nature ecology & evolution

ARTICLES

https://doi.org/10.1038/s41559-022-01815-x

Check for updates

Neuron numbers link innovativeness with both absolute and relative brain size in birds

Daniel Sol[1]✉, Seweryn Olkowicz[2], Ferran Sayol[1,3], Martin Kocourek[2], Yicheng Zhang[2], Lucie Marhounová[2], Christin Osadnik[4], Eva Corssmit[1], Joan Garcia-Porta[5], Thomas E. Martin[6], Louis Lefebvre[7]✉ and Pavel Němec[2]✉

A longstanding issue in biology is whether the intelligence of animals can be predicted by absolute or relative brain size. However, progress has been hampered by an insufficient understanding of how neuron numbers shape internal brain organization and cognitive performance. On the basis of estimations of neuron numbers for 111 bird species, we show here that the number of neurons in the pallial telencephalon is positively associated with a major expression of intelligence: innovation propensity. The number of pallial neurons, in turn, is greater in brains that are larger in both absolute and relative terms and positively covaries with longer post-hatching development periods. Thus, our analyses show that neuron numbers link cognitive performance to both absolute and relative brain size through developmental adjustments. These findings help unify neuro-anatomical measures at multiple levels, reconciling contradictory views over the biological significance of brain expansion. The results also highlight the value of a life history perspective to advance our understanding of the evolutionary bases of the connections between brain and cognition.

Encephalization—the evolutionary increase of the brain beyond that expected for a given body size[1]—has long been thought to be a major factor in the evolution of intelligence[2,3]. Comparisons across species have provided some support for this theory, showing that encephalization is associated with several facets of intelligence like innovativeness, learning and culture[4–8]. The theory has also stimulated an extended research programme on the ecological and evolutionary implications of brain size and architecture[9–11]. Yet, the reasons why a disproportionately larger brain should provide cognitive advantages remain unclear[3,12,13].

The rationale of the encephalization theory, as originally envisioned by Jerison[14], is that the 'extra tissue' that makes the brain larger than expected for a given body size (that is, larger relative brain size) reflects extra neurons that are available for cognitive tasks. However, the notion that cognitive performance depends on neuron numbers and increases with encephalization is backed by insufficient evidence[3,15,16]. Moreover, given that neuron numbers increase with absolute brain size[3,17], should we not expect that cognitive differences across species will be better predicted by absolute rather than relative brain size? There is indeed evidence that absolute brain size sometimes predicts cognitive performance across species better than relative measures of the brain[18–20]. Such contrasting results are not surprising given that increases in relative brain size can be reached by both brain enlargement and body size reduction and therefore may not always be associated with an increase in brain information-processing capacity[21,22]. The debate regarding the biological significance of absolute and relative brain sizes has been further complicated by the finding that not all brains are made in the same way; rather, brains may show different neuron densities and distributions among brain areas across species[12,15,23–25]. Thus, the intuitively appealing notion that larger brains translate into greater intelligence remains contentious[3,12,13].

To address this longstanding controversy, we provide theoretical and empirical grounds for the hypothesis that increased intelligence—operationally defined here as the ability to solve problems through mental or behavioural flexibility[3]—requires brains that are large in both absolute and relative terms (Fig. 1). This possibility has probably gone unrecognized because previous studies have used an 'either/or' approach and pitted absolute against relative brain size measures[18,20]. Yet if enhanced cognition requires more neurons in sensory, associative and premotor areas of the telencephalon—the pallial areas in birds and the neocortex in mammals[3,24]—and these areas represent a large fraction of the telencephalon and the whole brain[26], then the accumulation of a disproportionately large number of pallial neurons should produce brains that are larger both in absolute terms and relative to body size[27,28]. Such covariation between absolute and relative brain size should be more accentuated if the selective advantages of accumulating greater numbers of pallial neurons is higher for larger species than for small ones. This is to be expected because body size is a major correlate of longevity[29] and a long life increases the fitness value of gathering information and learning[30–33] while reducing the costs of delaying reproduction[34,35]. One mechanism that may allow a greater accumulation of pallial neurons is, according to some evo-devo models, an extension of development periods, particularly the later stages in altricial offspring that are born underdeveloped[36,37]. Thus, selection on cognition might link intelligence with larger absolute and relative brain size through developmental adjustments (Fig. 1).

