Post-print of: Sayol, F.; Lefebvre, L. and Sol, D. "Relative brain size and its relation with the associative pallium in birds" in Brain, behavior and evolution (Karger), vol. 87, issue 2 (2016), p. 69-77. The final version is available at DOI 10.1159/000444670

[Article accepted in Brain, Behaviour and Evolution]

Relative brain size and its relation with the associative pallium in birds

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Running title: Brain size and pallium areas

Tables: 1

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Key words: Encephalization, Brain size, Cognition, Pallium, Mosaic evolution, Concerted evolution.

Abstract

Despite growing interest in the evolution of enlarged brains, the biological significance of brain size variation remains controversial. Much of the controversy is over the extent to which brain structures have evolved independently of each other (mosaic evolution) or in a coordinated way (concerted evolution). If larger brains have evolved by the increase of different brain regions in different species, it follows that comparisons of the whole brain might be biologically meaningless. Such an argument has been used to criticize comparative attempts to explain existing variation in whole brain size among species. Here, we show that pallium areas associated with domain-general cognition represent a large fraction of the entire brain, are disproportionally larger in large-brained birds and accurately predict variation in the whole brain when allometric effects are appropriately accounted for. While this does not question the importance of mosaic evolution, it suggests that examining specialized, small areas of the brain is not very helpful for understanding why some birds have evolved such large brains. Instead, the size of the whole brain reflects consistent variation in associative pallium areas and hence is functionally meaningful for comparative analyses.

Introduction

The phylogenetic-based comparative approach has become a major tool in investigating the evolution of the vertebrate neural architecture. Much of past effort has been devoted to assess whether existing variation in brain size among species predicts differences in cognitively-demanding behaviours. This has yielded ample evidence that larger brains are associated with enhanced domain-general cognition [Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016; Lefebvre, Whittle, & Lascaris, 1997; Reader, Hager, & Laland, 2011; Reader & Laland, 2002] and function to facilitate behavioural adjustments to socio-environmental changes [Reader & Laland, 2002; Schuck-Paim, Alonso, & Ottoni, 2008; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Székely, Liker, & Lefebvre, 2007; Sol, 2009]. Despite the progress, the biological significance of brain size variation across species is not exempt of criticisms [Healy & Rowe, 2007]. A main argument has been that because brains are divided into functionally distinct areas, the analyses should focus on the areas to which a particular function could be ascribed [Healy & Rowe, 2007].

In fact, the validity of the above criticism depends on the classic, unresolved debate over the extent to which brain areas evolve independently of each other in a mosaic fashion [Barrett & Kurzban, 2006; Barton & Harvey, 2000; Iwaniuk & Hurd, 2005] or in a concerted way as a result of conserved developmental programs [Anderson & Finlay, 2013; Charvet, Striedter, & Finlay, 2011]. If information processing in the brain is massively modular [Barrett & Kurzban, 2006], then larger brains can evolve by the increase of different brain regions in different species, making comparisons of whole brain size biologically meaningless [Harvey & Krebs, 1990; Healy & Rowe, 2007]. However, if only some areas evolve in a concerted way, but together occupy a large part of the brain, then a disproportionate increase in these brain areas would be reflected in a larger brain regardless of the fact that smaller, more specialized, brain regions might evolve independently. This could be the case of brain areas like the avian mesopallium and nidopallium (which together form the associative pallium, AP) and the mammalian isocortex [Rehkämper, Frahm, & Zilles, 1991]. If the most important part of whole brain size variation is driven by these large, concertedly evolving areas, then focusing on the whole brain in comparative studies would be a good proxy for variation in these areas. Comparative evidence suggests that taxonomic variation in the size of the primate isocortex and avian AP is associated with variation in a suite of correlated, domain-general cognitive abilities [Lefebvre, Reader, & Sol, 2004; Reader et al., 2011] that include feeding innovation and tool use [Lefebvre, Nicolakakis, & Boire, 2002; Mehlhorn, Hunt, Gray, Rehkämper, & Güntürkün, 2010; Reader & Laland, 2002; Timmermans, Lefebvre, Boire, & Basu, 2000]. Enhanced demands on domain-general cognition could thus be reflected in an enlarged cortex and AP, as well as an enlarged brain.

The debate over models of brain size evolution has not yet been settled in part due to disagreements on how brain size should be best quantified. In primates, as many as 26 different metrics have been used in large scale studies exploring ecological, life history and cognitive correlates of encephalization (reviewed in Lefebvre [2012]). The comparative literature on birds is similarly based on a variety of metrics, which go from residuals to fractions and proportions of the whole or of parts of the brain (see table 1). The different ways in which the data are combined in the analyses adds additional uncertainties about what the size of the whole brain really means [Healy and Rowe, 2007].

In this paper, we use the most complete dataset on avian brain regions currently available [Iwaniuk and Hurd, 2005] to ask what really means the variation in brain size in terms of underlying structures. We use phylogenetically controlled analyses based on the current Bird Tree project [Jetz, Thomas, Joy, Hartmann, & Mooers, 2012] to examine inter-relationships between brain size, body size and the volume of six major brain parts, and assess the validity of several data transformation metrics used to control for allometry. We predict that a bigger brain should mainly correspond to an increase in AP, and hence that variation in these areas would strongly predict variation in the whole brain when using appropriate methods to remove allometric effects.

Methods

Data sources and phylogenetic hypotheses

Data on the whole brain and on volume of six brain parts were taken from Iwaniuk and Hurd [2005]. Three regions part of the telencephalon which are the nidopallium - which includes also all of the nidopallial subregions (but see [Iwaniuk & Hurd, 2005] for more details)-, the mesopallium and the hyperpallium. Three other non-telencephalic regions include the cerebellum, the diencephalon and the brainstem – which is the sum of the mesencephalon and the myelencephalon.. The six areas together form between 70 and 87 % of avian brain volume. Body mass data (g) were obtained from Dunning [2007]. The phylogenetic hypotheses we used were taken from the Bird Tree project [Jetz et al., 2012], where randomly sampled trees were taken from 2 different backbone coming from two independent studies [Ericson, 2012; Hackett et al., 2008]. We removed one species (*Pavo meleagris*) from the Iwaniuk and Hurd database, as in this set of phylogenetic trees it is considered the same species as *Meleagris gallopavo*, already present in the database (See supplementary fig. S1 for an example of one of the phylogenetic hypothesis used).

Statistical analyses

We first calculated a correlation matrix between the six brain areas. We used the “phyl.vcv” function in R [R, 2013] with optimization of the parameter Lambda using maximum likelihood criteria [Revell, 2012] to account for phylogenetic non-independence of the data.

