



Research

Cite this article: Keirnan AR, Cunha F, Citron S, Prideaux G, Iwaniuk AN, Weisbecker V. 2025 Avian telencephalon and cerebellum volumes can be accurately estimated from digital brain endocasts. *Biol. Lett.* **21**: 20240596.

<https://doi.org/10.1098/rsbl.2024.0596>

Received: 16 October 2024

Accepted: 15 December 2024

Subject Category:

Evolutionary Biology

Subject Areas:

evolution, palaeontology, neuroscience, behaviour

Keywords:

endocast, comparative neuroanatomy, telencephalon, cerebellum, birds, vertebrate brain

Author for correspondence:

Aubrey R. Keirnan

e-mail: aubrey.keirnan@flinders.edu.au

[†]Andrew N. Iwaniuk and Vera Weisbecker are joint senior authors.

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.7601386>.

THE ROYAL SOCIETY
PUBLISHING

Avian telencephalon and cerebellum volumes can be accurately estimated from digital brain endocasts

Aubrey R. Keirnan¹, Felipe Cunha², Sara Citron², Gavin Prideaux¹, Andrew N. Iwaniuk^{2,†} and Vera Weisbecker^{1,†}

¹College of Science and Engineering, Flinders University, Adelaide, South Australia, Australia

²Department of Neuroscience, University of Lethbridge, Lethbridge, Alberta, Canada

ARK, 0000-0002-4033-6217; FC, 0000-0002-3656-732X; SC, 0009-0006-8138-3905; GP, 0000-0002-9958-0265; ANI, 0000-0001-9273-3655; VW, 0000-0003-2370-4046

For studies of the evolution of vertebrate brain anatomy and potentially associated behaviours, reconstructions of digital brain endocasts from computed tomography scans have revolutionized our capacity to collect neuroanatomical data. However, measurements from digital endocasts must be validated as reflecting actual brain anatomy, which is difficult because the collection of soft tissue information through histology is laborious and time-consuming. In birds, the reliability of digital endocast measurements as volume proxies for the two largest brain regions—the telencephalon and cerebellum—remains to be validated despite their use as proxies, e.g. of cognitive performance or flight ability. We here use the largest dataset of histology and digital endocasts to date, including 136 species from 25 avian orders, to compare digital endocast surface area measurements with actual brain volumes of the telencephalon, cerebellum and whole-brain endocast. Using linear and phylogenetically informed regression analyses, we demonstrate that endocast surfaces are strongly correlated with their brain volume counterparts for both absolute and relative size. This provides empirical support for using endocast-derived cerebellar and telencephalic surface areas in existing and future studies of living and extinct birds, with potential to expand to the dinosaur—bird transition in the future.

1. Introduction

Over the past two decades, digital endocasts have become an increasingly important tool in the study of neural and behavioural evolution in vertebrates [1–6]. Using computed tomography (CT) scanned skulls, the brain cavity is digitally ‘filled’ to approximate the volume and shape of the brain [7]. These methods are largely non-destructive, allowing research into the neuroanatomy of rare [8] and extinct species [9], including fossil specimens [10,11]. For preservation purposes, such as museum specimens or fossils embedded in sedimentary matrix, CT scanning offers non-destructive access to otherwise unattainable information [12,13]. To date, endocasts have been used to study brain evolution across all vertebrate classes, including fishes [5], amphibians [2], birds [14], non-avian reptiles [15,16] and mammals [6,17,18]. Therefore, our understanding of the brain-to-endocast relationship is fundamental to the study of vertebrate brain evolution.

Our knowledge of evolutionary patterns in brain size [13,19], shape [6,20] and composition [21] has advanced substantially over the past century through endocast comparisons [13,22]. For example, early endocast research on pterosaur fossils, an extinct clade of flying reptiles, revealed similarities

between their brains and those of modern birds [23]. These included the positions of the optic lobes (or midbrain) and the cerebellum, distinguishing pterosaurs and birds from other reptiles [23]. More recently, endocast studies have been used to infer brain–behaviour relationships, including social behaviour in big cats [24], nocturnality in birds [8,9,25] and the habitats of snakes [16]. However, there is substantial variation in the brain–endocast relationships among vertebrates [26], yet the use of endocast measurements relies on the assumption that they are indicative of the brain region of interest [2,3,12]. While some studies have verified the brain–endocast correlations for particular brain regions [27,28], measurement modalities such as shape or volume are not necessarily interchangeable [4,6], meaning that both must be tested to establish the validity of these methods. For fishes, amphibians and non-avian reptiles, in which brains do not fill the cranial cavity, inferences are limited as endocasts overestimate brain size [2,4,29]. This can be an issue, particularly at the root of iconic radiations such as dinosaurs, whose closest living non-avian relatives—the crocodiles—have brains that typically occupy less than half of their endocranial space in adults [26,30]. In contrast, the endocranial volume in birds is strongly correlated with brain volume [31].

The brains of birds have been the subject of extensive efforts to establish the relationship between the endocranial cavity and brain tissue [22,28,31–33]. Their endocasts are remarkably faithful to the shape of the brain itself, and endocranial volume is a valid proxy for actual brain volume and widely used in studies of brain size (e.g. [14,31,34,35]). Further, several brain regions are discernible in endocasts [10,12,22,28]. The endocast surface areas of two of these brain regions, the wulst and optic lobes, are reliable estimates of the underlying hyperpallium and optic tectum regions, respectively, of the brain [28]. However, inferences have also been drawn from endocast measurements of the telencephalon and cerebellum, even though the reliability of measuring these brain regions from endocasts remains untested. Changes in the size of both regions are important in the evolution of differences in avian cognition [36] and the brain becoming ‘flight-ready’ [37,38]. For example, the expansion of the telencephalon is a key anatomical change in the evolution of the avian brain [37,39] and is associated with higher rates of innovative behaviour [40]. Similarly, changes in relative cerebellum size, and part of the cerebellum, are associated with behavioural differences across avian clades [41,42]. They also comprise the majority of brain volume [43] and the endocast surface. Exploiting the potential of these two brain regions in explaining major transitions in avian brain evolution therefore requires validation of how faithfully their endocast imprints reflect their soft tissue volume.

Here, we determine the brain–endocast relationships of the telencephalon and cerebellum using the largest, phylogenetically diverse sample of bird species to date. While brain regions are typically measured as volumes, endocasts lack the internal anatomical landmarks needed to accurately divide them into volumes. This is especially true of the avian cerebellum, because its anterior surface is covered by the posterior telencephalon. While surface area may not be interchangeable with volume [6], we hypothesized that this comparison would show a typical isometric relationship, close to or equal to a 2:3 ratio or surface area increasing at a rate of 0.67 to that of the volume. However, as the relative size of these brain regions is often important for studying neurobehavioural evolution [3,26,32,44,45], we also asked whether their relative size when measured from endocasts was comparable to that of brains. We expected that, if the endocast reliably estimates the relative size of these regions, they would produce comparable relationships, which would result in similar slopes.