[1]CSIC-CREAF (Centre for Ecological Research and Applied Forestries), Cerdanyola del Vallès, Catalonia, Spain. [2]Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic. [3]Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, UK. [4]Department of General Zoology, University of Duisburg-Essen, Essen, Germany. [5]Departament de Genètica, Microbiologia i Estadística, Facultat de Biologia & Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Catalonia, Spain. [6]Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT, USA. [7]Department of Biology, McGill University, Montréal, Québec, Canada. ✉e-mail: d.sol@creaf.uab.cat; louis.lefebvre@mcgill.ca; pgnemec@natur.cuni.cz

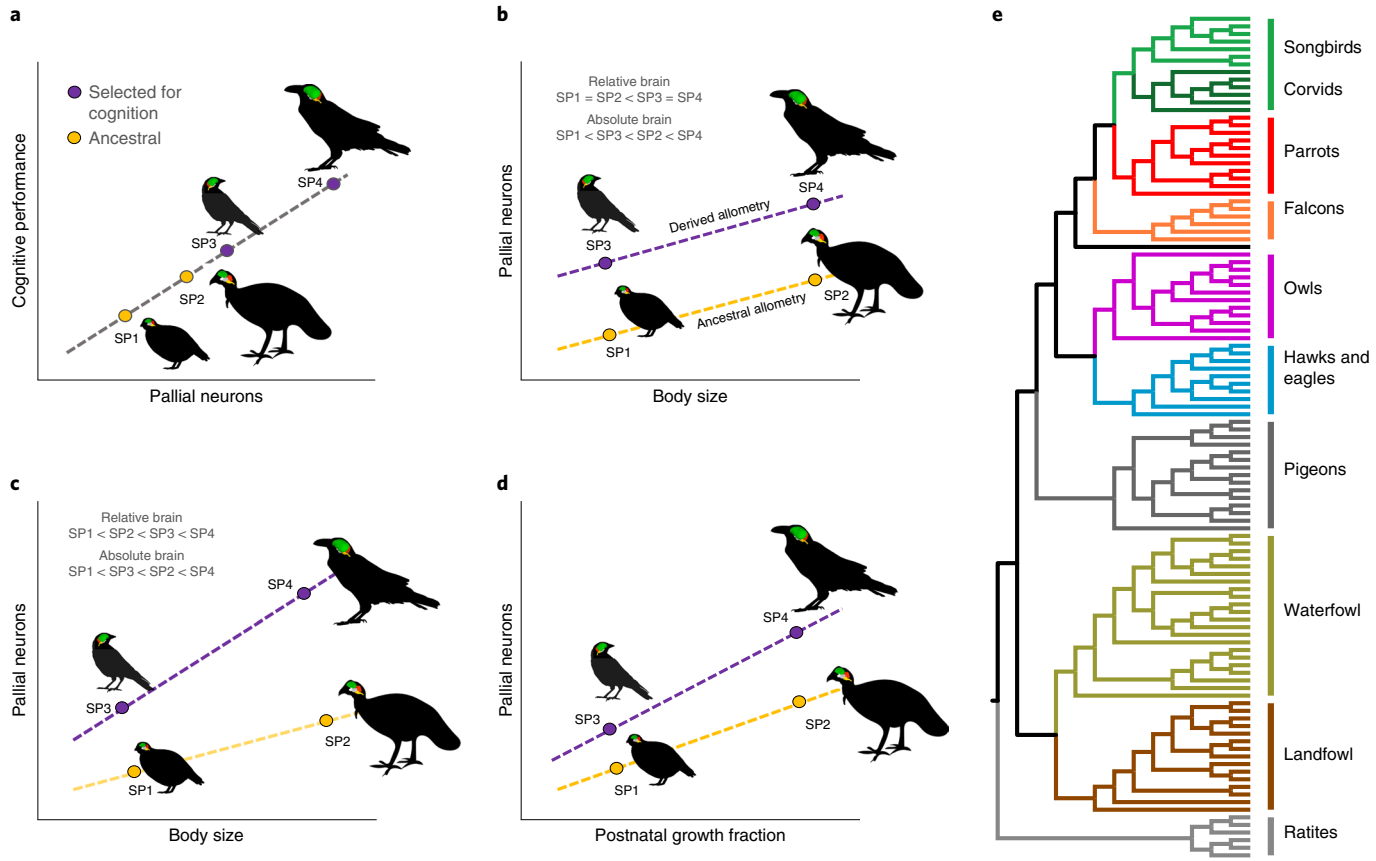

Fig. 1 | Framework linking cognition, neuron numbers and brain size. a, Enhanced cognition is assumed to require more neurons in the pallial telencephalon and perhaps also in the cerebellum. Thus, an increase in pallial neurons relative to the ancestor is expected in species that have been selected for higher intelligence. **b**, Because the pallium comprises a large fraction of the mass of the brain, a disproportionate accumulation of neurons in this area should enlarge the brain relative to body size. **c**, If the net benefits of enhanced cognition increase with body size, selection for cognition should further increase brain size in larger species. As a result, species that excel at cognitive performance should have brains that are large in both absolute and relative terms. **d**, A mechanism that may allow accumulation of more neurons in the pallium is to extend the period of development, particularly in the later stages. According to some evo-devo theories, extending the later stages of development increases neurogenesis in the areas of the brain where progenitor cell multiplication stops later, that is, the pallial areas of the telencephalon. Thus, if a longer development period facilitates neurogenesis in pallial regions, it may be targeted by selection for increased intelligence. **e**, Phylogenetic relationships among the species analysed for neuron numbers to address possibilities **a**–**d** (for a tree with species names see Supplementary Fig. 1). Silhouette illustrations are from PhyloPic (http://phylopic.org), contributed by F. Sayol and J. Louys under public domain licence.