We then compared different ways of removing allometric effects for each brain part, using either body mass, volume of the entire brain or of a basal part, the brainstem. For a given brain part, for example the nidopallium, we tested the following measures: (1) absolute nidopallium volume; (2) residuals of nidopallium volume from a log-log regression against body mass or (3) brainstem volume; (4) nidopallium volume divided by brainstem volume, similar to the executive brain ratio used for primates; (5) nidopallium volume divided by the volume of the rest of the brain (fraction); or (6) by the volume of the entire brain (proportion). Measures 2 and 3 are thus residuals of log-log regressions and measures 4, 5 and 6 can be calculated using untransformed or log transformed volumes. We thus had nine different measures that we compared and tested for potential remaining effects of body size using phylogenetically corrected least-squares regressions (PGLS) using the R package “caper" [Orme et al., 2013]. This method, compared to a non-corrected regression, controls for the non-independence of data due to shared ancestry. Contrary to independent contrasts, however, it first determines the strength of the phylogenetic signal in the data (parameter lambda, which varies between 0 and 1 and is calculated using Maximum Likelihood; Pagel, 1999) and controls it accordingly, without assuming, as do contrasts, that lambda is 1. To this purpose, we used a set of 20 phylogenetic trees and calculated means over the 20 models.

For all further analyses, we used residuals only, as other metrics do not eliminate the effect of body mass (see Results). We next analyzed the extent to which each brain region is associated with body size using PGLS models with log-transformed variables. To see which brain part best predicts whole brain variation, we took the residuals of whole brain volume against body mass and examined their relationship with the residuals of each brain part regressed against body mass. To illustrate these relationships, we plotted positive and negative whole brain residuals in different shades (black for positive and white for negative) and graphed them against brain part residuals. A brain part that predicts whole brain size well will yield clearly separated clouds of white and black points; in contrast, a brain part that does not predict whole brain size well will yield overlapping black and white data points. The extent to which positive and negative whole brain residuals are well separated in each graph can then be expressed by a histogram illustrating overlaps. We also used a set of PGLS models to determine which allometrically corrected brain part best explains variation in allometrically corrected whole brain size. A possible problem in the last two analyses is that we are correlating two variables that are residuals from the same predictor (body size), which might lead to some circularity. However, when using brainstem to remove allometry in the brain regions and body size to remove allometry in the whole brain, we obtained exactly the same results in terms of which parts explain most variation in the whole brain.

Finally, we conducted a phylogenetic reconstruction of whole brain residuals and associative pallium residuals - all corrected for body mass by taking phylogenetic residuals- on a sample tree using the contMap function of the “phytools” R package [Revell, 2012]. This technique combines data on phylogeny and trait variation between clades to estimate evolutionary increases or decreases in different lineages.

Results

In terms of absolute size, all brain areas are positively associated with each other in phylogenetically corrected analyses (fig. 1a, table S1). Much of this trend is due to body size allometry, however, so we next examined the way different transformations of the original data affect the body size confound. Of all the metrics we tested, only those based on residuals and executive brain ratio calculated on log-transformed data completely removed the effects of body size (table S2). Analyses based on metrics such as fractions and proportions therefore do not deal exclusively with brain part variation, but also include body size.

When allometric effects are taken into account by estimating residuals, some areas show stronger inter-relationships than others, suggesting a combination of concerted and mosaic evolution (fig.1b, table S3). Concerted evolution is particularly evident for the areas forming the associative part of the telencephalon, notably the nidopallium and mesopallium ($r = 0.94$). These two areas show much larger amounts of variation independent of body size than do basal brain areas such as the brainstem (fig. 2, table S4). Phylogenetically corrected variation in nidopallium and mesopallium size correctly classifies 95 and 92% respectively of the positive and negative residuals of whole brain size regressed against body size (fig. 2a-b). In contrast, brainstem volume is strongly related to body size and does not discriminate between species with large versus small brain residuals (fig. 2e). As a consequence, brain to body size residuals are better predicted by variation in associative pallium residuals (mesopallium + nidopallium) than by other brain parts (fig. 3), regardless of whether allometry is corrected by body (table S5) mass or brainstem volume (table S6). In fact, brain size and associative pallium (after corrections for allometric effects) are almost indistinguishable measures of encephalization (fig. 4; PGLS: $R^2 = 0.91$, $p < 0.001$). Inferring the evolution of avian brains with phylogenetic reconstructions yields virtually identical results with the two metrics (fig. 5), were we can see independent shifts in the increase of both relative brain and associative pallium sizes in crows and parrots and the reduction of these two measures in three practically independent clades (rheids, galliforms and swifts).

Discussion

Our analyses lead to three main conclusions regarding the evolution of the avian brain. First, all six brain parts analyzed here tended to increase in a concerted way, a trend that was not simply a consequence of allometry or phylogeny. Second, some areas, notably those belonging to the associative pallium, evolved in a more concerted way than others. Finally, large brains primarily resulted from a disproportionate increase in these pallial areas. These areas are not only anatomically well delineated (thus minimizing measurement error), but also comprise a large fraction of the brain, in particular the nidopallium. Thus, the same proportional increase of these areas is likely to have a stronger effect on the size of the whole brain than that of smaller areas, an idea previously proposed by Rehkämper et al's [1991].

The associative pallium areas are known to have key roles in avian cognition. The nidopallium, in particular its caudolateral part, the NCL, is the closest avian equivalent of the mammalian pre-frontal cortex. Several lines of evidence, using different approaches and techniques (connectome: [Shanahan et al., 2013]; single unit recording: [Lengersdorf et al., 2015, Rose and Colombo, 2005, Veit and Nieder, 2013]; receptor architecture: [Herold et al., 2011, Rose et al., 2010]; temporary inactivation: [Helduser and Güntürkün, 2012]; lesions: [Mogensen and Divac, 1993]) point to the importance of NCL in avian executive control. Comparative work also suggests that the nidopallium is the brain area most closely correlated with avian tool use [Lefebvre et al., 2002], while the other part of the associative pallium, the mesopallium, is most closely correlated with innovation rate [Timmermans et al., 2000]. The mesopallium is significantly enlarged in the bird with the most sophisticated form of tool use, the New Caledonian crow (*Corvus moneduloides*) [Mehlhorn et al., 2010]. The very tight relationship between nidopallium and mesopallium size, once phylogeny and allometry have been removed, further suggests that evolutionary changes in the two structures are strongly linked. Together, the two structures are the closest avian equivalent of the mammalian non-visual cortex. These areas appear to be a crucial to domain-general cognitive abilities.

Our results suggest caution in the use of absolute brain size to study the neural basis of cognitive skills, at least in birds. Given that this measure is confounded with body size, traits associated with body size (e.g. range, energetics, prey size) will confound any comparative test of brain size correlates. Using relative measures could be a solution to remove allometric effects, but we found here that dividing brain part volume by the volume of the whole (proportions) or the rest of the brain (fractions), with or without prior log transforms of the volumes, leaves significant body size confounds (Table 1 appendix). Studies using these metrics (e.g. [Burish, Kueh, & Wang, 2004; Clark, Mitra, & Wang, 2001]) thus contain a hidden confound that might affect conclusions about evolutionary trends.