2. Methods

(a) Specimens

Data on whole brain, telencephalon and cerebellum volumes were compiled from the literature [41,43,46–56] and supplemented with previously unpublished data from a histological collection maintained by A.N.I. [57]. These specimens were provided to A.N.I. dead and were not euthanized for the purpose of this study. Further, all procedures were completed in accordance with the guidelines and policies of the Canada Council on Animal Care. These brains were gelatin-embedded and serially sectioned in the coronal plane at a thickness of 40 μm . After mounting and staining with thionin acetate, the volumes were measured using unbiased stereology in StereoInvestigator (Microbrightfield Inc., VT, USA) by F.C. For some species, the telencephalon and cerebellum volumes were measured from different individuals, so brain volumes for both individuals were included. More details on these methods are described in [46]. All data and their sources are provided in electronic supplementary material [58].

To compare the brain volumes with surface areas from endocasts, we collected existing micro-CT scans through the online repository Morphosource (project ID: 000642669) [28,59–66], our previous studies [8,25] as well as completing additional scans. The source, museum identification, and the scanning parameters for each specimen are provided in electronic supplementary material [58]. In total, we had brain volume measurements and CT scans from 136 species, representing 58 families and 25 orders. However, for four species, the volumes for either the telencephalon or cerebellum were unavailable—two species from each region—reducing the total to 134 species for these brain regions.

(b) Endocasts

All endocast reconstruction and measurements were completed by A.R.K. We imported the CT scans into the image processing software Materialise Mimics (v. 24.0; released in 2021 by Materialise NV) and exported reconstructed skulls. Meshes of the inner surface of the brain cavity—the endocast—were derived using the endomaker function from the Arothron package [67] in R [68] with the meshes decimated to 20 000 but otherwise using the base settings for all reconstructions. The meshes were incomplete due to natural openings or damage to the skull and often included excess material. To complete the endocasts, these were imported into Geomagic Wrap (v. 2021.2.2; released in 2023 by 3D Systems) to remove excess material and patch openings using

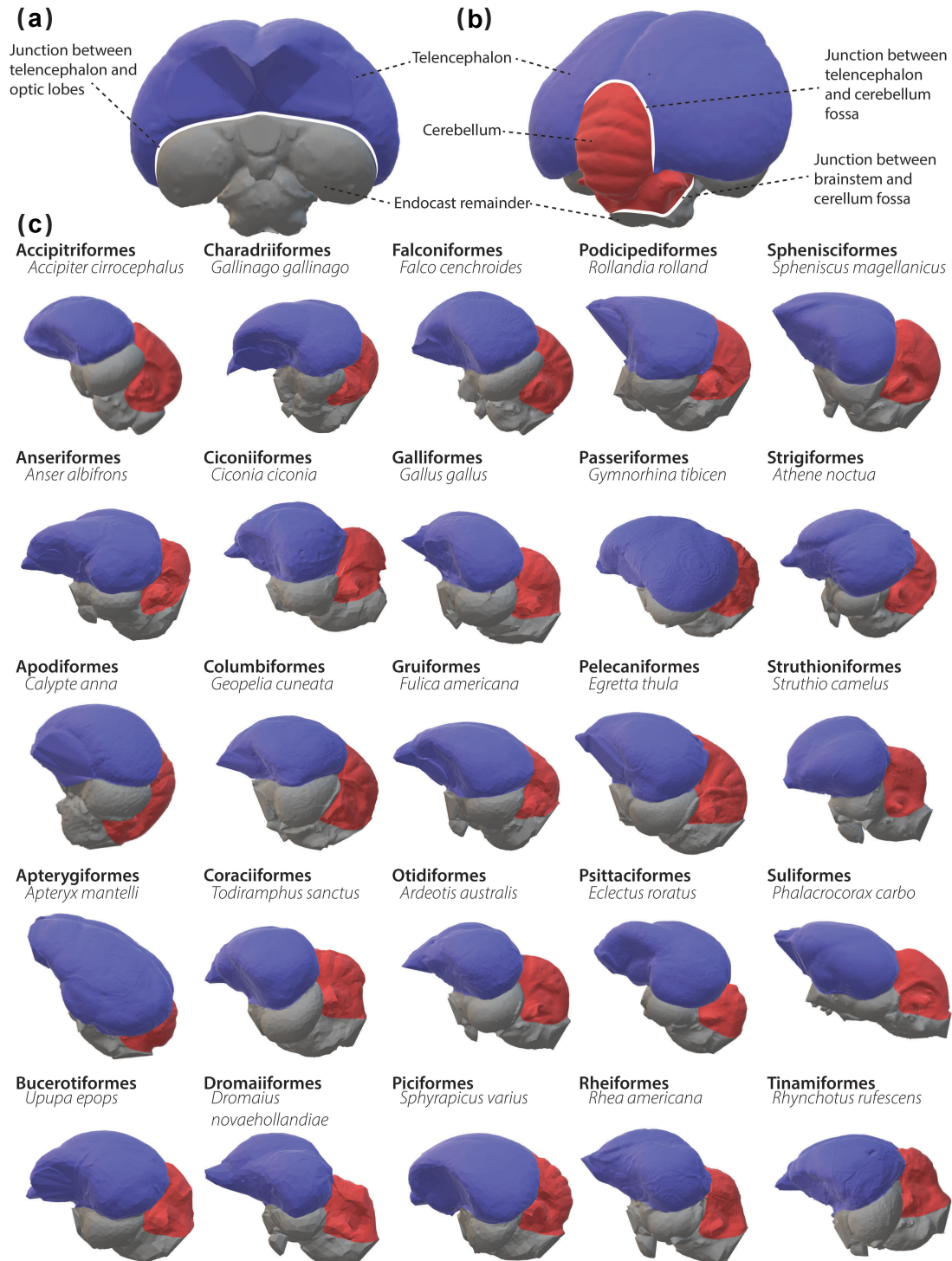


Figure 1. The endocast of a Eurasian treecreeper (*Certhia familiaris*) in rostral (a) and caudal views (b). Both images show osteological landmarks used to delineate the endocast telencephalon and cerebellum for measurements. The telencephalon is blue, the cerebellum is red and the rest of the endocast is grey. (c) Endocasts of a representative species of each of the orders examined in this study using the same colour coding as in (a) and (b). Note that endocast images shown here are of reduced resolution and are not to scale.

the ‘flat’ fill setting. Bumps and crevices were also removed and subsequently patched with the ‘flat’ fill along with the removal and patching of nerves and blood vessels, following best practices as outlined by Balanoff *et al.* [33] (example in electronic supplementary material, figure S1). As is to be expected, there was some variation in the amount removed and patching needed for each specimen. However, efforts were made to keep the reconstructions consistent and maintain the surface details of all the endocasts for accuracy.

We defined the borders for the telencephalon and cerebellum by consulting previous studies that partitioned endocasts for volume, surface area or landmark-based measurements [4,8,21,28,69]. We used the surface areas within these borders, which encompass the visible imprints of both regions, to estimate their sizes from the endocasts (figure 1a,b). We collected all measurements using Geomagic Wrap by following the borders outlined above. In figure 1c, we provide examples of these selections from each of the 25 clades in this study. Our detailed description of these borders is available in the electronic supplementary material.