Testing the above tenets is challenging owing to the difficulties of accurately estimating neuron numbers of different brain regions for many species[15]. The isotropic fractionator—a new method of assessing neuron numbers[38]—now makes it possible. Our study is based on a substantially updated dataset[24,25,39] quantifying neuron numbers in the whole brain and three brain areas (the pallium, the cerebellum and the brainstem) for 111 species of 24 avian families, representing both basal and crown avian lineages (Fig. 1e and Supplementary Fig. 1) and encompassing a large fraction of the morphospace occupied by avian brains (Supplementary Fig. 2). To test associations with cognition, we focus on a major component of intelligence—innovativeness[40]—by quantifying its product—innovation frequency[4–6,8]. Our innovation data were extracted from a database including >4,400 published reports of bird species using novel foods or new feeding techniques in the wild[41]. On this basis, we first ask whether innovation propensity increases with the number of neurons in the pallium (and potentially also in the cerebellum, which is thought to co-evolve and function in tandem with the pallium[42,43]) but not with those in areas less directly involved in cognition, like the brainstem. Next, we investigate whether the proliferation of neurons in the pallium makes the brain increase disproportionally with body size, linking innovativeness with both absolute and relative brain size. Finally, we test whether the accumulation of neurons in the pallium is associated with an extension of later stages of development. We test these predictions by combining random forests, a type of machine-learning algorithm that allows us to accommodate complex nonlinear interactions among predictors with minimal assumptions[44], with Bayesian mixed models that explicitly account for phylogenetic relatedness among species[45]. Because nocturnal species are difficult to observe, and hence are not present in the innovation dataset, we exclude owls from all the analyses that follow; results with the entire dataset are shown in the Supplementary Information.