In contrast, residual brain size seems to better describe how brains increase due to a disproportionate enlargement of specific, large brain areas. Using residuals completely removes allometric effects on the brain but might face a problem of interpretation, as it is unclear what a disproportionately large area means in functional terms. The underlying assumption for existing variation in brain size among species is that any increase in size provides some increase in function. Although this is supported by growing evidence linking residual brain to enhanced cognition [Benson-Amram et al., 2016; Sol et al., 2005] (but see a revision by Lefebvre and Sol [2008]), why should a disproportionate increase matter at all? Because the brain processes information, and this is done by discrete neurons acting together via neurotransmitters and receptors, the functional significance of volume differences might not be clear. In mammals, different orders have different scaling relationships of neuron numbers to brain area volume [S. Herculano-Houzel, 2012; Suzana Herculano-Houzel, 2011]. Similar differences might well characterize bird brains. One can imagine, for example, that a corvid or a parrot mesopallium might have more neurons per mm^3 than a quail brainstem. Knowing this would obviously be important, but it would not change correlational trends of the type we report here, or the associations with cognition reported in the literature. We might in fact be underestimating selection on brain areas associated with cognition by focusing on mass or volume rather than neuron numbers if differences in density go in the same direction as differences in classical metrics of encephalization. This also assumes that neuron numbers is the main determinant of information processing capacity, not their connectedness or the density and type of neurotransmitters and receptors. Comparative studies of receptor density and gene expression in brain areas will shed new light on the functional significance enlarged brains [Goodson, Kelly, & Kingsbury, 2012].

The finding that enlarged brains have primarily evolved by the concerted increase of certain brain regions does not deny the importance of mosaic evolution. Indeed, the fact that some areas evolve more concertedly than others can be interpreted as a combination of mosaic and concerted evolution. Theoretical work on other biological systems (e.g. metabolic networks, [Ravasz, Somera, Mongru, Oltvai, & Barabási, 2002]) suggests that modular units are organized into hierarchical clusters, a principle that might reconcile modular and concerted views on the way in which the neural substrate of cognitive abilities operate and evolve. Moreover, mosaic evolution could be more important for small areas specialized in particular behaviours, which have not been evaluated here. A case in point is the network of song nuclei that has been extensively studied in oscines. Nuclei of this type are absent in non-oscines, with the exception of parrots and hummingbirds [Jarvis, 2007], and at least one of them, HVC, varies strongly as a result of sexual selection on repertoire size [Devoogd, Krebs, Healy, & Purvis, 1993; Moore, Székely, Büki, & Devoogd, 2011]. If there is one clear case of adaptive specialization of brain areas in birds, it is the case of oscine song nuclei, which could evolve independently from other brain regions. However, these findings do not deny that, as our study suggests, the main variation in whole brain size is due to concerted changes in pallial areas, allowing the use of relative brain size as a proxy for relative pallium size in comparative studies.

Acknowledgements

We are grateful to members of Sol's Laboratory for helpful discussion. We also thank two anonymous reviewers for their comments and José Luis Ordóñez for his help with the figures. This research was supported by funds from the Spanish government (CGL2013-47448-P) to DS. FS was supported by a PhD fellowship FI-DGR 2014 from the Catalan government.

References

Anderson M L, & Finlay B L (2013): Allocating structure to function: the strong links between neuroplasticity and natural selection. *Front. Hum. Neurosci. 7*:918.

Barrett H C, & Kurzban R (2006): Modularity in cognition: framing the debate. *Psychol. Rev. 113*:628.

Barton R A, & Harvey P H (2000): Mosaic evolution of brain structure in mammals. *Nature 405*:1055–8.

Benson-Amram S, Dantzer B, Stricker G, Swanson E M, & Holekamp K E (2016): Brain size predicts problem-solving ability in mammalian carnivores. *Proc. Natl. Acad. Sci.* 201505913.

Burish M J, Kueh H Y, & Wang S S-H (2004): Brain architecture and social complexity in modern and ancient birds. *Brain. Behav. Evol. 63*:107–24.

Charvet C J, Striedter G F, & Finlay B L (2011): Evo-devo and brain scaling: candidate developmental mechanisms for variation and constancy in vertebrate brain evolution. *Brain. Behav. Evol. 78*:248–57.

Clark D a, Mitra P P, & Wang S S (2001): Scalable architecture in mammalian brains. *Nature 411*:189–193.

Devoogd T J, Krebs J R, Healy S D, & Purvis A (1993): Relations between song repertoire size and the volume of brain nuclei related to song: comparative evolutionary analyses amongst oscine birds. *Proc. R. Soc. London B Biol. Sci. 254*:75–82.

Dunning J B (2007): *Handbook of Avian Body Masses* (J.B. Dunning Jr., Ed.) (Second). CRC Press.

Ericson P G P (2012): Evolution of terrestrial birds in three continents: biogeography and parallel radiations. *J. Biogeogr. 39*:813–824.

Franklin D C, Garnett S T, Luck G W, Gutierrez-Ibanez C, & Iwaniuk A N (2014): Relative brain size in Australian birds. *Emu* 160–170.

Fuchs R, & Winkler H (2014): Brain Geometry and its Relation to Migratory Behavior in Birds. *J. Adv. Neurosci. Res. 1*:1–9.

Goodson J L, Kelly A M, & Kingsbury M a. (2012): Evolving nonapeptide mechanisms of gregariousness and social diversity in birds. *Horm. Behav. 61*:239–250.

Gutiérrez-Ibáñez C, Iwaniuk A N, Moore B a, Fernández-Juricic E, Corfield J R, Krilow J M, … Wylie D R (2014): Mosaic and concerted evolution in the visual system of birds. *PLoS One 9*:e90102.

Hackett S J, Kimball R T, Reddy S, Bowie R C K, Braun E L, Braun M J, … Yuri T (2008): A phylogenomic study of birds reveals their evolutionary history. *Science 320*:1763–8.

Harvey P H, & Krebs J R (1990): Comparing brains. *Science (80-.). 249*:140–146.

Healy S D, & Rowe C (2007): A critique of comparative studies of brain size. *Proc. R. Soc. B Biol. Sci. 274*:453–464.

Helduser S, & Güntürkün O (2012): Neural substrates for serial reaction time tasks in pigeons. *Behav. Brain Res. 230*:132–143.

Herculano-Houzel S (2011): Scaling of brain metabolism with a fixed energy budget per neuron: implications for neuronal activity, plasticity and evolution. *PLoS One 6*:e17514.

Herculano-Houzel S (2012): The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost. *Proc. Natl. Acad. Sci. 109*:10661–10668.

Herold C, Palomero-Gallagher N, Hellmann B, Kröner S, Theiss C, Güntürkün O, & Zilles K (2011): The receptor architecture of the pigeons' nidopallium caudolaterale: an avian analogue to the mammalian prefrontal cortex. *Brain Struct. Funct. 216*:239–254.

Isler K, & van Schaik C (2006): Costs of encephalization: the energy trade-off hypothesis tested on birds. *J. Hum. Evol. 51*:228–43.

Iwaniuk A N, Dean K M, & Nelson J E (2004): A mosaic pattern characterizes the evolution of the avian brain. *Proc. Biol. Sci. 271 Suppl* :S148–51.

Iwaniuk A N, Heesy C P, Hall M I, & Wylie D R W (2008): Relative Wulst volume is correlated with orbit orientation and binocular visual field in birds. *J. Comp. Physiol. A 194*:267–282.