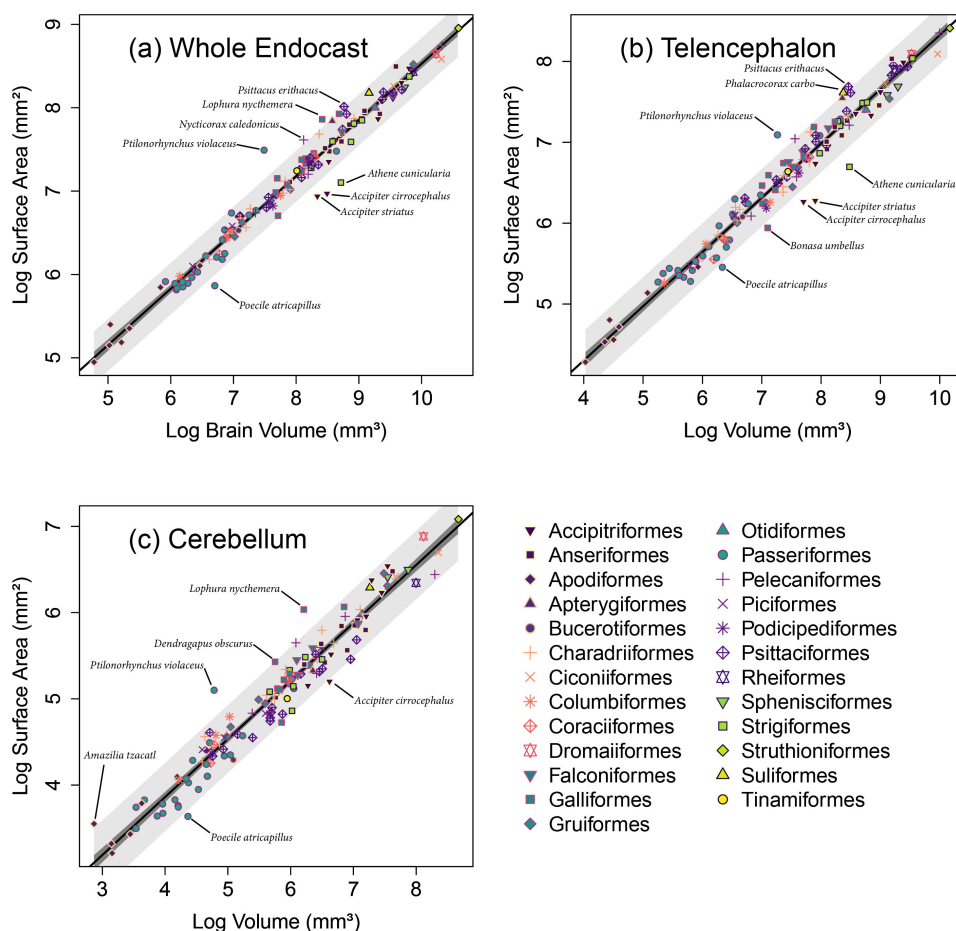


Figure 2. Log-transformed measurements of the (a) whole endocast, (b) telencephalon and (c) cerebellum surface areas measured from endocasts regressed against their brain volume counterparts for 136 species of birds. The orders from these data are represented by unique combinations of colours with point shapes. The black line represents the ordinary least-squares linear model regression; dark grey area represents 95% confidence intervals; light grey area represents 95% prediction intervals.

(c) Statistical analysis

All data were natural log transformed for analyses. To assess whether the absolute size of the endocast surface areas is an appropriate proxy of the absolute size of their brain counterpart, we completed ordinary least-squares (OLS) regression analyses with brain region volume as the predictor and endocast surface area as the response variable in R [68]. From these, we calculated confidence intervals (CIs; the confidence of the fit), prediction intervals (PIs; the confidence with which an unknown specimen could be given a value) and the line of best fit for each set of measurements: whole endocast, telencephalon and cerebellum. We expected the endocast surface areas to scale isometrically with the brain volume, with surface area scaling at two-thirds the volume (i.e. yielding slopes of 0.67). To test this, we assessed the slope coefficients of the linear relationships and additionally used Wald tests in the *car* package [70], which uses the model coefficients and coefficient-covariance matrix to determine whether the relationship significantly deviated from the isometric slope of 0.67 [71]. Note that the relationship between brains and endocasts is not expected to be impacted by the phylogenetic structure of the data. For this reason, linear modelling was the preferred statistical procedure. However, phylogenetic generalized least-squares (PGLS) models were also computed using the *evomap* package [72] to assess whether phylogenetic relationships impact the estimates of the slope [73].

As we have previously shown that the variation in voxel sizes of the CT scans may cause minor discrepancies for endocast measurements [8], we tested whether this may have had an artificial effect on endocast size. We did this by comparing the residuals of OLS regression analyses using the voxel size as the predictor variable for both endocast and brain measurements. We expected these residuals to scale similarly to the brain-to-endocast comparison.

We also computed the relative size for both the telencephalon and cerebellum by scaling them with the remainder of the brain as the dependent variable [74], both in the surface area (endocast-based) data and the volume (histology-based) data. This was to confirm that the slopes of the scaling relationships were comparable between the two datasets. Because phylogenetic relationships exert a significant effect on the relative size of brain regions [43,73,75,76], we used both OLS modelling and PGLS modelling to derive the slopes and intercepts.

We derived our phylogeny by pruning the family-level phylogeny by Stiller *et al.* [77] and used Mesquite [78] to place species on this tree using order-specific phylogenetic studies [79–89]. We then completed the PGLS regression analyses and calculated phylogenetic CIs for each of the regions against the remainder of either the endocast or brain using the *evomap* package [72].

Table 1. Results from ordinary least-squares (OLS) regression analyses and Wald tests. OLS results show the significant ($p \leq 0.05$) relationships between the endocast surface area measurements and the brain volume measurements. Wald test results show that slopes do not significantly ($p \geq 0.05$) differ from the expected isometric relationship between surface area and volume measurements (0.67). Cere., cerebellum; Endo., endocast; SA, surface area; Tele., telencephalon; Vol., volume.

dependent	predictor	d.f.	F-statistic	p-value	y intercept	R ²	slope	Wald test p-value
log Endo. SA	log brain Vol.	134	3969	<0.01	1.78	0.97	0.68	0.64
log Tele. SA	log Tele. Vol.	132	2954	<0.01	1.62	0.96	0.67	0.99
log Cere. SA	log Cere. Vol.	132	2324	<0.01	1.17	0.95	0.67	0.84

3. Results

Our comparisons of the surface area measurements for the whole endocast, telencephalon and cerebellum against their brain volume counterparts yielded highly significant associations (figure 2; table 1), which are unlikely to be influenced by the voxel size (see electronic supplementary material, figure S2). Furthermore, the resulting slopes indicate isometric relationships (table 1), which are not significantly different from the expected 0.67 according to the Wald test comparison (table 1). While this overall pattern is highly consistent, some species fell outside of the PIs for the whole sample, meaning that their surface area measurements were not expected given their corresponding volumes. In total, nine species fell outside of the PIs for at least one of the regressions with three outside of the PIs for all regressions (figure 2).

