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Is the Western Scrub-Jay *(Aphelocoma californica)* Really an Underdog among Food-Caching Corvids when It Comes to Hippocampal Volume and Food Caching Propensity?

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Abstract
Food caching has been linked to better performance on spatial memory tasks and enlarged hippocampal volume in both birds and mammals. Within food-caching birds, it has also been predicted that species less reliant on stored food should have inferior spatial memory and a smaller hippocampus compared to species that depend heavily on food caches. Several comparisons suggest that North American corvids have a significantly smaller hippocampus and overall brain volume compared to the Eurasian corvid species and that western scrub-jays (*Aphelocoma californica*) have a smaller hippocampus compared to the more specialized Clark's nutcracker. Here we present the largest data set of scrub-jay brains and, in contrast to previous reports, show that relative to body mass western scrub-jays have a brain size similar to the largest brain size of Eurasian corvids. The relative hippocampal volume of scrub-jays is also among the largest of all investigated corvids. These findings may not be surprising considering that scrub-jays have been reported to have remarkable cognitive capacities such as episodic-like memory and experience projection. Our data suggest that many previously made assumptions about western scrub-jays as less specialized food hoarders might be an oversimplification and that simple categorization of species into specialized and non-specialized hoarders might not provide useful insights into the evolution of memory and the hippocampus.

Introduction

Some bird species regularly cache food for future consumption and such food caches are thought to be crucial for survival [Vander Wall, 1990; Pravosudov and Grubb, 1997]. Many of the food-caching species scatter their hoards over substantial home ranges and successful cache retrieval is thought to be critical for the evolution of food-caching behavior [Krebs et al., 1996]. It has been well documented that food-caching birds successfully find their own caches and rely, at least in part, on spatial memory to do so [Shettleworth, 1995; Krebs et al., 1996]. In

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addition, it is well established that the hippocampus is involved in spatial memory processing [O'Keefe and Nadel, 1978; Sherry and Vaccarino, 1989; Hampton and Shettleworth, 1996].

The adaptive specialization hypothesis predicts that increased demands for memory processing stemming from the necessity to find thousands of previously hidden food caches resulted in increased selection pressure on spatial memory and the hippocampus in food caching birds [Krebs et al., 1989, 1996]. Following the adaptive specialization hypothesis, food-caching birds should have better performance on spatial memory tasks and an enlarged hippocampal volume compared to non-caching species; and much research has been carried out testing this prediction [Krebs et al., 1989; Sherry et al., 1989; Healy and Krebs, 1992, 1996; Basil et al., 1996]. Most work focused on representatives of two families with many food-caching species: i.e., the Corvidae and the Paridae. Initial comparisons made separately within each family supported the adaptive specialization hypothesis and suggested that food-caching species have larger hippocampal volumes than their non-caching family members [Krebs et al., 1989; Sherry et al., 1989; Healy and Krebs, 1992, 1996; Basil et al., 1996].

However, when Brodin and Lundberg [2003] analyzed all data sets combined, including all available data on corvids and parids, they failed to find a significant relationship between food-caching behavior and hippocampal volume. Lucas et al. [2004] suggested that the lack of a relationship between food caching behavior and hippocampal volume presented by Brodin and Lundberg [2003] stemmed from the fact that there is a difference in the volume of the hippocampus and overall brain size between Eurasian and North American species. When continent of origin was added as a factor to the model, the relationship between food caching and hippocampal volume reappeared [Lucas et al., 2004]. Garamszegi and Eens [2004] added a larger set of non-caching species to the data set and found an effect of food-caching specialization on hippocampal volume without adding continent effects. Thus, the latest large-scale comparison supports the adaptive specialization hypothesis. However, it remains unclear why North American species would have a smaller brain size than their relatives in Eurasia.