Results and discussion

Cognitive performance has long been thought to depend on the number of neurons in the brain[46,47] but this idea is currently backed by surprisingly little empirical evidence[15]. A comparison of apes, corvids and pigeons in five cognitive domains concluded that neuron number is a poor predictor of absolute cognitive performance

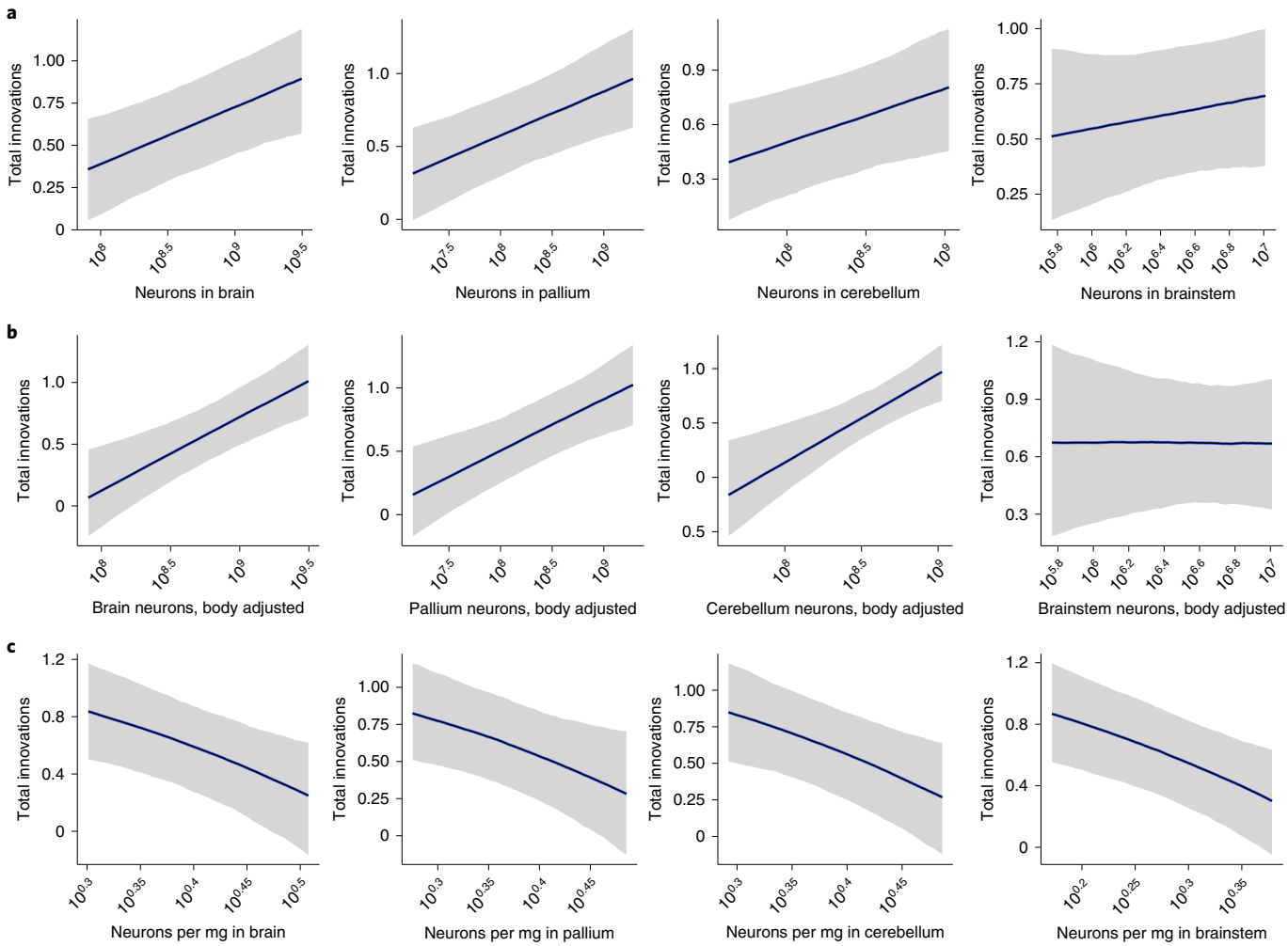

Fig. 2 | Neurons and innovation propensity. Relationship between neuron numbers and innovation propensity for the entire brain and the pallium, cerebellum and brainstem, as predicted by models. **a**, Absolute neuron numbers. **b**, Neuron numbers adjusted by body size by including body mass (previously subtracting brain mass) as covariate in the model. **c**, Density of neurons (cells per mg). All models account for the effect of phylogeny, biogeographic realm and confounding variables (Supplementary Tables 1 and 2). Lines show the values predicted by Bayesian phylogenetic mixed models and the lower and upper bounds are the credibility intervals representing the uncertainty interval of the prediction. Sample size is 99 species, as nocturnal specialists (owls) are excluded from the innovation database.