For the comparisons of the relative sizes of the telencephalon and cerebellum, the surface area for these regions regressed against the endocast remainder yielded similar slopes to that of the region volume regressed against the brain remainder for both the OLS and PGLS (figure 3; table 2). Parrots (Psittaciformes) appear to deviate more from the regression lines in figure 3 for both regions. This is because parrots have relatively large telencephala and small cerebella compared with other species [43]. The surface area measurements show a somewhat larger deviation for the telencephalon, which could arise from the relationship between surface area and volume or that the optic lobes are smaller in parrots [43,90], allowing the telencephalon to spread out more. One species, the Kākāpō (*Strigops habroptilus*), is outside of the PGLS CI for the expected range of the telencephalon surface area scaled against the endocast remainder surface area (figure 3a). This species is a uniquely nocturnal and flightless parrot that is neuroanatomically distinct within its clade [54], which may then result in an atypical relationship between endocast and brain measurements. Overall, these results indicate that the scaling relationship for both brain regions is similar when measured from endocast surface areas and brain volumes.

4. Discussion

Our results reveal that avian endocast surface areas for the whole endocast, the telencephalon and the cerebellum exhibit tight isometric relationships with the volume of their brain counterparts. This result is in spite of a sample size of one individual per species for the endocast measurements and a reliance on different individuals for the endocast and brain measurements, both of which could have reduced the strength of the association between the two datasets [31]. By including a broad range of species, our validation supports the use of endocast measurements for these regions in future studies while also supporting the conclusions from previous studies that relied on such measurements [8,9,25,36,37,91,92]. This result is particularly beneficial for studies on rare species [8,25], and palaeontological specimens [9,93] for which brain measurements are not attainable.

We also found that the relative sizes for both the telencephalon and cerebellum regions are consistent between the endocast surface areas and the soft tissue brain volumes, supporting their use in comparisons of brain composition [43]. This is in spite of the absence of the entire anterior lobe of the cerebellum in endocasts, which is generally hidden from external view by the telencephalon, and the cerebellar surface often obscured by the occipital sinus [3,32,94,95]. For other endocast validation research, such as that of the optic lobes and wulst [28], the regions are typically clearly defined and largely unobscured. Nonetheless, our findings strongly suggest that the portion of the cerebellum visible in endocasts is sufficient for estimating its relative volume.

While there is a strong brain–endocast association despite our reliance on different individuals, some species showed disparities between specimens, likely due to intraspecific variation in brain size and composition arising from sexual dimorphism [96–98] or subspecific, clinal, and other regional variation [99]. In fact, in a previous study, we found substantial skull and endocast size differences for two collared sparrowhawk specimens, likely due to sexual dimorphism [25]. Within this study, we suspect variation from sexual dimorphism in hawks [96,98] and pheasants [56,100] and regional variation for the bowerbird [97], chickadee [101], burrowing owl [102] and cormorant [103]. Furthermore, as variation occurred when comparing volumes and surface areas directly to one another but did not appear to be present in the analyses of relative brain region size, we suspect this variation stems from using different specimens for both datasets. While variation is expected, this raises concerns regarding the sample size needed to represent a species in comparative studies, particularly of narrow taxonomic scope. We nevertheless note the high correspondence between the brain and endocast datasets, suggesting that these measurements can generally be used with small sample sizes.

The telencephalon and cerebellum make up the majority of the brain and endocast surface, making their inclusion necessary for studies on brain composition [43]. By using known brain–behaviour associations, such as the telencephalon size with cognitive abilities [36,40,104], and the cerebellum with flight abilities [37,38,42], some aspects of ecology and behaviours may

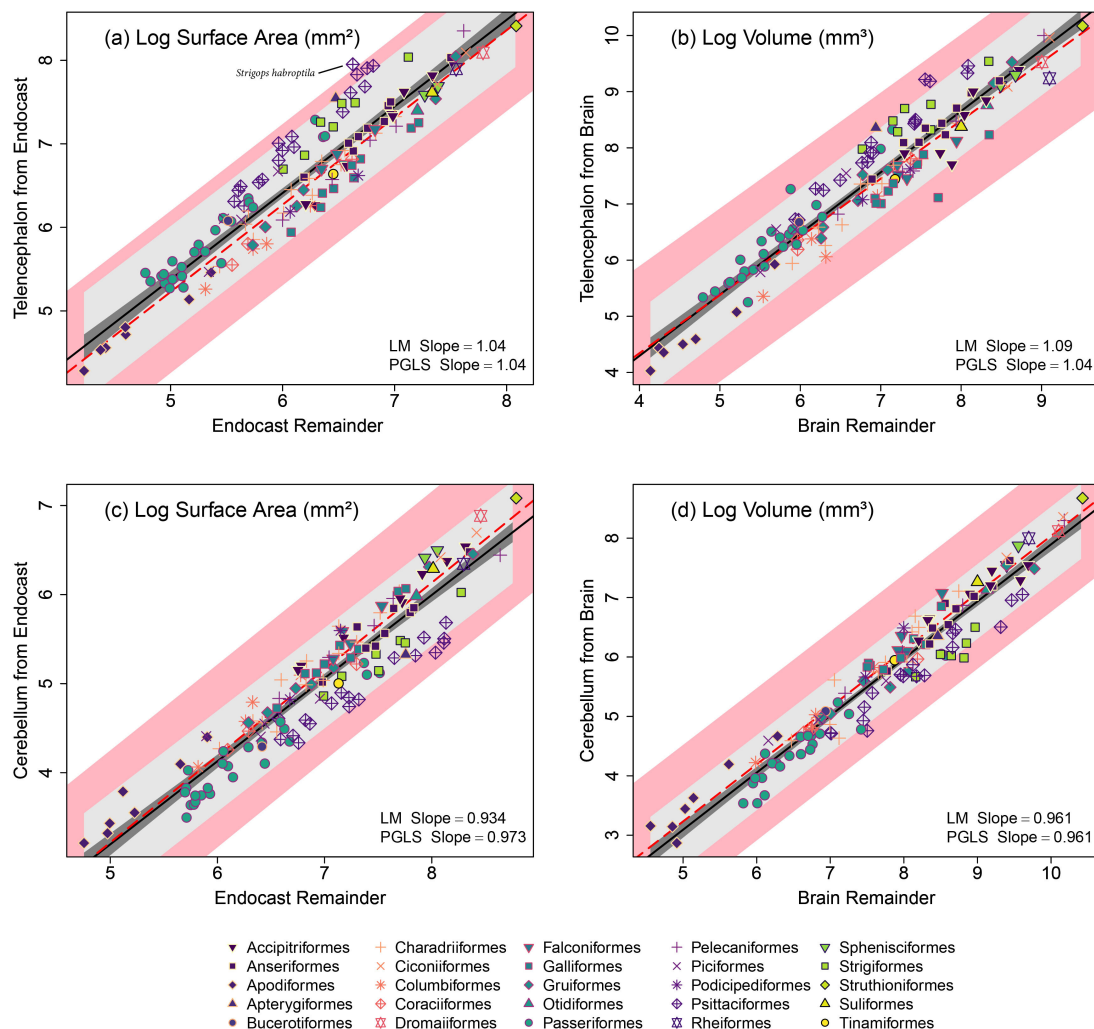


Figure 3. Log-transformed measurements comparing the scaling relationships of the telencephalon for (a) the surface area against endocast remainder and (b) the volume against brain remainder, as well as the cerebellum for (c) the surface area against endocast remainder and (d) the volume against brain remainder for 136 species of birds. The orders from these data are represented by unique combinations of colours with point shapes. Ordinary least-squares regression (LM slope) is shown by the black line; dark grey for the 95% confidence intervals; light grey for the 95% prediction intervals. Phylogenetic generalized least-squares (PGLS) regression is shown by the dashed red line; pink area shows the 95% confidence intervals of the PGLS.