On a finer scale the adaptive specialization hypothesis also predicts that food-caching species that rely heavily on food caches for survival should have better spatial memory and larger hippocampal volumes compared to species that depend less on cached food. North American corvids have been extensively used to test this prediction: western scrub-jays (*Aphelocoma californica*) and grey-breasted jays (*A. ultramarina*) have been categorized as non-specialized hoarders that are not well adapted to food-caching. By contrast, pinyon jays (*Gymnorhinus cyanocephalus*) and Clark's nutcrackers (*Nucifraga columbiana*) have been characterized as highly specialized hoarders that depend on cached food for survival [Balda and Kamil, 1989; Kamil et al., 1994; Olson et al., 1995]. Extensive testing has not led to any conclusive results; in some tests Clark's nutcracker and pinyon jays demonstrated better spatial memory than western scrub-jays and Mexican jays [Kamil et al., 1994; Olson et al., 1995], whereas others found western scrub-jays to be superior to nutcrackers and pinyon jays [Gould-Beierle, 2000]. Balda and Kamil [1989] emphasized that Clark's nutcrackers and pinyon jays can remember cache locations for long periods of time; caches made during autumn can frequently be used as late as spring and early summer. Western scrub-jays, on the other hand, do not seem to use their caches over such extended periods. Instead, western scrub-jays cache and retrieve their caches on a short-term time scale. Yet, Bednekoff et al. [1997] failed to find significant differences in long-term spatial memory between these species. So, despite the report of Basil et al. [1996] showing that Clark's nutcrackers have a relatively larger hippocampus than western scrub-jays, these species do not show consistent differences in adaptations to caching behavior.

It is possible that some of the assumptions made about the degree of caching specialization of scrub-jays are oversimplified. Western scrub-jays do not seem to be well adapted for caching large quantities of pine seeds over short periods of time. They do not have the morphological adaptations to carry many seeds, such as the pouches of Clark's nutcrackers [Bock et al., 1973] and pinyon jays [VanderWall and Balda, 1981]. However, western scrub-jays cache year round [Curry et al., 2002; personal observations] whereas the Clark's nutcracker and the pinyon jays show distinct peaks in caching behavior that coincide with the availability of their favorite seeds. The amount of caching by western scrub-jays could also be underestimated because the assessment is based on the numbers of pine seeds cached. Although western scrub-jays cache fewer pine seeds compared to hoarding specialists such as the Clark's nutcracker [Balda and Kamil, 1989], they also cache a large number of other food types [Curry et al., 2002]. It is unclear how these two distinct types of caching, namely, the concentrated-in-time and food-type-specific caching of the Clark's nutcracker and the continuous and versatile caching of the western scrub-jay, compare in the demand on spatial memory. In addition, it has been demonstrated that western scrub-jays have remarkable episodic-like memory for their caches; not only do they remember where they made a cache but they also remember the content of the cache and the time it was made [Clayton and Dickinson, 1998; Clayton et al., 2003]. Because western scrub-jays cache food types that perish at different rates (e.g., invertebrates and seeds), selection pressure on the memory of when a cache was made and its content, in addition to the memory of where it was cached, could have been particularly strong. In contrast, a species that specializes in caching non-perishable seeds only needs to remember the location for successful cache retrieval. It has been suggested that like spatial memory, episodic memory might depend on the hippocampus [Jefferey, 2004] and thus episodic-like memory in the western scrub-jays might pose an additional selection pressure on hippocampal volume. Considering that western scrub-jays memory use is more complex than would be expected from simply considering them non-specialized hoarders, it would be important to re-evaluate their hippocampal and brain size and to re-examine how their brain size compares to that of other corvids.

Here, we present new data on western-scrub jay's brain size using the largest sample size available for any corvid species and compare them with the brain size in other corvids.

Materials and Methods

Twenty-four western scrub-jays were collected from nests between March and April 2003 and hand raised for behavioral experiments investigating the effects of nutrition during early post-hatching development on spatial memory and the hippocampus [Pravosudov et al., in press]. All birds were sacrificed at about one year of age for brain analyses. Jays were anesthetized with Nembutal-sodium solution and perfused transcardially with 4% paraformaldehyde in phosphate buffer. After perfusion, the brain was placed in 4% paraformaldehyde for 1 week. The brains were cryoprotected in a 30% sucrose solution, frozen in dry ice and kept at –70°C until processing. We cut coronal sections at 40 μm on a sliding freezing microtome. All details of perfusions and brain preparations have been described in detail previously [Pravosudov et al., 2002, in press; Pravosudov and Clayton, 2002; Pravosudov and Omanska, 2005a, b].