Iwaniuk A N, & Hurd P L (2005): The evolution of cerebrotypes in birds. *Brain. Behav. Evol. 65*:215–30.

Iwaniuk A N, & Wylie D R W (2006): The evolution of stereopsis and the Wulst in caprimulgiform birds: A comparative analysis. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 192*:1313–1326.

Jarvis E D (2007): Neural systems for vocal learning in birds and humans: a synopsis. *J. Ornithol. 148*:35–44.

Jetz W, Thomas G H, Joy J B, Hartmann K, & Mooers a O (2012): The global diversity of birds in space and time. *Nature 491*:444–8.

Kawabe S, Shimokawa T, Miki H, Okamoto T, Matsuda S, Itou T, … Endo H (2013): Relationship Between Brain Volume and Brain Width in Mammals and Birds. *Paleontol. Res. 17*:282–293.

Lefebvre L (2012): *Primate encephalizationProgress in Brain Research* (1st ed., Vol. 195). Elsevier B.V.

Lefebvre L, Gaxiola A, Dawson S, Timmermans S, Rosza L, & Kabai P (1998): Feeding innovations and forebrain size in Australasian birds. *Behaviour 135*:1077–1097.

Lefebvre L, Nicolakakis N, & Boire D (2002): Tools and brains in birds. 939–973.

Lefebvre L, Reader S M, & Sol D (2004): Brains , Innovations and Evolution in Birds and Primates. *Brain. Behav. Evol. 63*:233–246.

Lefebvre L, & Sol D (2008): Brains, lifestyles and cognition: are there general trends? *Brain. Behav. Evol. 72*:135–44.

Lefebvre L, Whittle P, & Lascaris E (1997): Feeding innovations and forebrain size in birds. *Anim. Behav. 53*:549–560.

Lengersdorf D, Marks D, Uengoer M, Stüttgen M C, & Güntürkün O (2015): Blocking NMDA-receptors in the pigeon's "prefrontal" caudal nidopallium impairs appetitive extinction learning in a sign-tracking paradigm. *Front. Behav. Neurosci. 9*:85.

Mehlhorn J, Hunt G R, Gray R D, Rehkämper G, & Güntürkün O (2010): Tool-Making New Caledonian Crows Have Large Associative Brain Areas. *Brain. Behav. Evol. 75*:63–70.

Mogensen J, & Divac I (1993): Behavioural effects of ablation of the pigeon-equivalent of the mammalian prefrontal cortex. *Behav. Brain Res. 55*:101–107.

Møller A P (2010): Brain size, head size and behaviour of a passerine bird. *J. Evol. Biol. 23*:625–635.

Moore J M, Székely T, Büki J, & Devoogd T J (2011): Motor pathway convergence predicts syllable repertoire size in oscine birds. *Proc. Natl. Acad. Sci. U. S. A. 108*:16440–5.

Nicolakakis N, & Lefebvre L (2000): Forebrain size and innovation rate in European birds: feeding, nesting and confounding variables. *Behaviour 137*:1415–1429.

Nottebohm F (2005): The neural basis of birdsong. *PLoS Biol. 3*:0759–0761.

Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, & Pearse W (2013): caper: Comparative Analyses of Phylogenetics and Evolution in R. .

Pagel M (1999): Inferring the historical patterns of biological evolution. *Nature 401*:877–84.

R C T (2013): R: A language and environment for statistical computing. *R Found. Stat. Comput.* Vienna,Austria.

Ravasz E, Somera A L, Mongru D A, Oltvai Z N, & Barabási A-L (2002): Hierarchical organization of modularity in metabolic networks. *Science (80-.). 297*:1551–1555.

Reader S M, Hager Y, & Laland K N (2011): The evolution of primate general and cultural intelligence. *Philos. Trans. R. Soc. B Biol. Sci. 366*:1017–1027.

Reader S M, & Laland K N (2002): Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl. Acad. Sci. U. S. A. 99*:4436–41.

Rehkämper G, Frahm H D, & Zilles K (1991): Quantitative Development of Brain and Brain Structures in Birds (Galliformes and Passeriformes) Compared to that in Mammals (Insectivores and Primates)(Part 2 of 2). *Brain. Behav. Evol. 37*:135–143.

Revell L J (2012): phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol. 3*:217–223.

Rose J, & Colombo M (2005): Neural correlates of executive control in the avian brain. *PLoS Biol. 3*:1139–1146.

Rose J, Schiffer A-M, Dittrich L, & Güntürkün O (2010): The role of dopamine in maintenance and distractability of attention in the “prefrontal cortex” of pigeons. *Neuroscience 167*:232–237.

Schuck-Paim C, Alonso W J, & Ottoni E B (2008): Cognition in an ever-changing world: climatic variability is associated with brain size in Neotropical parrots. *Brain. Behav. Evol. 71*:200–15.

Shanahan M, Bingman V P, Shimizu T, Wild M, & Güntürkün O (2013): Large-scale network organization in the avian forebrain: a connectivity matrix and theoretical analysis. *Front. Comput. Neurosci. 7*:89.

Shultz S, & Dunbar R I M (2010): Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biol. J. Linn. Soc. 100*:111–123.

Sol D (2009): Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biol. Lett. 5*:130–3.

Sol D, Duncan R P, Blackburn T M, Cassey P, & Lefebvre L (2005): Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. U. S. A. 102*:5460–5.

Sol D, Székely T, Liker A, & Lefebvre L (2007): Big-brained birds survive better in nature. *Proc. R. Soc. London, Ser. B 274*:763–9.

Timmermans S, Lefebvre L, Boire D, & Basu P (2000): Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. *Brain Behav. Evol.* 196–203.

Veit L, & Nieder A (2013): Abstract rule neurons in the endbrain support intelligent behaviour in corvid songbirds. *Nat. Commun. 4*.

Winkler H, Leisler B, & Bernroider G (2004): Ecological constraints on the evolution of avian brains. *J. Ornithol. 145*:238–244.

Zorina Z a., & Obozova T a. (2012): New data on the brain and cognitive abilities of birds. *Biol. Bull. 39*:601–617.

Table 1. Encephalization metrics used in the comparative literature on birds. Res = residual; tel = telencephalon; region = varies according to study (e.g. mesopallium, nidopallium, hyperpallium, visual areas); rest of brain or tel = volume of the brain or telencephalon minus volume of the region studied.