Table 2. Results from phylogenetic generalized least-squares (PGLS) regression models used to compare the scaling relationship of endocast surface area and brain volume measurements of the telencephalon and cerebellum. Cere., cerebellum; Endo., endocast; SA, surface area; Tele., telencephalon; Vol., volume.

dependent	predictor	d.f.	t-value	p-value	y intercept	slope
Tele. SA	Endo. remainder	134	32.2	<0.01	0	1.04
Tele. Vol.	brain remainder	134	28.97	<0.01	0.2	1.04
Cere. SA	Endo. remainder	134	29.35	<0.01	-1.65	0.97
Cere. Vol.	brain remainder	134	33.48	<0.01	-1.57	0.96

be inferred from these regions [40,46,105–107]. Furthermore, even though some behaviourally relevant brain regions (such as the hippocampus [108]) are hidden within the brain, holistic approaches to endocast comparisons can improve the accuracy of inferences by accounting for the influences that changes in brain region sizes can have on one another [14,43,107,109]. For example, the relative size of the telencephalon in owls is comparable with that of parrots [104], but this is largely due to their hypertrophied wulst in relation to vision [43] and not the regions of the telencephalon associated with cognition [110].

Overall, this study has confirmed the strong relationships between the surface areas of endocasts and brain volumes in birds for absolute and relative size, both wholly and when divided into the telencephalon and cerebellum regions. This result is in concordance with other endocast validations [28,31], and we suggest that further expanding the use of avian endocasts is plausible. However, these methods remain speculative beyond the crown group Aves, such as for non-avian dinosaurs [2,4,29]. Outside of validating bird endocasts, comparisons with other living archosaurs, the crocodylians, may assist with resolving the brain–endocast correspondence [2] and provide further evidence for the strengths and limitations of these methods [4,30]. With the increased accessibility that CT scanning and associated digital reconstruction methods present [1,10,111], expanding and refining endocast uses has the potential to shed light on the lives of extinct species and further resolve our understanding of vertebrate brain evolution.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data and R code are available via the Zenodo Digital Repository: <https://zenodo.org/records/14590397> [58].

Endocasts and CT scan files specimens available through Morphosource: <https://www.morphosource.org/projects/000642669> [66].

Supplementary material is available online [112].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.R.K.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; F.C.: data curation, methodology, writing—review and editing; S.C.: data curation, methodology, writing—review and editing; G.P.: conceptualization, investigation, methodology, supervision, writing—review and editing; A.N.I.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—review and editing; V.W.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. Funding was received from the Australian Research Council Future Fellowship grant no. FT180100634 to V.W.

References

- Degrange FJ. 2023 Anatomy and Evolution of Avian Brain and Senses: What Endocasts Can Tell Us. In *Paleoneurology of amniotes: new directions in the study of fossil endocasts* (ed MT Dozo), pp. 333–364. Cham, Switzerland: Springer International Publishing.
- Clement AM, Mensforth CL, Challands TJ, Collin SP, Long JA. 2021 Brain reconstruction across the fish–tetrapod transition; insights from modern amphibians. *Front. Ecol. Evol.* **9**, 9. (doi:10.3389/fevo.2021.640345)
- Balanoff A, Bever GS. 2017 The Role of Endocasts in the Study of Brain Evolution. In *Evolution of nervous systems* (ed. JH Kaas), pp. 223–241. San Diego, CA: Academic Press. (doi:10.1016/B978-0-12-804042-3.00023-3)
- Watanabe A. 2019 Are endocasts good proxies for brain size and shape in archosaurs throughout ontogeny? *J. Anat.* **234**, 291–305. (doi:10.1111/joa.12918)
- Clement AM. 2022 Morphometric analysis of lungfish endocasts elucidates early dipnoan palaeoneurological evolution. *eLife* **11**, e73461. (doi:10.7554/eLife.73461)
- Weisbecker V. 2021 Global elongation and high shape flexibility as an evolutionary hypothesis of accommodating mammalian brains into skulls. *Evol. Int. J. Org. Evol.* **75**, 625–640. (doi:10.1111/evo.14163)
- Kubo D. 2008 Accuracy and precision of CT-based endocranial capacity estimations: a comparison with the conventional millet seed method and application to the Minatogawa 1 skull. *Anthropol. Sci.* **116**, 77–85. (doi:10.1537/ase.070502)
- Iwaniuk AN, Keirnan AR, Janetzi H, Mardon K, Murphy S, Leseberg NP, Weisbecker V. 2020 The endocast of the night parrot (*Pezoporus occidentalis*) reveals insights into its sensory ecology and the evolution of nocturnality in birds. *Sci. Rep.* **10**, 9258. (doi:10.1038/s41598-020-65156-0)
- Torres CR, Clarke JA. 2018 Nocturnal giants: evolution of the sensory ecology in elephant birds and other palaeognaths inferred from digital brain reconstructions. *Proc. R. Soc. B* **285**, 1890. (doi:10.1098/rspb.2018.1540)
- Knoll F, Kawabe S. 2020 Avian palaeoneurology: reflections on the eve of its 200th anniversary. *J. Anat.* **236**, 965–979. (doi:10.1111/joa.13160)
- Heingård M. 2021 New remains of *Scandiavis mikkelsenii* Inform avian phylogenetic relationships and brain evolution. *Diversity* **13**, 12. (doi:10.3390/d13120651)
- Walsh SA, Knoll MA. 2011 Directions in palaeoneurology. *Spec. Pap. Palaeontol.* **86**, 263–279. (doi:10.1111/J.1475-4983.2011.01085.x)
- Buchholtz EA, Seyfarth EA. 2001 The Study of 'Fossil Brains': Tilly Edinger (1897–1967) and the Beginnings of Paleoneurology. *Bioscience* **51**, 674–682. (doi:10.1641/0006-3568(2001)051[0674:TSOFBT]2.0.CO;2)
- Ksepka DT *et al.* 2020 Tempo and pattern of avian brain size evolution. *Curr. Biol.* **30**, 2026–2036. (doi:10.1016/j.cub.2020.03.060)
- Beyrand V. 2019 Multiphase progenetic development shaped the brain of flying archosaurs. *Sci. Rep.* **9**, 10807. (doi:10.1038/s41598-019-46959-2)
- Allemand R, Boistel R, Daghfous G, Blanchet Z, Cornette R, Bardet N, Vincent P, Houssaye A. 2017 Comparative morphology of snake (Squamata) endocasts: evidence of phylogenetic and ecological signals. *J. Anat.* **231**, 849–868. (doi:10.1111/joa.12692)
- Todorov OS. 2022 Down a rabbit hole: burrowing behaviour and larger home ranges are related to larger brains in Leporidae. *J. Mamm. Evol.* **29**, 957–967. (doi:10.1007/s10914-022-09624-6)
- Marino L. 2003 Reconstructing cetacean brain evolution using computed tomography. *Anat. Rec. Part B New Anat.* **272B**(1), 107–117. (doi:10.1002/ar.b.10018)
- Montgomery SH, Capellini I, Barton RA, Mundy NI. 2010 Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and *Homo floresiensis*. *BMC Biol.* **8**, 9. (doi:10.1186/1741-7007-8-9)
- Carril J, Tambussi CP, Degrange FJ, Benitez Saldivar MJ, Picasso MJB. 2016 Comparative brain morphology of Neotropical parrots (Aves, Psittaciformes) inferred from virtual 3D endocasts. *J. Anat.* **229**, 239–251. (doi:10.1111/joa.12325)
- Balanoff AM, Smaers JB, Turner AH. 2016 Brain modularity across the theropod–bird transition: testing the influence of flight on neuroanatomical variation. *J. Anat.* **229**, 204–214. (doi:10.1111/joa.12403)
- Edinger T. 1975 Paleoneurology 1804–1966: an annotated bibliography. *Adv. Anat. Embryol. Cell Biol.* **49**, 3–258.
- Edinger T. 1941 The brain of Pterodactylus. *Am. J. Sci.* **239**, 665–682. (doi:10.2475/ajs.239.9.665)
- Sakai ST, Arsznov BM, Hristova AE, Yoon EJ, Lundrigan BL. 2016 Big Cat Coalitions: A Comparative Analysis of Regional Brain Volumes in Felidae. *Front. Neuroanat.* **10**, 99. (doi:10.3389/fnana.2016.00099)
- Keirnan A, Worthy TH, Smaers JB, Mardon K, Iwaniuk AN, Weisbecker V. 2022 Not like night and day: the nocturnal letter-winged kite does not differ from diurnal congeners in orbit or endocast morphology. *R. Soc. Open Sci.* **9**, 220135. (doi:10.1098/rsos.220135)
- Jerison HJ. 1975 Evolution of the Brain and Intelligence. *Curr. Anthropol.* **16**, 403–426. (doi:10.1086/201571)
- Sakai ST, Arsznov BM, Lundrigan BL, Holekamp KE. 2011 Virtual endocasts: an application of computed tomography in the study of brain variation among hyenas. *Ann. N. Y. Acad. Sci.* **1225**, E160–70. (doi:10.1111/j.1749-6632.2011.05988.x)
- Early CM, Iwaniuk AN, Ridgely RC, Witmer LM. 2020 Endocast structures are reliable proxies for the sizes of corresponding regions of the brain in extant birds. *J. Anat.* **237**, 1162–1176. (doi:10.1111/joa.13285)