We used the StereoInvestigator software (version 3.15a, Microbrightfield, Colchester, Vt., USA) for all stereological measurements. We used the Cavalieri principle [Gunderson and Jensen, 1987] to measure the volume of the right and left sides of the hippocampus and the rest of the telencephalon on Nissl-stained sections [Pravosudov et al., in press]. We used the optical fractionator method to estimate the total number of neurons in the right and left sides of the hippocampus using the same sections as for the analyses of the hippocampal volume [Pravosudov et al., in press]. The details of all these methods have been described previously [Pravosudov et al., 2002; Pravosudov and Clayton, 2002; Pravosudov and Omanska 2005a, b]. Scrub-jays in this study were divided into two groups; one group was reared on ad libitum food supply whereas the other group was fed a moderately restricted diet until the birds started to eat independently [Pravosudov et al., in press]. After birds in both groups became nutritionally independent they were maintained on an ad libitum diet. Birds in both groups demonstrated development rates within a range commonly observed in natural broods. All birds have been regularly tested on spatial memory tests consisting of a food caching and cache-recovery task and a one-trial associative learning task following the same protocol until they were sacrificed when they were about one year old [Pravosudov et al., in press]. Thus all birds had extensive experience in food caching and cache retrieval. Relative hippocampal volume was smaller in birds that experienced nutritional deficits but here we conservatively used data from all brains irrespective of specific experimental conditions during development [Pravosudov et al., in press]. Because some birds died during the experiment, only 21 brains were available for the analyses.

We used brain measurements for other corvid species from Healy and Krebs [1992a], Basil et al. [1996], and Brodin and Lundberg [2003] but we only used species for which two or more data points were available to provide a measure of variance. For statistical analyses we used a General Linear Model (GLM) with species as a factor on log transformed brain volume estimates (Log(x+1)). We used either the remainder of the telencephalon volume or body mass as a covariate to compare relative hippocampal volume. All comparisons were made using least squares means, which are mean values adjusted for the variation in either telencephalon volume or body mass.

Results

Absolute volume of the hippocampus of western scrub-jays in this study was more than two times larger (76.19 ± 6.9 mm^3 (SD)) than that reported in Basil et al. [1996] (32.06 ± 3.6 mm^3 (SD) adjusted for shrinkage; t test, $t_{21} = -12.54$, $p < 0.001$; fig. 1). Relative to the telencephalon volume, hippocampal volume of western scrub-jays in this study was also larger (ca. 57%, $F_{1,20} = 8.67$, $p < 0.01$) than that in Basil et al. [1996]. Similar significant differences between the studies were observed in telencephalon minus the hippocampus volume (2,158.3 ± 172.1 mm^3 (SD) in our study and 1,094.6 ± 55.6 mm^3 (SD) in Basil et al. [1996], adjusted for shrinkage; t test, $t_{21} = -11.77$, $p < 0.001$; fig. 1).

When telencephalon was used as a covariate, hippocampal volume differed significantly between the species ($F_{7,54} = 32.6$, $p < 0.001$; fig. 2A, 3A), and the effect of telencephalon was also significant ($F_{1,54} = 32.6$, $p < 0.001$). Post-hoc analyses revealed that relative hippocampal volume of western scrub-jays was significantly larger than