but it may predict learning speed and the ability to plastically adjust rules to novel situations[46]. A broader comparative analysis across primates and birds revealed that performance in a cognitive task (the detour test) does tend to increase with the total number of cortical/pallial neurons[15], yet this study did not rule out the possibility that the association was driven by phylogenetic relatedness.

Using Bayesian phylogenetic mixed models, we found that the number of neurons in the entire brain is positively associated with behavioural innovation propensity (Fig. 2a), particularly technical innovations that are assumed to require more advanced cognition[5] (Supplementary Table 1). The pattern holds when body mass is included as a covariate in the model (Fig. 2b and Supplementary Table 2), suggesting that innovation propensity is higher in birds with a disproportionately larger number of neurons than expected on the basis of body size. While we find that the brain of innovative species contains more neurons than the brain of less innovative species, there is no parallel increase in neuron density; rather, innovation propensity decreases with neuron density (Fig. 2c). Because avian neuron densities tend to decrease with brain size and the total number of neurons, these results support the notion that cognitive performance is primarily limited by the absolute and relative number of neurons rather than by neuron densities.

Additional analyses revealed that the number of neurons in the pallium and, to a lesser extent, the cerebellum are better predictors of innovation propensity than are neurons in the brainstem, a brain area less directly involved in cognition (Fig. 2 and Supplementary Tables 1 and 2). Although pallial areas are thought to co-evolve and function in tandem with the cerebellum[42,43], it remains to be determined whether the avian cerebellum subserves motor skills only (as its association with technical innovations but not resource innovations suggests; Supplementary Table 2) or is also directly involved in cognitive functions like the mammalian cerebellum[42]. Nonetheless, our findings align with growing evidence that cognitive processes associated with intelligence are controlled by widely distributed networks integrating several brain areas[48].

Corvids and parrots are regarded as the most innovative birds, a conclusion that is backed by ample experimental evidence[46,47,49,50]. These taxa also share both the highest inferred rates of brain–body size evolution among Neoaves and the steepest allometric slopes among all birds[51]. This contrasts with less innovative taxa