Metric	Reference
Frequently used metrics	
Log brain mass	[Lefebvre & Sol, 2008]; [Shultz & Dunbar, 2010]
Res log (brain) log (body)	[Isler & van Schaik, 2006]; [Franklin, Garnett, Luck, Gutierrez-Ibanez, & Iwaniuk, 2014]
Res log (tel) log (body)	[Nicolakakis & Lefebvre, 2000]; [Lefebvre & Sol, 2008];[Iwaniuk & Wylie, 2006]
Res log (tel) log (rest of brain)	[Iwaniuk & Wylie, 2006]
Volume tel/brainstem	[Lefebvre et al., 1997]
Volume tel/brain	[Burish et al., 2004]
Volume tel/rest of brain	[Shultz & Dunbar, 2010]
Log region	[Lefebvre & Sol, 2008]
Res log (region) log (body)	[Mehlhorn et al., 2010; Timmermans et al., 2000]
Res log (region) log (body) log (other regions)	[Iwaniuk, Dean, & Nelson, 2004]
Res log (region) log (tel)	[Fuchs & Winkler, 2014]
Res log (region) log rest of brain)	[Gutiérrez-Ibáñez et al., 2014; Iwaniuk & Wylie, 2006]
Res log (region) log (rest of tel)	[Iwaniuk & Wylie, 2006];[Iwaniuk, Heesy, Hall, & Wylie, 2008]
Volume region/brainstem	[Lefebvre & Sol, 2008]
Volume region/ brain	[Fuchs & Winkler, 2014; Iwaniuk & Hurd, 2005]
Rarely used metrics	
Martin EQ	[Lefebvre & Sol, 2008]
Head volume	[Møller, 2010]
Shape based on absolute values	[Kawabe et al., 2013]
Shape based on regressions against body size	[Kawabe et al., 2013]
Telencephalon/brainstem of galliforme	[Lefebvre et al., 1997; Zorina & Obozova, 2012]
Log tel/brainstem of galliforme	[Lefebvre et al., 1998]
Skull height	[Winkler, Leisler, & Bernroider, 2004]

FIGURE LEGENDS

Fig. 1. Phylogenetic correlations between different brain regions, using (a) absolute values or (b) residuals from log-log regressions against body size.

Fig. 2. Log size of the six brain parts against log body mass, distinguishing species with positive brain residuals (black data points) and species with negative brain residuals (open data points). In the right of each plot, we present two histograms, one for each set of dots from the plots (black and open), corresponding to positive and negative brain residuals

.

Fig. 3. Relationship between residuals of different brain parts and whole brain residuals, all regressed against log body mass, with the R^2 for PGLS models represented on a schematic avian brain (redrawn based on Nottebohm, 2005).

Fig. 4. Residual of whole brain size against body size plotted against residual of associative pallium size against brainstem size. The data points represent actual species, while the line represents the PGLS model. The slightly lower slope of the regression with respect to the cloud of data points is due to the phylogenetic corrections.

Fig. 5. Phylogenetic reconstruction in a sample phylogenetic hypothesis of birds in our dataset, representing residual brain size evolution and residual associative pallium size evolution.