29. Morhardt AC, Ridgely RC, Witmer LM. 2018 Gross Anatomical Brain Region Approximation (GABRA): a new landmark-based approach for estimating brain regions in dinosaurs and other archosaurs. *FASEB J* **31**, 251. (doi:10.1096/fasebj.31.1_supplement.251.2)
30. Jirak D, Janacek J. 2017 Volume of the crocodylian brain and endocast during ontogeny. *PLoS One* **12**, e0178491. (doi:10.1371/journal.pone.0178491)
31. Iwaniuk A, Nelson J. 2002 Can endocranial volume be used as an estimate of brain size in birds? *Can J Zool Can. J. Zool.* **80**, 16–23. (doi:10.1139/z01-204)
32. Witmer LM. 2008 Using CT to Peer into the Past: 3D Visualization of the Brain and Ear Regions of Birds, Crocodiles and nonavian dinosaurs. In *Anatomical imaging* (eds H Endo, R Frey), pp. 67–87. Tokyo, Japan: Springer.
33. Balanoff AM *et al.* 2016 Best practices for digitally constructing endocranial casts: examples from birds and their dinosaurian relatives. *J. Anat.* **229**, 173–190. (doi:10.1111/joa.12378)
34. Smaers JB *et al.* 2021 The evolution of mammalian brain size. *Sci. Adv.* **7**, eabe2101. (doi:10.1126/sciadv.abe2101)
35. Weisbecker V, Goswami A. 2010 Brain size, life history, and metabolism at the marsupial/placental dichotomy. *Proc. Natl Acad. Sci. USA* **107**, 16216–16221. (doi:10.1073/pnas.0906486107)
36. Walsh SA, Knoll F. 2017 The evolution of avian intelligence and sensory capabilities: the fossil evidence. In *Digital endocasts. replacement of neanderthals by modern humans series* (eds E Bruner, N Ogiwara, H Tanabe), pp. 59–69. Tokyo, Japan: Springer.
37. Balanoff AM, Bever GS, Rowe TB, Norell MA. 2013 Evolutionary origins of the avian brain. *Nature* **501**, 93–96. (doi:10.1038/nature12424)
38. Witmer LM, Chatterjee S, Franzosa J, Rowe T. 2003 Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. *Nature* **425**, 950–953. (doi:10.1038/nature02048)
39. Striedter GF, Northcutt RG. 2019 *Brains through time: a natural history of vertebrates*. New York, NY: Oxford University Press. (doi:10.1093/oso/9780195125689.001.0001)
40. Lefebvre L. 1997 Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549–560. (doi:10.1006/anbe.1996.0330)
41. Cunha F, Gutiérrez-Ibáñez C, Racicot K, Wylie DR, Iwaniuk AN. 2021 A quantitative analysis of cerebellar anatomy in birds. *Brain Struct. Funct.* **226**, 2561–2583. (doi:10.1007/s00429-021-02352-2)
42. Iwaniuk AN, Hurd PL, Wylie DR. 2007 Comparative Morphology of the Avian Cerebellum: II. Size of Folia. *Brain Behav. Evol.* **69**, 196–219. (doi:10.1159/000096987)
43. Iwaniuk AN, Hurd PL. 2005 The Evolution of Cerebrotypes in Birds. *Brain Behav. Evol.* **65**, 215–230. (doi:10.1159/000084313)
44. Sol D, García N, Iwaniuk A, Davis K, Meade A, Boyle WA, Székely T. 2010 Evolutionary Divergence in Brain Size between Migratory and Resident Birds. *PLoS One* **5**, e9617. (doi:10.1371/journal.pone.0009617)
45. Sol D, Lefebvre L, Rodríguez-Teijeiro JD. 2005 Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proc. R. Soc. B* **272**, 1433–1441. (doi:10.1098/rspb.2005.3099)
46. Cunha F. 2021 Allometric relationships and the evolution of the avian brain. PhD thesis, University of Lethbridge, Lethbridge, Canada.
47. Iwaniuk AN, Nelson JE. 2003 Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Can. J. Zool.* **81**, 1913–1928. (doi:10.1139/z03-190)
48. Portmann A. 1947 Etudes sur la cérébralisation des oiseaux. II. Les indices intra-cérébraux. *Alauda* **15**, 1–15.
49. Kalisińska E. 2005 Anseriform Brain and Its Parts versus Taxonomic and Ecological Categories. *Brain Behav. Evol.* **65**, 244–261. (doi:10.1159/000084315)
50. Corfield JR, Wild JM, Parsons S, Kubke MF. 2012 Morphometric analysis of telencephalic structure in a variety of neognath and paleognath bird species reveals regional differences associated with specific behavioral traits. *Brain Behav. Evol.* **80**, 181–195. (doi:10.1159/000339828)
