C + BM + BV	0.006	0.41 (0.0003–0.99)	88.7	0.3
Brain	BV + BM	0.005	0.36 (0.0002–0.98)	90.6	2.2

Model terms are volume of anterior cerebrum (AC), body mass (BM), volume of brainstem and cerebellum (BS/CL), volume of total brain (BV), volume of total cerebrum (C), and volume of posterior cerebrum (PC). 95% CI, 95% credible interval.

Our results are similar to those obtained in the work by MacLean et al. (12), which examined relationships among brain size, social complexity, and self-control in 23 species of primates. In both that study and our own study, species with the largest brains showed the best performance in problem-solving tasks. However, in neither primates nor carnivores did social complexity predict problem-solving success. This finding is also consistent with results obtained in the work by Gittleman (41), with analysis of 153 carnivore species that revealed no difference in brain size relative to body size between social and solitary species. Nevertheless, in this study, we were only able to present carnivores with a single problem-solving task, and we were only able to test one to nine individuals per species. Ideally, future studies will present a large array of carnivores with additional cognitive challenges and will test more individuals per species.

A second hypothesis forwarded to explain the evolution of larger and more complex brains, the cognitive buffer hypothesis (42, 43), posits that large brains evolved to allow animals to cope with socioecological challenges and thus, reduce mortality in changing environments. Previous work has shown convincingly that diet is a significant predictor of brain size in carnivores (27), as it is in primates (12), and this study shows that carnivore species with larger brains are more likely to solve a novel technical problem. However, an explicit test of the cognitive buffer hypothesis has not yet been attempted with mammalian carnivores.

Overall, our finding that enhanced problem solving is related to disproportionally large brain size for a given body mass is important for several reasons. First, although there is correlational evidence for an association between absolute or relative brain size and problem-solving abilities, experimental evidence is extremely rare. The lack of experimental evidence has led to criticisms of the use of brain size as a proxy for problem-solving abilities (8, 9, 44). We offer experimental evidence that brain size is, indeed, a useful predictor of performance, at least in the single problem-solving task that we posed to our carnivore subjects. Although only brain size relative to body mass was a significant predictor of success with our puzzle box, species with larger absolute brain volumes also tended to be better than others at opening the puzzle box (Figs. 2 and 3 and Table S2). Second, the vast majority of work on this topic has focused on primates, fish, and birds (5, 10, 11, 13–16). Our results offer new evidence for the relationship between brain size and problem-solving abilities in mammalian carnivores. The previous lack of support for this relationship across a diverse set of taxa has limited both its validity and its generality. Thus, the findings presented here represent an important step forward in our understanding of why some animals have evolved large brains for their body size.

Materials and Methods

From 2007 to 2009, we presented puzzle boxes to myriad carnivores housed in nine North American zoos (Fig. 1A and Dataset S1). Because we were testing animals that ranged in size from roughly 2 to 300 kg, we used two steel mesh puzzle boxes; the larger box was 63.5 × 33 × 33 cm, and the smaller box was one-half that size. The smaller box was presented to species with an average body mass of <22 kg, such as river otters, kinkajous, sand cats, and other small-bodied carnivores (Dataset S1). The larger box was presented to species with an average body mass >22 kg, including snow leopards, wolves, bears, and other large-bodied species (Dataset S1). For cheetahs (species average

body mass = 50 kg) and wild dogs (species average body mass = 22.05 kg), both large and small boxes were used with some subjects, but their performance did not vary with box size (additional details are given in SI Text).

We videotaped all trials and extracted performance measures from videotapes using methods described elsewhere (24, 28, 45) (Movie S1). Extracted behaviors included the latency to approach the puzzle box, the total time spent trying to open the box, the number of different behaviors used in attempting to open the box, and a measure of manual dexterity (all described in SI Text). We then brought together data on success and performance measures during zoo trials with previously published data on total brain size and body mass (46).

We used Bayesian phylogenetic generalized linear mixed-effects models based on a Markov Chain Monte Carlo algorithm implemented in the R package MCMCglmm (47–49) to identify the variables predicting success or failure in solving this puzzle. These models allowed us to assess the effects of predictor variables on carnivores' success at opening the puzzle box after controlling for shared phylogenetic history.

For our analyses of how brain volume affected the ability of carnivores to open the puzzle box, we constructed 12 different models containing different combinations of the morphological, behavioral, and social characteristics of tested species or individuals (Table 1). In all models except that shown in Table S2, we included species' average body mass as a covariate so that we could assess the effects of brain volume on puzzle box performance relative to body mass (50, 51). We used DIC (51) to examine the relative degree of fit of the different models. DIC is analogous to Akaike's information criterion (52), and lower values for DIC suggest a better fit. We present DIC values for all models (Table 1) but only present results from the model with the lowest DIC (Table 2) (53).

In separate analyses, we performed five different Bayesian phylogenetic generalized linear mixed-effects models to determine whether the volume of any specific brain region better predicted success in opening the puzzle box than overall endocranial volume (Table 3). These models also included species' average body mass and total brain volume as covariates (27). Computed tomography data were available documenting both total endocranial volume and the volumes of specific brain regions from 17 different carnivore species in six families (Dataset S1). Overall endocranial volume was subdivided into (i) cerebrum anterior to the cruciate sulcus, (ii) cerebrum posterior to the cruciate sulcus, (iii) total cerebrum, and (iv) hindbrain, which includes both cerebellum and brainstem. The cerebrum anterior to the cruciate sulcus is comprised mainly of frontal cortex. Additional methodological details on the estimation of these brain region volumes can be found elsewhere (54–56) (SI Text).

Our response variable was binary (did or did not open puzzle box); therefore, we used a categorical error structure in MCMCglmm, and we fixed the prior for the residual variance to one ($V = 1$; fix = 1). We included random effects for species and individual identity in these models. We used weakly informative inverse γ-priors with a low degree of belief ($V = 1$; $\mu = 0.002$) for the random effect variance. All models were run for appropriate numbers of iterations, burn-ins, and thinning intervals to generate a minimum effective sample size of >2,000 for all parameters in all of the different models. We provide the mean, mode, and 95% credible interval from the posterior distribution of each parameter. We considered parameters to be statistically significant when the 95% credible intervals did not overlap zero and pMCMC was <0.05 (47). Detailed statistical methods are in SI Text.

Appropriate ethical approval was obtained for this work. This work was approved by Michigan State University Institutional Animal Care and Use Committee (IACUC) Approval 03/08-037-00 and also, the IACUCs at all nine zoos (St. Louis Zoo, Bergen County Zoo, Binder Park Zoo, Potter Park Zoo, Columbus Zoo, The Living Desert, Wild Canid Survival and Research Center, Turtle Back Zoo, and Denver Zoo) where testing was done.

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