Figure 1

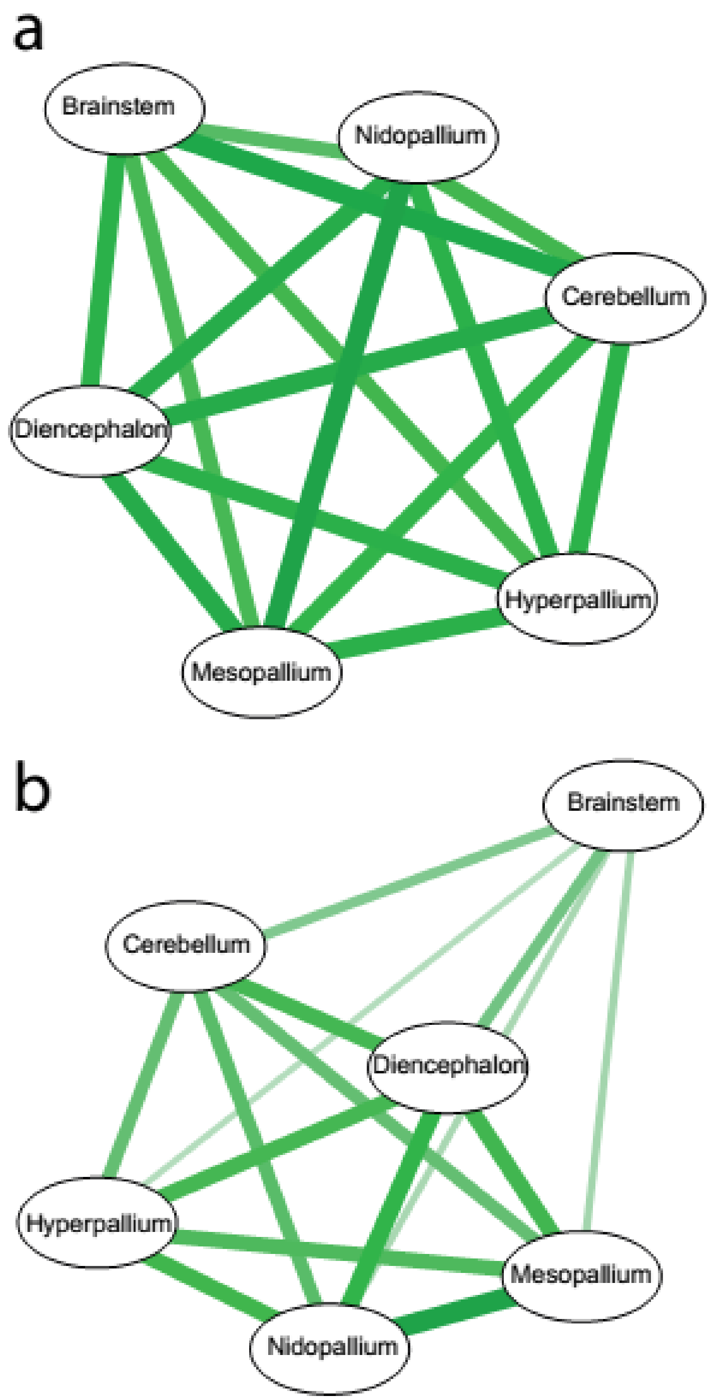
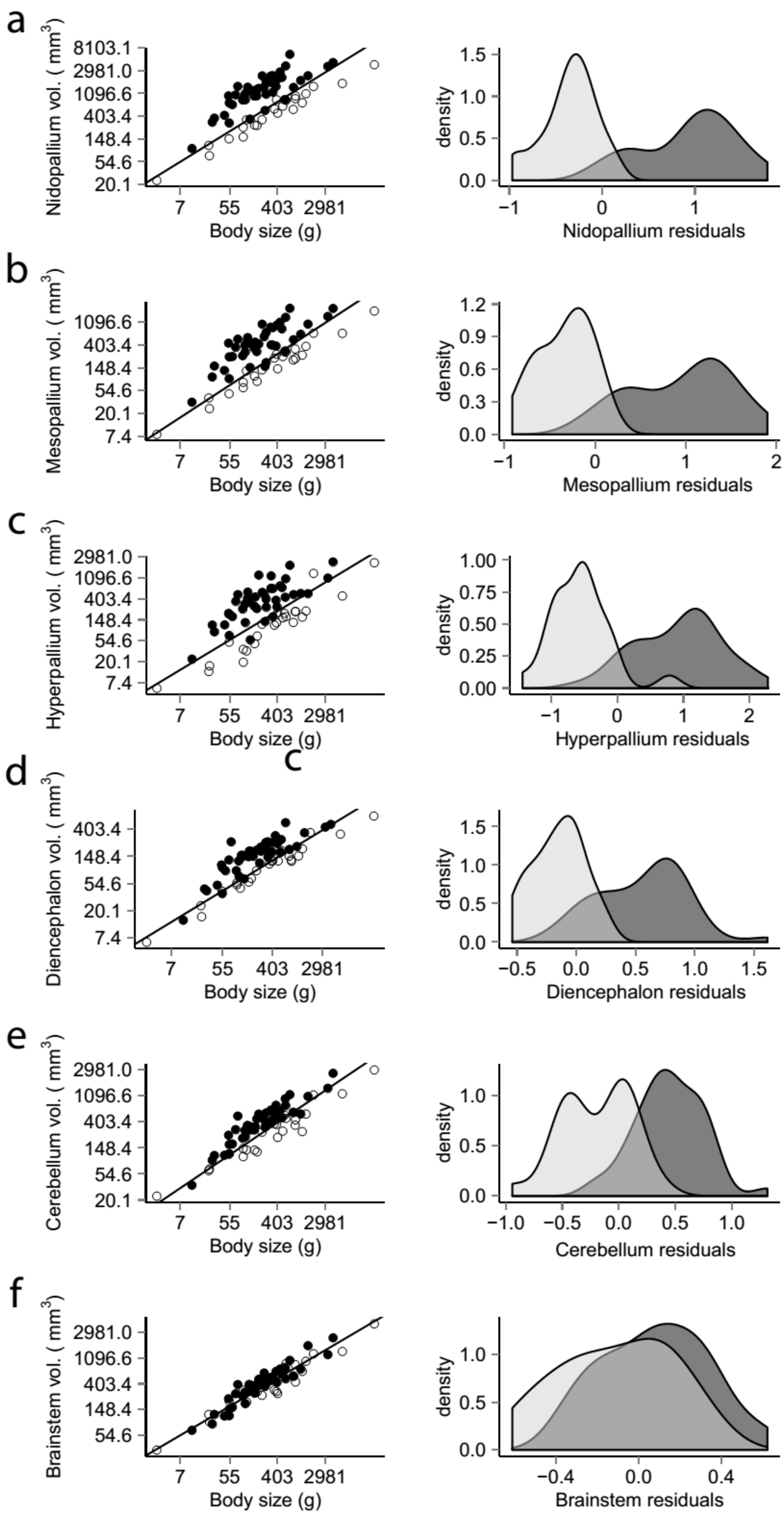
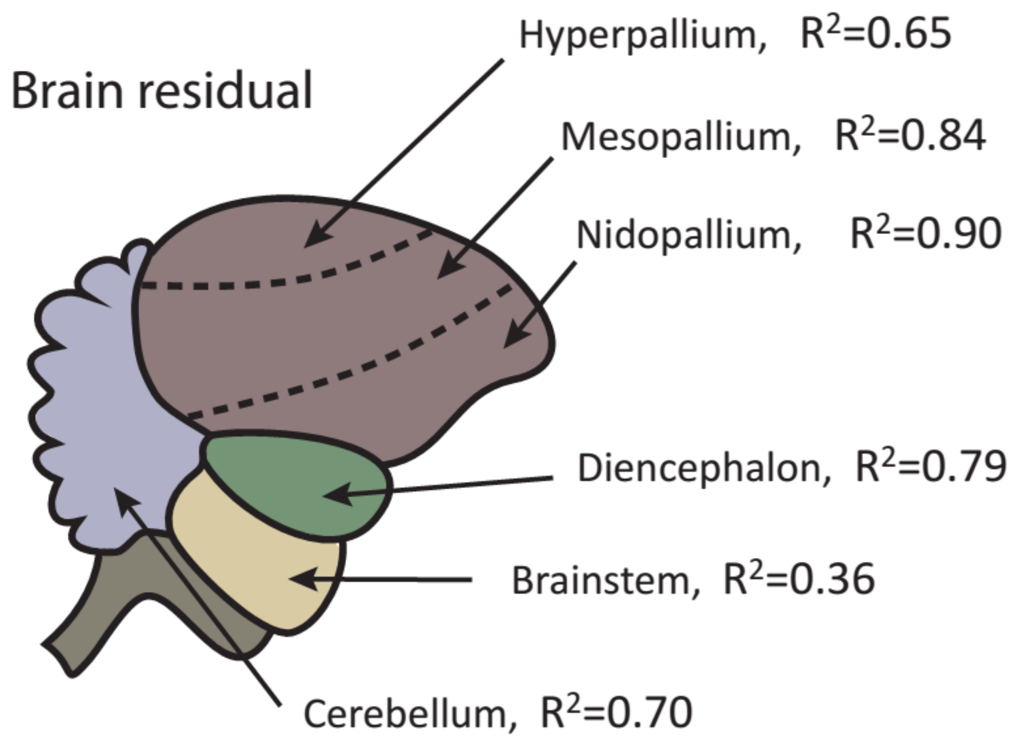

a
Brainstem
Nidopallium
Cerebellum
Diencephalon
Hyperpallium
Mesopallium
b
Brainstem
Cerebellum
Diencephalon
Hyperpallium
Mesopallium
Nidopallium

Figure 2



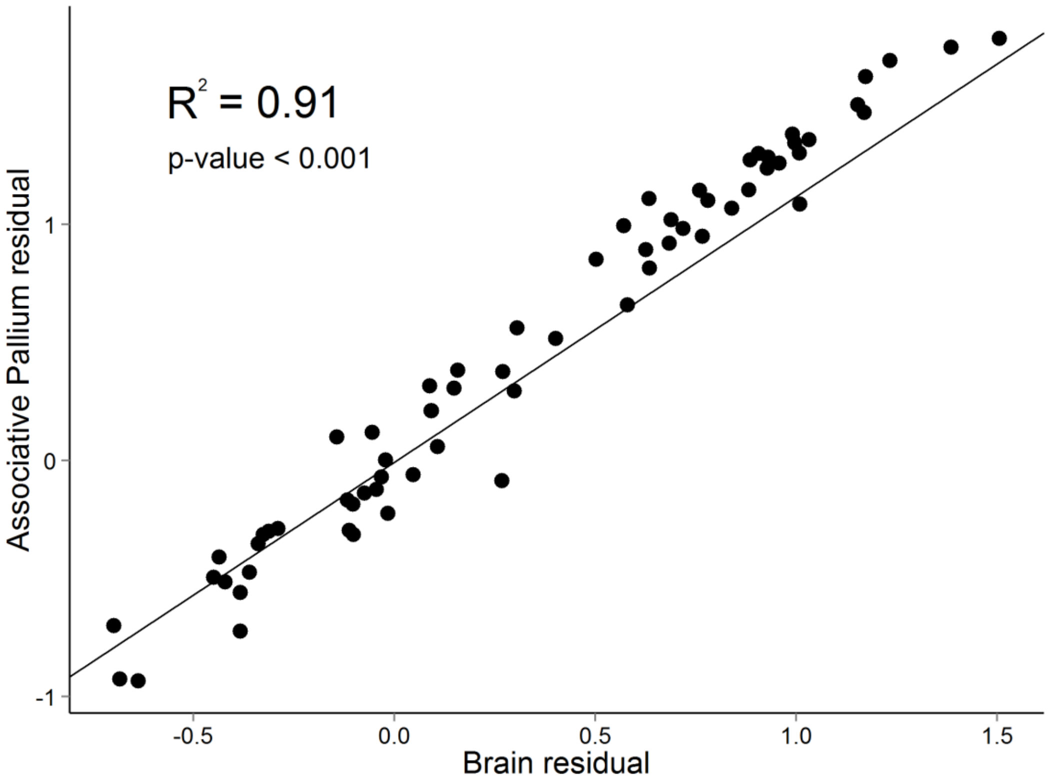
a
Nidopallium vol. (mm3)
8103.1
2981.0
1096.6
403.4
148.4
54.6
20.1
7
55
403
2981
Body size (g)
density
1.5
1.0
0.5
0.0
−1
0
1
Nidopallium residuals
b
Mesopallium vol. (mm3)
1096.6
403.4
148.4
54.6
20.1
7.4
Body size (g)
1.2
0.9
0.6
0.3
0.0
2
Mesopallium residuals
c
Hyperpallium vol. (mm3)
1.00
0.75
0.50
0.25
0.00
Hyperpallium residuals
d
Diencephalon vol. (mm3)
−0.5
0.0
0.5
1.0
1.5
Diencephalon residuals
e
Cerebellum vol. (mm3)
−1.0
Cerebellum residuals
f
Brainstem vol. (mm3)
−0.4
0.4
Brainstem residuals