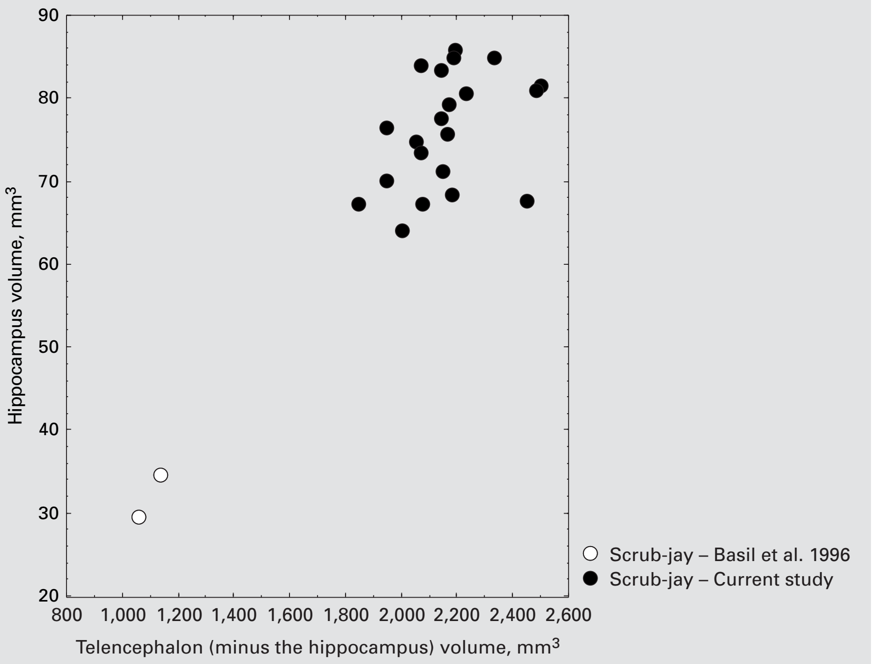

Fig. 1. The relationship between the hippocampal and telencephalon volumes in western scrub-jays, from Basil et al. [1996] (open circles) and from our study (filled circles).

that of pinyon and grey-breasted jays, Clark's nutcrackers and jackdaws (*Corvus monedula*), statistically indistinguishable from that of the carrion crow (*Corvus corone*) and the Eurasian magpie (*Pica pica*) and significantly smaller than that of the Eurasian jay (*Garullus glandarius*; table 1; fig. 3A).

When body mass was used as a covariate, hippocampal volume also differed significantly between the species ($F_{7,54} = 29.1$, $p < 0.001$; fig. 2B, 3B) and the effect of body mass was significant ($F_{1,54} = 5.2$, $p < 0.05$). The post-hoc analyses, however, revealed different results; relative hippocampal volume of western scrub-jays was now statistically indistinguishable from that of the Eurasian jay, the Eurasian magpie and the carrion crow, whereas it was significantly larger than that of all other species (table 1; fig. 3B). The main difference between using telencephalon and body mass as a covariate concerns just one species; the Eurasian jay that has been reported to have an unusually small telencephalon [Healy and Krebs, 1992; fig. 2, 3].

When we compared the total brain volume relative to body mass, species was a significant factor ($F_{7,54} = 20.6$, $p < 0.001$; fig. 4), as well as body mass ($F_{1,54} = 19.0$, $p < 0.001$). Post-hoc analyses showed that Eurasian jays had a significantly smaller brain volume relative to body mass than all other species except carrion crows (Tukey test, $p < 0.05$; fig. 4). Western scrub-jays, on the other hand, have a significantly larger total brain volume relative to body mass than all other species in this study (Tukey test, $p < 0.05$; fig. 4).

Table 1. Results of Tukey post-hoc tests comparing relative hippocampal volume (adjusted for either telencephalon volume or body mass) of western scrub-jays with that of other corvids

Species	Adjusted for telencephalon	Adjusted for body mass
Grey-breasted jay	$p < 0.05$ (+)	$p < 0.05$ (+)
Pinyon jay	$p < 0.05$ (+)	$p < 0.05$ (+)
Clark's nutcracker	$p < 0.05$ (+)	$p < 0.05$ (+)
Carrion crow	n.s.	n.s.
Jackdaw	$p < 0.05$ (+)	$p < 0.05$ (+)
Eurasian jay	$p < 0.05$ (–)	n.s.
Eurasian magpie	n.s.	n.s.

(+) indicates larger and (–) smaller relative hippocampal volume in scrub-jays. A complete General Linear Model included log-transformed hippocampal volume as a dependent variable, species as an independent variable and either telencephalon or body mass as a covariate.