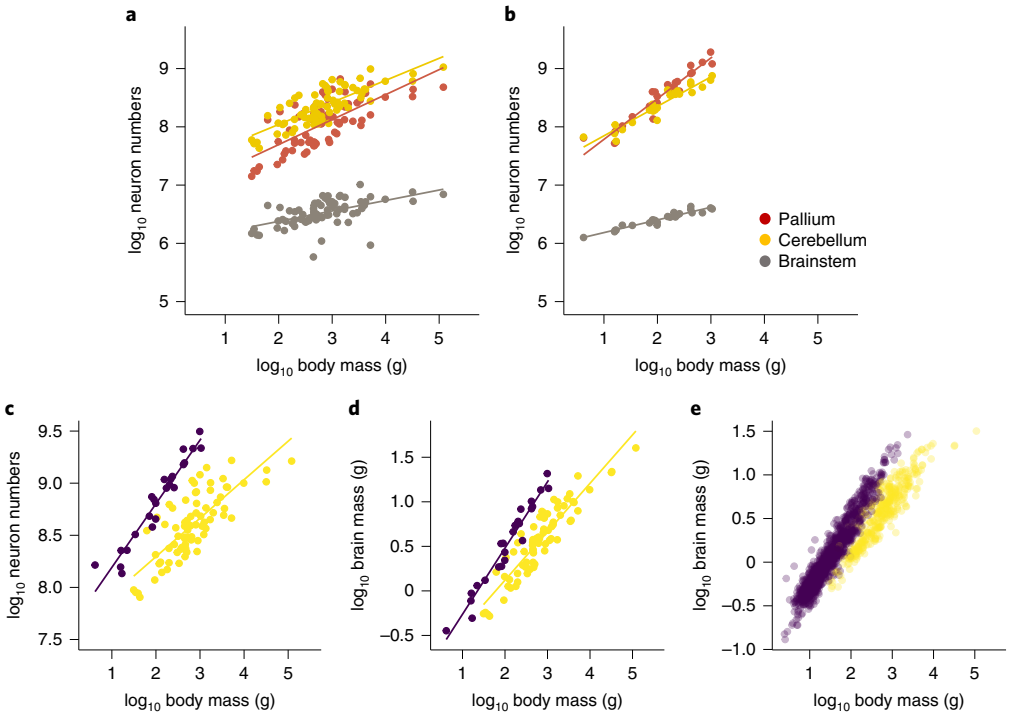

Fig. 3 | Neuron numbers and brain mass as a function of body size. a,**b**, Distribution of neuron numbers among pallium, cerebellum and brainstem for clades belonging to low-slope (**a**) and highest slope (**b**) grades. The assignation of species to each slope-grade group is based on ref. [51]. **c**, Variation in neuron numbers in the entire brain as a function of body size. **d**,**e**, Variation in brain mass as a function of body size for the sample of species used in analyses of neurons (**d**) and for the entire brain–body dataset (**e**). In **c**–**e**, clades with low-slope grades are shown in yellow while clades with the highest slope grades are shown in purple. In all plots, owls have been excluded. For plots based on the entire sample of species, see Supplementary Fig. 3.

like early-diverging birds (Palaeognathae, basal Neognathae), Anseriformes (waterfowl) and predatory core landbirds (hawks and eagles, falcons and owls), whose allometric exponents have diverged little from the ancestral avian grade and hence represent low-slope grades. To assess whether the proliferation of neurons in the pallium can explain deviations from the 'ancestral' allometric scaling relationship, we estimated the allometric exponents of the neuron numbers for clades with the highest slope and low-slope grades (sensu ref. [51]); we then compared these with the allometric exponents for the cerebellum and brainstem. We find that while the allometric exponents for the cerebellum and brainstem were similar between the two slope-grade groups, clades that share a high slope tended to accumulate disproportionately more neurons in the pallium as they become larger (Fig. 3 and Supplementary Figs. 3–5). Thus, as expected, the accumulation of pallial neurons makes the brain increase in both absolute and relative terms (Fig. 4 and Supplementary Figs. 6 and 7).

While the number of neurons in the whole brain and the pallium increases in a similar way with both absolute and relative brain size (Fig. 4), the number of neurons in the cerebellum is more strongly related to absolute brain size alone; those in the brainstem do not follow any clear pattern. These conclusions are consistent regardless of the method used to estimate relative brain size (Supplementary Fig. 7); they also hold when we include owls (Supplementary Figs. 6 and 7), whose large forebrain results in part from expanding the visual Wulst for sensory rather than associative purposes. Although the evolutionary repatterning of the brain–body relationship cannot be circumscribed to selection on brain size alone, our results support the notion that cognition can form a major driver of adaptive shifts to higher grades deviations from the 'ancestral' allometric scaling.

Presumably because brain cellular scaling rules can be clade-specific[15,23–25,52], and because avian neuron densities decrease with brain mass[24,25], the relationship between neuron numbers and brain size is complex. The relationship tends to be roughly linear for relative brain size, especially when we exclude owls, but only for the entire brain and the pallium (Fig. 4b). In contrast, neuron numbers tend to asymptote at larger absolute brain sizes in all cases (Fig. 4c). This last finding agrees with the notion that animals that have large brains merely because they have very big bodies are not necessarily the most intelligent, as it is the case for Ratites and large Galliformes.