Figure 3



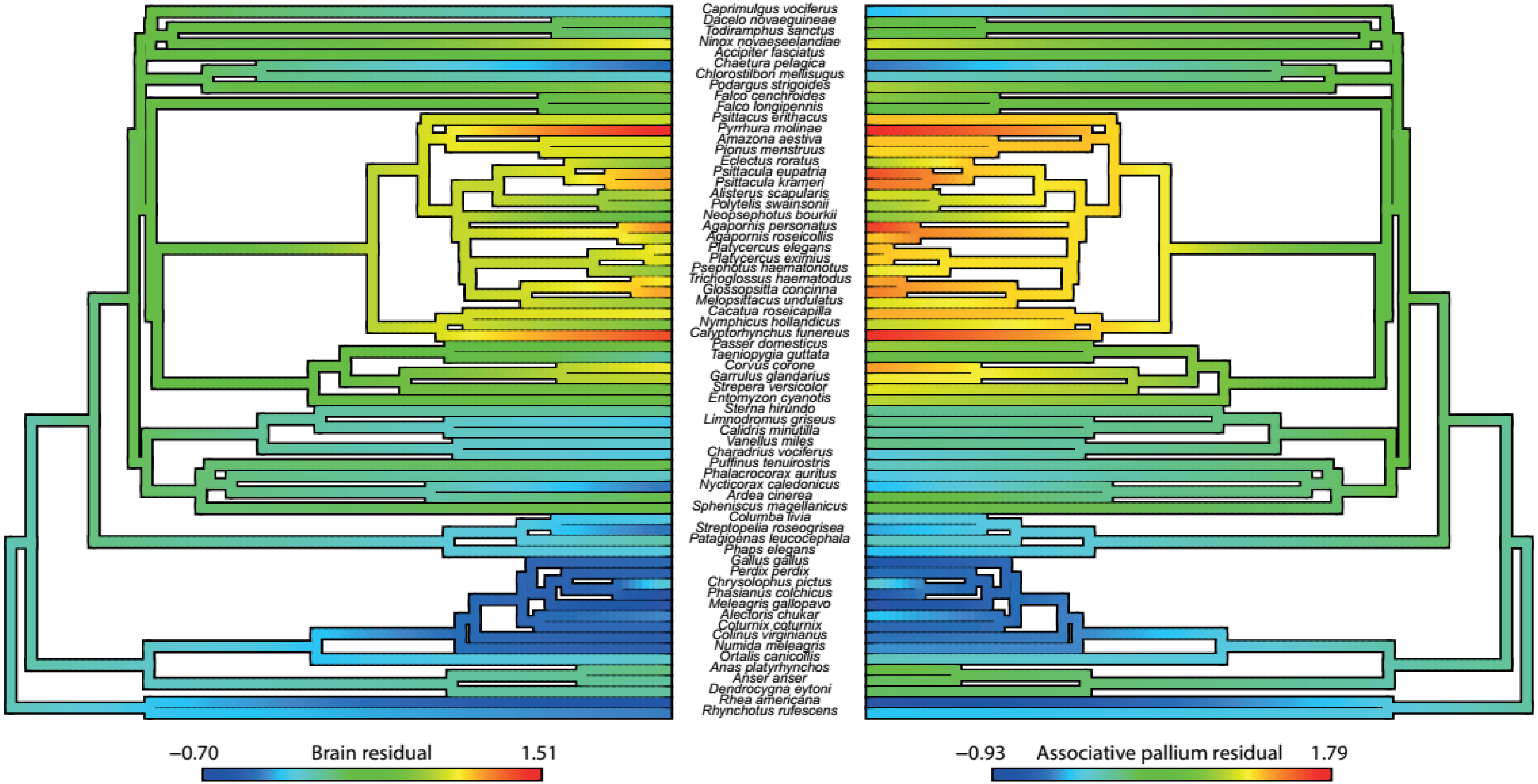
Brain residual
Hyperpallium, R2=0.65
Mesopallium, R2=0.84
Nidopallium, R2=0.90
Diencephalon, R2=0.79
Brainstem, R2=0.36
Cerebellum, R2=0.70

Figure 4



R² = 0.91
p-value < 0.001
Associative Pallium residual
Brain residual
-1
0
1
-0.5
0.0
0.5
1.0
1.5

Figure 5


Caprimulgus vociferus
Dacelo novaeguineae
Todiramphus sanctus
Ninox novaeseelandiae
Accipiter fasciatus
Chaetura pelagica
Chlorostilbon mellisugus
Podargus strigoides
Falco cenchroides
Falco longipennis
Psittacus erithacus
Pyrrhura molinae
Amazona aestiva
Pionus menstruus
Eclectus roratus
Psittacula eupatria
Psittacula krameri
Alisterus scapularis
Polytelis swainsonii
Neopsephotus bourkii
Agapornis personatus
Agapornis roseicollis
Platycercus elegans
Platycercus eximius
Psephotus haematonotus
Trichoglossus haematodus
Glossopsitta concinna
Melopsittacus undulatus
Cacatua roseicapilla
Nymphicus hollandicus
Calyptorhynchus funereus
Passer domesticus
Taeniopygia guttata
Corvus corone
Garrulus glandarius
Strepera versicolor
Entomyzon cyanotis
Sterna hirundo
Limnodromus griseus
Calidris minutilla
Vanellus miles
Charadrius vociferus
Puffinus tenuirostris
Phalacrocorax auritus
Nycticorax caledonicus
Ardea cinerea
Spheniscus magellanicus
Columba livia
Streptopelia roseogrisea
Patagioenas leucocephala
Phaps elegans
Gallus gallus
Perdix perdix
Chrysolophus pictus
Phasianus colchicus
Meleagris gallopavo
Alectoris chukar
Coturnix coturnix
Colinus virginianus
Numida meleagris
Ortalis canicollis
Anas platyrhynchos
Anser anser
Dendrocygna eytoni
Rhea americana
Rhynchotus rufescens
−0.70
Brain residual
1.51
−0.93
Associative pallium residual
1.79

Supplementary Tables (S1-S6) and Figures (S1)

Table S1. Correlation matrix between the raw volume of the six major brain parts controlling for phylogenetic non-independence of the species.