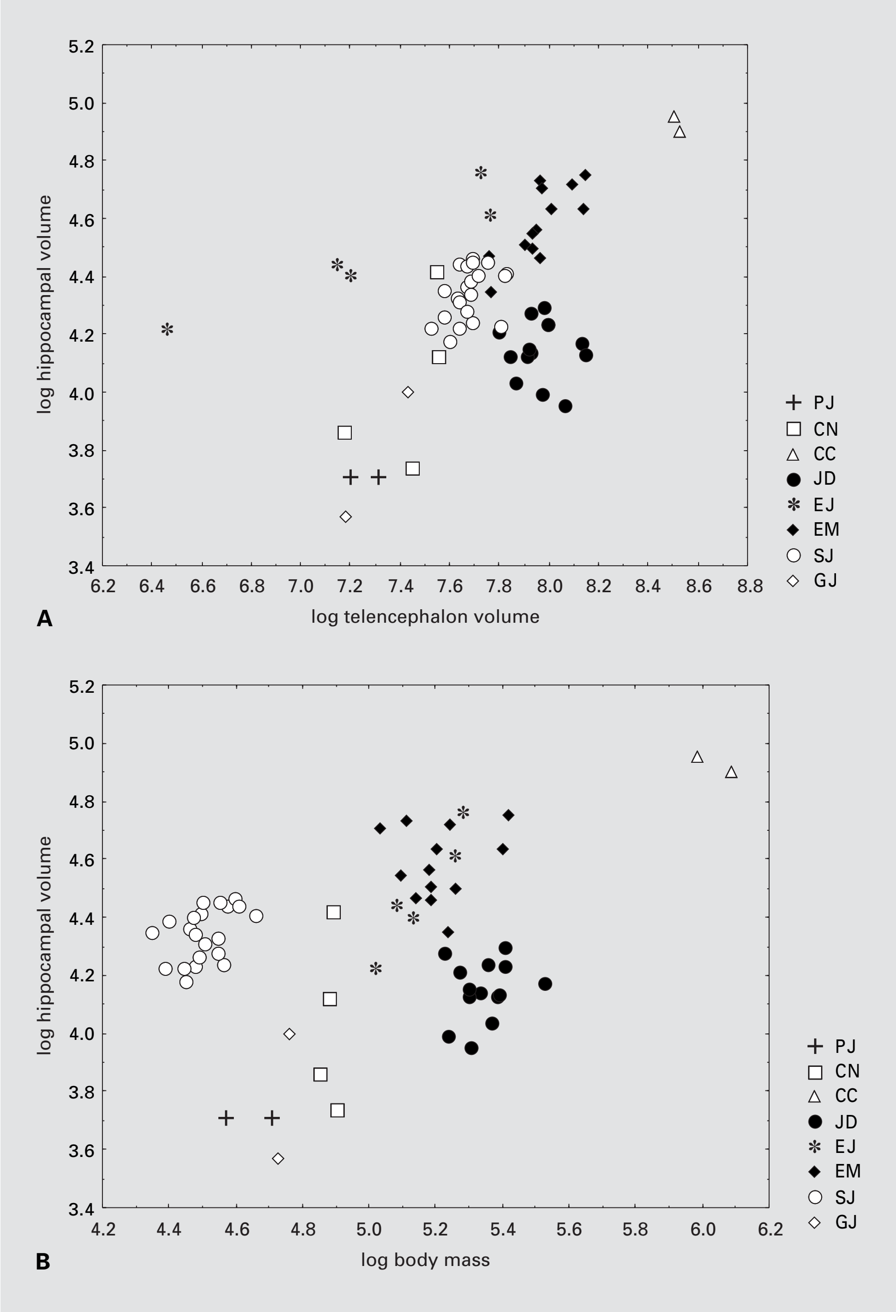

Fig. 2. The relationship between hippocampal and telencephalon volume (**A**) and between hippocampal volume and body mass (**B**) in corvids. PJ = Pinyon jay; GJ = grey-brested jay; CN = Clark's nutcracker; CC = carrion crow; JD = jackdaw; EJ = Eurasian jay; EM = Eurasian magpie; SJ = western scrub-jay.