51. Alama S, Bee-dee-Speroni N. 1992 Indices cerebrales y composición cuantitativa encefálica en *Athene cunicularia* y *Tyto alba* (Strigiformes: Strigidae y Tytonidae). *Facena* **9**, 19–37.
52. Boire D, Baron G. 1994 Allometric comparison of brain and main brain subdivisions in birds. *J. Hirnforsch.* **35**, 49–66.
53. Carezzano F, Speroni NB. 1995 Composicion volumetrica encefalica e indices cerebrales en tres aves de ambiente acuatico (Ardeidae, Podicipedidae, Rallidae). *Facena* **11**, 75–83.
54. Corfield JR, Gsell AC, Brunton D, Heesy CP, Hall MI, Acosta ML, Iwaniuk AN. 2011 Anatomical Specializations for Nocturnality in a Critically Endangered Parrot, the Kakapo (*Strigops habroptilus*). *PLoS ONE* **6**, e22945. (doi:10.1371/journal.pone.0022945)
55. Day LB, Westcott DA, Olster DH. 2005 Evolution of Bower Complexity and Cerebellum Size in Bowerbirds. *Brain Behav. Evol.* **66**, 62–72. (doi:10.1159/000085048)
56. Krilow JM, Iwaniuk AN. 2015 Seasonal Variation in Forebrain Region Sizes in Male Ruffed Grouse (*Bonasa umbellus*) *Brain Behav. Evol.* **85**, 189–202. (doi:10.1159/000381277)
57. Iwaniuk AN. 2011 The importance of scientific collecting and natural history museums for comparative neuroanatomy. *Ann. N. Y. Acad. Sci.* **1225**, E1–19. (doi:10.1111/j.1749-6632.2011.05977.x)
58. Keirman AR. akeirman/Avian_Endocast_Validation: Avian telencephalon and cerebellum volumes can be accurately estimated from digital brain endocasts. Zenodo. See <https://doi.org/10.5281/zenodo.14590396>.
59. Steell EM, Nguyen JMT, Benson RBJ, Field DJ. 2023 Comparative anatomy of the passerine carpometacarpus helps illuminate the early fossil record of crown Passeriformes. *J. Anat.* **242**, 495–509. (doi:10.1111/joa.13761)
60. Lowi-Merri TM, Benson RBJ, Claramunt S, Evans DC. 2021 The relationship between sternum variation and mode of locomotion in birds. *BMC Biol.* **19**, 165. (doi:10.1186/s12915-021-01105-1)
61. Choiniere JN *et al.* 2021 Evolution of vision and hearing modalities in theropod dinosaurs. *Science* **372**, 610–613. (doi:10.1126/science.abe7941)
62. Benson RBJ, Starmer-Jones E, Close RA, Walsh SA. 2017 Comparative analysis of vestibular ecomorphology in birds. *J. Anat.* **231**, 990–1018. (doi:10.1111/joa.12726)
63. Eliason CM, McCullough JM, Andersen MJ, Hackett SJ. 2021 Accelerated Brain Shape Evolution Is Associated with Rapid Diversification in an Avian Radiation. *Am. Nat.* **197**, 576–591. (doi:10.1086/713664)
64. Zeyl JN *et al.* 2022 Aquatic birds have middle ears adapted to amphibious lifestyles. *Sci. Rep.* **12**, 5251. (doi:10.1038/s41598-022-09090-3)
65. Blackburn DC *et al.* 2024 Increasing the impact of vertebrate scientific collections through 3D imaging: The openVertebrate (oVert) Thematic Collections Network. *Bioscience* **74**, 169–186. (doi:10.1093/biosci/biad120)
66. Keirman AR. Endocast surface area validation study. Morphosource. See <https://www.morphosource.org/projects/000642669>.
67. Profico A. 2020 Endomaker, a new algorithm for fully automatic extraction of cranial endocasts and the calculation of their volumes. *Am. J. Phys. Anthropol.* **172**, 511–515. (doi:10.1002/ajpa.24043)
68. R Core Team. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing
69. Kawabe S, Shimokawa T, Miki H, Matsuda S, Endo H. 2013 Variation in avian brain shape: relationship with size and orbital shape. *J. Anat.* **223**, 495–508. (doi:10.1111/joa.12109)
70. Fox J, Weisberg S. 2018 *An R companion to applied regression*. Thousand Oaks, CA: Sage Publications.
71. Goldman CA. 1990 Principles of allometry. In *Tested Studies for Laboratory Teaching. Proc. of the 11th Workshop/Conf. of the Association for Biology Laboratory Education (ABLE)* (ed. CA Goldman), pp. 43–72, vol. **11**. Toronto, CA: Association for Biology Laboratory Education.
72. Smaers J, Mongle C. 2014 evomap: R package for the evolutionary mapping of continuous traits GitHub. See <https://github.com/JeroenSmaers/evomap>.