Several developmental mechanisms, including differences in early morphogen patterning and expansion of stem cell pool, diversification of neural progenitors, variation of cell-cycle rates and protracted neurogenesis are responsible for expansion of the telencephalon in amniotes[37,53–55]. We asked whether these mechanisms were reflected in the duration of embryonic and post-hatching development periods. We found that longer development time leads to a greater accumulation of number of neurons in the pallium of clades with high-slope grades than in those showing low-slope grades (Fig. 5 and Supplementary Fig. 8). This accumulation of neurons is associated with an extension of the postnatal (fledging) development relative to the embryonic period. Importantly, scaling of pallial neuron counts with development strongly resembles that found for the total number of brain neurons, reinforcing the notion that the number of pallial neurons largely accounts for the much larger number of neurons in the brains of altricial species.

Growing evidence suggests that different mechanisms underlie telencephalon growth and maturation in precocial and altricial birds, leading to relatively larger relative brains in the latter. Precocial birds like ducks and grouse enlarge their telencephalon early in development (before the onset of neurogenesis) presumably by an increase in the number of telencephalic progenitors[56]. In contrast, expansion of the telencephalon in altricial birds like songbirds and parrots is associated with protracted neurogenesis and delayed neuronal maturation[57]. Our analyses are consistent with these patterns (Supplementary Fig. 9), showing that longer