Discussion

Our study showed that previously used estimates of western scrub-jay brains do not represent reliable values. Total brain volume in this study was more than 2 times larger than that reported in Basil et al. [1996]. The new estimates showed that western scrub-jays have one of the largest hippocampal volumes relative to body mass and the largest total brain volume relative to the body mass among all investigated corvids.

Why is there such a discrepancy between our study and Basil et al. [1996]? One major difference is that we used frozen tissue similar to most other studies, whereas Basil et al. [1996] embedded brain tissue in paraffin. Basil et al. [1996] corrected for tissue shrinkage referring to Fite et al. [1993] and these corrected values have been used in

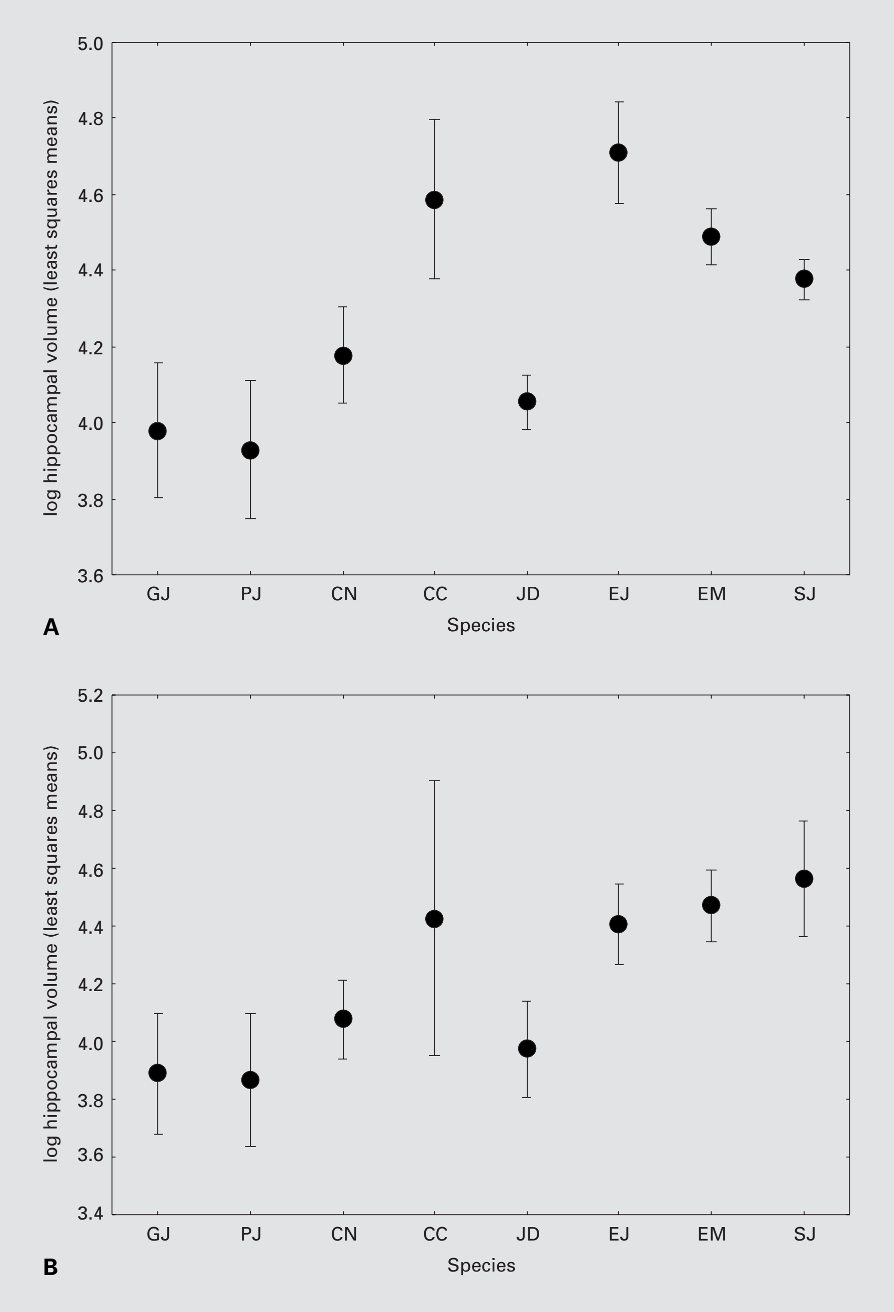

Fig. 3. A Hippocampal volume relative to the remainder of the telencephalon volume in corvids. **B** Hippocampal volume relative to the body mass in corvids. Vertical lines represent 95% confidence interval. Species acronyms as in figure 2.