73. Garland, Jr., T, Ives AR. 2000 Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* **155**, 346–364. (doi:10.1086/303327)
74. Deacon TW. 1990 Fallacies of progression in theories of brain-size evolution. *Int. J. Primatol.* **11**, 193–236. (doi:10.1007/BF02192869)
75. Garland T, Bennett AF, Rezende EL. 2005 Phylogenetic approaches in comparative physiology. *J. Exp. Biol.* **208**, 3015–3035. (doi:10.1242/jeb.01745)
76. Corfield JR, Price K, Iwaniuk AN, Gutierrez-Ibañez C, Birkhead T, Wylie DR. 2015 Diversity in olfactory bulb size in birds reflects allometry, ecology, and phylogeny. *Front. Neuroanat.* **9**, 102. (doi:10.3389/fnana.2015.00102)
77. Stiller J *et al.* 2024 Complexity of avian evolution revealed by family-level genomes. *Nature* **629**, 851–860. (doi:10.1038/s41586-024-07323-1)
78. Maddison WP, Maddison DR. 2023 Mesquite: a modular system for evolutionary analysis, v. 3.81. See <http://www.mesquiteproject.org>.
79. Fuchs J, Johnson JA, Mindell DP. 2015 Rapid diversification of falcons (Aves: Falconidae) due to expansion of open habitats in the Late Miocene. *Mol. Phylogenetics Evol.* **82**, 166–182. (doi:10.1016/j.ympev.2014.08.010)
80. Prum RO. 2015 A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**, 569–573. (doi:10.1038/nature15697)
81. Andersen M. 2017 A phylogeny of kingfishers reveals an Indomalayan origin and elevated rates of diversification on oceanic islands. *J. Biogeogr.* **45**, 45. (doi:10.1111/jbi.13139)
82. Shakya SB. 2017 Tapping the woodpecker tree for evolutionary insight. *Mol. Phylogenetics Evol.* **116**, 182–191. (doi:10.1016/j.ympev.2017.09.005)
83. García-R JC. 2020 Phylogenomic Reconstruction Sheds Light on New Relationships and Timescale of Rails (Aves: Rallidae) Evolution. *Diversity* **12**, 70. (doi:10.3390/d12020070)
84. Kimball RT, Hosner PA, Braun EL. 2021 A phylogenomic supermatrix of Galliformes (landfowl) reveals biased branch lengths. *Mol. Phylogenetics Evol.* **158**, 107091. (doi:10.1016/j.ympev.2021.107091)
85. Wink M, El-Sayed A, Sauer-Gurth H, Gonzalez J. 2009 Molecular Phylogeny of Owls (Strigiformes) Inferred from DNA Sequences of the Mitochondrial Cytochrome b and the Nuclear RAG-1 gene. *Ardea*. **97**, 581–591. (doi:10.5253/078.097.0425)
86. Černý D, Natale R. 2022 Comprehensive taxon sampling and vetted fossils help clarify the time tree of shorebirds (Aves, Charadriiformes). *Mol. Phylogenetics Evol.* **177**, 107620. (doi:10.1016/j.ympev.2022.107620)
87. Hruska JP. 2023 Ultraconserved elements resolve the phylogeny and corroborate patterns of molecular rate variation in herons (Aves: Ardeidae). *Ornithology* **140**, ukad005. (doi:10.1093/ornithology/ukad005)
88. Catanach TA, Halley MR, Pirro S. 2024 Enigmas no longer: using ultraconserved elements to place several unusual hawk taxa and address the non-monophyly of the genus *Accipiter* (Accipitriformes: Accipitridae). *Biol. J. Linn. Soc.* (doi:10.1093/biolinnean/bla028)
89. Smith BT *et al.* 2023 Phylogenomic Analysis of the Parrots of the World Distinguishes Artifacts from Biological Sources of Gene Tree Discordance. *Syst. Biol.* **72**, 228–241. (doi:10.1093/sysbio/syaa055)
90. Iwaniuk AN, Gutierrez-Ibanez C, Pakan JMP, Wylie DR. 2010 Allometric Scaling of the Tectofugal Pathway in Birds. *Brain Behav. Evol.* **75**, 122–137. (doi:10.1159/000311729)
91. Early CM, Ridgely RC, Witmer LM. 2020 Beyond endocasts: using predicted brain-structure volumes of extinct birds to assess neuroanatomical and behavioral inferences. *Diversity* **12**, 34. (doi:10.3390/d12010034)
92. Milner AC, Walsh SA. 2009 Avian brain evolution: new data from Palaeogene birds (Lower Eocene) from England. *Zool. J. Linn. Soc.* **155**, 198–219. (doi:10.1111/j.1096-3642.2008.00443.x)
93. Smith NA, Clarke JA. 2012 Endocranial Anatomy of the Charadriiformes: Sensory System Variation and the Evolution of Wing-Propelled Diving. *PLoS One* **7**, e49584. (doi:10.1371/journal.pone.0049584)
94. Ksepka DT, Balanoff AM, Walsh S, Revan A, Ho AMY. 2012 Evolution of the brain and sensory organs in Sphenisciformes: new data from the stem penguin *Paraptenodytes antarcticus*. *Zool. J. Linn. Soc.* o–no. (doi:10.1111/j.1096-3642.2012.00835.x)
95. Walsh SA, Iwaniuk AN, Knoll MA, Bourdon E, Barrett PM, Milner AC, Nudds RL, Abel RL, Sterpaio PD. 2013 Avian Cerebellar Floccular Fossa Size Is Not a Proxy for Flying Ability in Birds. *PLoS One* **8**, e67176. (doi:10.1371/journal.pone.0067176)
96. Debus S. 2012 *Birds of prey of Australia: a field guide*. Melbourne, Australia: CSIRO Publishing.
97. Menkhurst P. 2017 *The Australian bird guide*. Melbourne, Australia: CSIRO Publishing.
98. Dunne P, Karlson KT. 2017 *Birds of prey: hawks, eagles, falcons, and vultures of North America*. New York, NY: Houghton Mifflin Harcourt.
99. Baladrón AV. 2015 Body size and sexual dimorphism in the southernmost subspecies of the burrowing owl (*Athene cunicularia cunicularia*). *J. Raptor Res.* **49**, 479–485. (doi:10.3356/rapt-49-04-479-485.1)
100. McGowan PJK, Kirwan GM. 2020 *Silver pheasant (Lophura nycthemera), version 1.0*. Birds of the world. (eds J Hoyo, A Elliott, J Sargatal, DA Christie, E Juana), Cornell Lab of Ornithology. See <https://doi.org/10.2173/bow.silphe.01>.
101. Roth TC II, Pravosudov VV. 2009 Hippocampal volumes and neuron numbers increase along a gradient of environmental harshness: a large-scale comparison. *Proc. R. Soc. B* **276**, 401–405. (doi:10.1098/rspb.2008.1184)
102. Poulin RG. 2020 *Burrowing Owl (Athene cunicularia), version 1.0*. Birds of the world. (ed. AF Poole), Cornell Lab of Ornithology. See <https://doi.org/10.2173/bow.buowl.01>.
103. Hatch JJ. 2020 *Great Cormorant (Phalacrocorax carbo), version 1.0*. Birds of the world. (ed. SM Billerman), Cornell Lab of Ornithology. See <https://doi.org/10.2173/bow.grecor.01>.
104. Iwaniuk AN, Dean KM, Nelson JE. 2005 Interspecific Allometry of the Brain and Brain Regions in Parrots (Psittaciformes): Comparisons with Other Birds and Primates. *Brain Behav. Evol.* **65**, 40–59. (doi:10.1159/000081110)
105. Burish MJ, Kueh HY, Wang SSH. 2004 Brain Architecture and Social Complexity in Modern and Ancient Birds. *Brain Behav. Evol.* **63**, 107–124. (doi:10.1159/000075674)
106. Lefebvre L. 1998 Feeding Innovations and Forebrain Size in Australasian Birds. *Behaviour* **135**, 1077–1097. (doi:10.1163/156853998792913492)
107. Iwaniuk AN, Dean KM, Nelson JE. 2004 A mosaic pattern characterizes the evolution of the avian brain. *Proc. R. Soc. Lond. B* **271**, S148–S151. (doi:10.1098/rsbl.2003.0127)
108. Todorov OS. 2019 Primate hippocampus size and organization are predicted by sociality but not diet. *Proc. R. Soc. B* **286**, 20191712. (doi:10.1098/rspb.2019.1712)
109. Carlisle A. 2017 Testing hypotheses of developmental constraints on mammalian brain partition evolution, using marsupials. *Sci. Rep.* **7**, 4241. (doi:10.1038/s41598-017-02726-9)
110. Sayol F, Maspons J, Lapedra O, Iwaniuk AN, Székely T, Sol D. 2016 Environmental variation and the evolution of large brains in birds. *Nat. Commun.* **7**, 13971. (doi:10.1038/ncomms13971)
111. Davies TG. 2017 Open data and digital morphology. *Proc. R. Soc. B* **284**, 20170194. (doi:10.1098/rspb.2017.0194)
112. Keirman AR, Cunha F, Citron S, Prideaux GJ, Iwaniuk AN, Weisbecker V. 2024 Supplementary material from: Avian telencephalon and cerebellum volumes can be accurately estimated from digital brain endocasts. Figshare. (doi:10.6084/m9.figshare.c.7601386)