	Nidopallium	**Mesopallium**	**Hyperpallium**	**Diencephalon**	**Cerebellum**
Mesopallium	0.975	-	-	-	-
Hyperpallium	0.864	0.872	-	-	-
Diencephalon	0.896	0.907	0.869	-	-
Cerebellum	0.756	0.823	0.853	0.911	-
Brainstem	0.649	0.728	0.759	0.863	0.940

Table S2. Relationships between log body mass and different encephalization metrics used in other studies. Ndp: Nidopallium; Brn: Brainstem.

Brain Measure	**Predictor**	**Intercept ±SE**	**Slope ±SE**	**Pr(>|t|)**	**R^2**	**Lambda**
Absolute measures						
Log (absolute Ndp)	Log (body size)	1.43 ±0.40	0.66 ±0.04	<0.001	0.82	1.00
Residuals						
Ndp residual (against Brn)	Log (body size)	-343.97 ±477.59	0.00 ±0.01	0.935	0.00	1.00
Ndp residual (against body)	Log (body size)	-326.93 ±582.85	0.05 ±0.05	0.374	0.00	1.00
Proportions						
Ndp / brain	Log (body size)	0.24 ±0.05	0.01 ±0.05	0.001	0.09	1.00
Log (Ndp) / Log (brain)	Log (body size)	0.73 ±0.02	0.02 ±0.02	<0.001	0.48	1.00
Fractions						
Ndp / brain - Ndp	Log (body size)	0.23 ±0.15	0.04 ±0.02	0.001	0.09	1.00
Log (Ndp) / Log (brain - Ndp)	Log (body size)	0.79 ±0.03	0.02 ±0.00	<0.001	0.27	1.00
Executive ratios						
Ndp / Brn	Log (body size)	-0.65 ±1.39	0.36 ±0.14	0.010	0.08	0.97
Log (Ndp) / Log (Brn)	Log (body size)	1.06 ±0.07	0.01 ±0.01	0.319	0.00	0.98

Table S3. Correlation matrix between the six major brain parts after removing the allometric effect of body mass by means of residuals and controlling for phylogenetic non-independence of the species.

	Nidopallium	**Mesopallium**	**Hyperpallium**	**Diencephalon**	**Cerebellum**
Mesopallium	0.942	-	-	-	-
Hyperpallium	0.737	0.664	-	-	-
Diencephalon	0.796	0.726	0.710	-	-
Cerebellum	0.609	0.572	0.573	0.713	-
Brainstem	0.273	0.297	0.232	0.490	0.434

Table S4. Body size and brainstem size as predictors of whole brain size and the different brain parts, using PGLS models.

Brain area	**Predictor**	**Intercept ±SE**	**Slope ±SE**	**Pr(>|t|)**	**Adj R^2**	**lambda**
Log (whole brain)	Log(Body size)	4.24±0.24	0.63±0.03	<0.001	0.85	0.97
Log (Nidopallium)	Log(Body size)	2.72 ±0.33	0.65 ±0.04	<0.001	0.81	0.98
Log(Mesopallium)	Log(Body size)	1.49 ±0.35	0.69 ±0.04	<0.001	0.80	0.91
Log(Hyperpallium)	Log(Body size)	1.32 ±0.48	0.68 ±0.05	<0.001	0.71	1.00
Log(Cerebellum)	Log(Body size)	2.23 ±0.24	0.62 ±0.03	<0.001	0.85	0.69
Log(Diencephalon)	Log(Body size)	1.48 ±0.26	0.53 ±0.03	<0.001	0.82	0.87
Log(Brainstem)	Log(Body size)	2.94 ±0.15	0.55 ±0.02	<0.001	0.89	0.19
Log(Nidopallium)	Log(Brainstem)	0.01 ±0.49	1.07 ±0.07	<0.001	0.80	1.00
Log(Mesopallium)	Log(Brainstem)	-1.57 ±0.49	1.15 ±0.07	<0.001	0.82	0.97
Log(Hyperpallium)	Log(Brainstem)	-1.61 ±0.72	1.13 ±0.10	<0.001	0.66	0.96
Log(Cerebellum)	Log(Brainstem)	-0.59 ±0.32	1.06 ±0.05	<0.001	0.88	0.50
Log(Diencephalon)	Log(Brainstem)	-1.14 ±0.35	0.96 ±0.05	<0.001	0.85	0.83

Table S5. Relationship of different brain parts with brain size after removing allometry by means of residuals from body size and using PGLS models to control for phylogenetic non-independence of the species.

Response	**Predictor**	**Intercept ±SE**	**Slope ±SE**	**Pr(>|t|)**	**Adj R^2**	**lambda**
Brain size	Nidopallium	0.00 ±0.05	0.76 ±0.03	<0.001	0.90	0.72
Brain size	Mesopallium	0.00 ±0.06	0.70 ±0.04	<0.001	0.84	0.71
Brain size	Hyperpallium	0.01 ±0.09	0.46 ±0.04	<0.001	0.65	0.74
Brain size	Diencephalon	0.00 ±0.08	0.88 ±0.06	<0.001	0.79	1.00
Brain size	Cerebellum	-0.01 ±0.11	0.77 ±0.06	<0.001	0.70	1.00
Brain size	Brainstem	0.00 ±0.16	0.58 ±0.09	<0.001	0.36	1.00

Table S6. Relationship of different brain parts with brain size after removing the allometric effect by means of residuals from brainstem size and using PGLS models to control for phylogenetic non-independence of the species

Response	**Predictor**	**Intercept ±SE**	**Slope ±SE**	**$Pr(>\vert t\vert)$**	**Adj R^2**	**lambda**
Brain size	Nidopallium	-0.03 ±0.13	0.48 ±0.07	<0.001	0.39	0.59
Brain size	Mesopallium	-0.04 ±0.14	0.46 ±0.08	<0.001	0.34	0.67
Brain size	Hyperpallium	-0.05 ±0.15	0.29 ±0.05	<0.001	0.29	0.72
Brain size	Diencephalon	0.00 ±0.13	0.57 ±0.11	<0.001	0.27	0.72
Brain size	Cerebellum	-0.01 ±0.17	0.29 ±0.12	<0.001	0.07	0.87

Figure S1. Example of one of the 20 phylogenetic hypotheses used in the analyses.