subsequent comparative studies [Brodin and Lundberg, 2003; Lucas et al., 2004; Garamszegi and Eens, 2004]. However, Fite et al. [1993] did not mention shrinkage of paraffin-embedded tissue as they used Polybed 812, which might have different properties than paraffin. Fite et al. [1993] also did not present any data supporting their estimation of 24% shrinkage in Polybed-embedded tissue. Basil et al. [1996] used 23% correction, which is not mentioned in Fite et al. [1993]. It is possible that paraffin-embedded tissue shrinks more than Polybed-embedded tissue, however there were no data to validate any of the corrections used. Polybed 812 is an Epon resin and there have been reports that embedding in paraffin results in greater tissue shrinkage compared to embedding in plastic such as Polybed [Nielsen et al., 1995]. Because there is a substantial discrepancy between the western

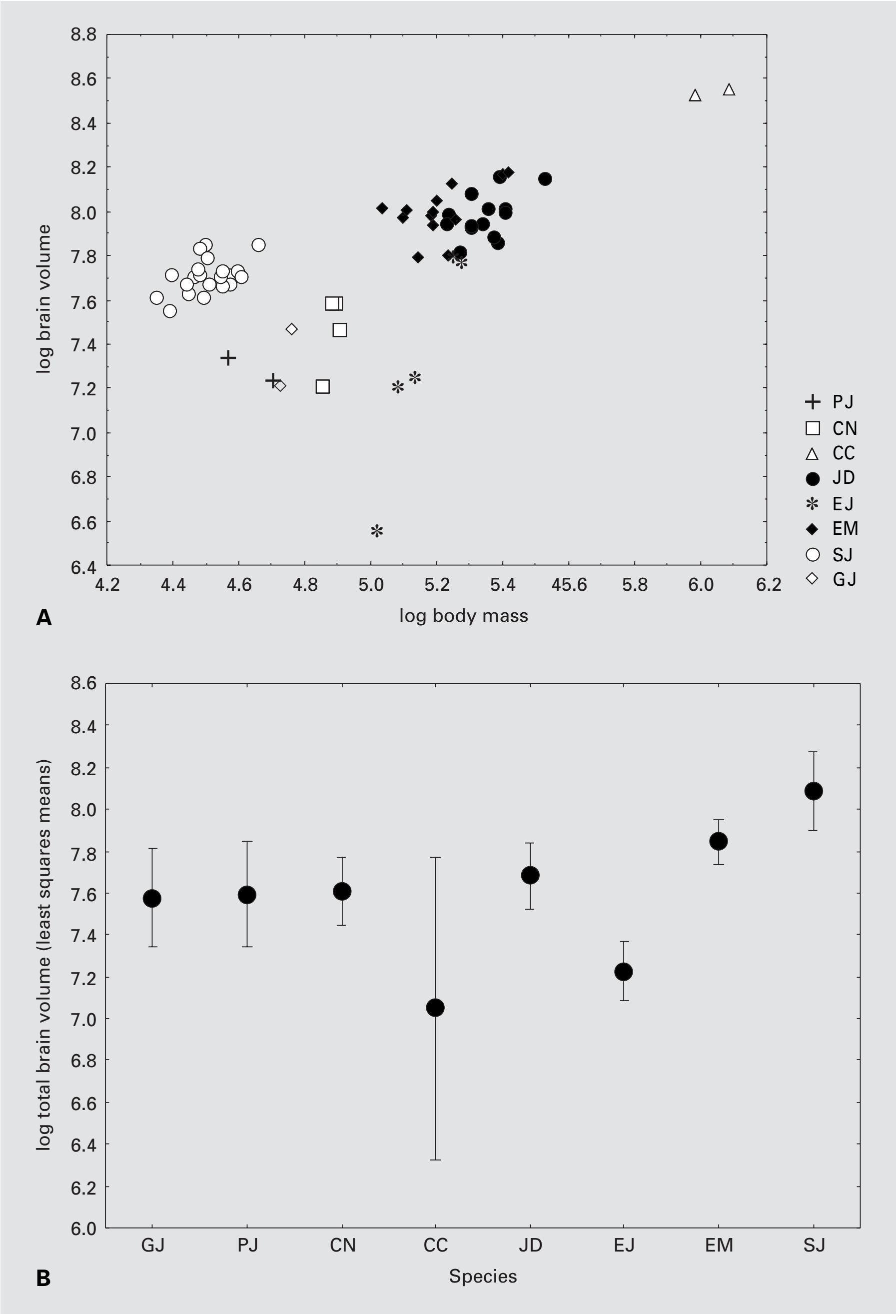

Fig. 4. The relationship between total brain volume and body mass (**A**); and total brain volume relative to body mass in corvids (**B**). Vertical lines represent 95% confidence interval. Species acronyms as in figure 2.

scrub-jay measurements of Basil et al. [1996] and our measurements, it is plausible to assume that all measurements of other North American corvids in that paper were also noncomparable to the measurements from frozen tissue. We used the data from Basil et al. [1996] for illustrative purposes, but we suggest that these data should not be used in future comparative studies until more data on these species can either confirm or refute our conclusions. It is plausible that the shrinkage of both the hippocampus and the rest of the telencephalon is proportional when tissue is embedded in paraffin, however, hippocampal volume relative to the rest of the telencephalon in this study was significantly different from that in Basil et al. [1996]. Therefore, it might be possible that shrinkage of the hippocampus and the rest of the telencephalon is not proportional when the tissue is embedded in paraffin. Alternatively and more likely, it is possible that the small sample size (n = 2) in Basil et al. [1996] contributed to the differences between the studies.

Lucas et al. [2004] reported that North American corvids have significantly smaller hippocampi than Old World corvids irrespective of their degree of food-caching specialization. However, data for all except one North American corvid [blue jay (*Cyanocitta cristata*) – only a single data point is available, which seems to be an outlier within American corvids for hippocampal volume relative to telencephalon volume; Lucas et al., 2004] come from a single study by Basil et al. [1996], which, as we argue here, does not provide comparable data. Based on the current data, western scrub-jays have a relative hippocampus as large as the largest hippocampus in Old World corvids, whereas their relative overall brain size is actually larger than that of any investigated Old World corvid. Thus, conclusions about continental differences in corvid brain size [Lucas et al., 2004] might be premature.

It is interesting that when we used the telencephalon as a covariate, Eurasian jays had the largest hippocampus of all corvids, whereas when we used body mass as a covariate, the trend disappeared and Eurasian jays had hippocampi similar in size to those in Eurasian magpie and western scrub-jays. When we looked at the volume of the entire brain, Eurasian jays also have a significantly smaller brain volume than most other corvid species. Although it is not clear why Eurasian jays have a smaller brain size, overall our results suggest that relative hippocampal size in scrub-jays is comparable to that of Eurasian jays.

This study shows that the western scrub-jay has a relatively large hippocampus compared to other corvids, despite its usual categorization as a non-specialized food cacher. Caching and retrieving relatively small amounts of food throughout the year, such as the western scrub-jay does might provide as much selection pressure for memory and the hippocampus as caching large amounts of food during only a brief period, such as the specialized cachers do. In addition, caching food items that perish at different rates (e.g., seeds vs insects) might provide an additional selection pressure on memory and the hippocampus. Thus comparing species with seemingly different degrees of hoarding specialization might not be informative with respect to the evolution of memory and the hippocampus. The current study also strongly suggests that more data are needed to justify generalizations about brain evolution in birds and to avoid possible spurious correlations.

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