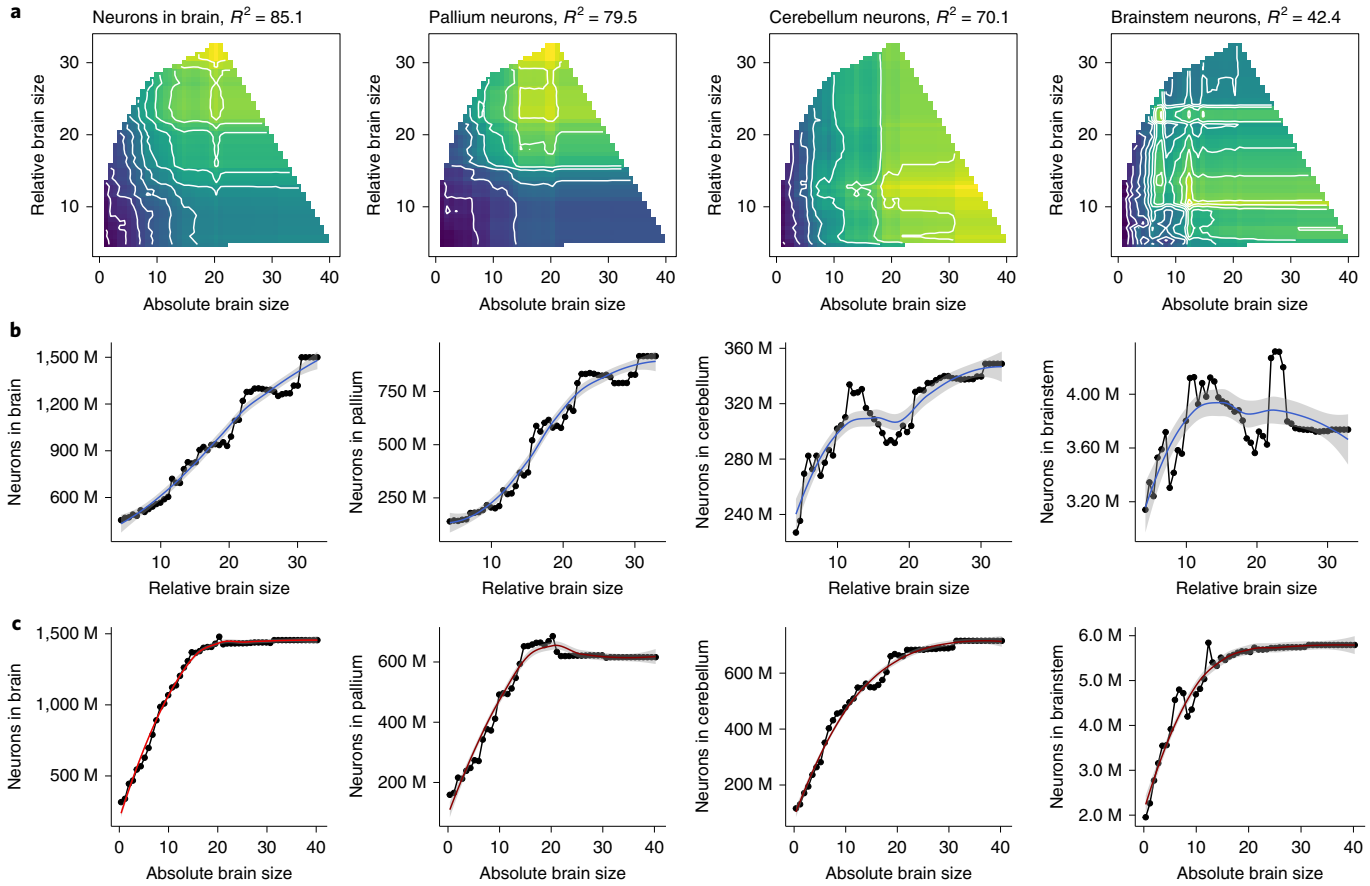

Fig. 4 | Neuron numbers as a function of absolute and relative brain size. a, Bivariate dependence plots representing neuron numbers in the entire brain and main brain regions as a function of absolute and relative brain size, based on the predictions from random forests. Colours describe neuron numbers, with low numbers represented by dark-blue colours and higher numbers by yellow-green colours. Relative brain size was estimated by means of the normalized scaled brain index, with the allometric exponent estimated excluding clades that have been found to exhibit substantial grade shifts in brain:body allometries ($NSBI_{grades}$; Methods). **b**, Univariate representations (partial dependence plots) for relative brain size to further interpret the bivariate dependence plots. The plots show the dependence between neuron numbers and relative brain size, marginalizing over the values of absolute brain size. **c**, Univariate representation of the bivariate dependence plot for absolute brain size. In **b** and **c**, lines show the values predicted by random forests and the lower and upper bounds are the credibility intervals representing the uncertainty of the prediction. In all analyses, owls have been excluded. For analyses with the entire sample of species, see Supplementary Figs. 6 and 7. M, million.

development time leads to greater accumulation of neurons in the pallium in altricial than in precocial species. Indeed, all species from our dataset belonging to the highest slope-grade category show high degree of altriciality (that is, they are classified as super-altricial). Altogether, our results are consistent with the view that increases in absolute and relative brain size are made possible through the evolutionary transition to altriciality and changes in neurogenesis schedules related to a disproportionate lengthening of the later stages of development. While this pattern is predicted by some models of brain development, like the 'late is large' rule[37], additional research is needed to elucidate the exact mechanisms.

Our analyses unify neuro-anatomical measures at multiple levels. First, we provide firm support for the intuitively appealing notion that cognitive performance is limited by the number of neurons in the pallium and, to a lesser extent, the cerebellum. Thus, our results support the hypothesis[14] that intelligence reflects a disproportionate allocation of neurons to cognitive tasks but also aligns with suggestions that cognitive performance ultimately depends on the total number of neurons and the way neurons connect different brain areas[3,15,23]. Second, we show that an increase in the number of neurons in the areas most closely involved in cognitive performance, the pallium, increases brain size in both absolute and relative terms. Although the number of neurons in the cerebellum scaled primarily with absolute brain size, the effect of total neuron numbers on relative brain size persisted because, in birds, larger brains contain increasing proportions of neurons in the pallium and decreasing proportions in the cerebellum and other brain regions[24]. Third, we provide an adaptive explanation for some of the patterns of brain–body covariation in deep time detected by ref. [51]: clades that have a higher brain–body slope than others tend to be the ones that are most innovative. A higher brain–body slope means that as body size gets bigger, the brain increases disproportionately more in size than it does in non-innovative clades; this increase in both absolute and relative brain size is, according to our analyses, mostly due to an increase in pallial neurons. Finally, we provide a developmental rationale for the observed patterns, suggesting that the elongation of the fledging period in altricial species links neuron numbers with absolute and relative brain size. The failure to find a similar pattern in precocial species supports the notion that not all brains are made in a same way[25,52], highlighting the key role of life history in brain evolution (Supplementary Fig. 10).

The reason why the dual role of absolute and relative brain size in cognition has been underappreciated in the past probably reflects the common practice of removing the allometric effects of body size

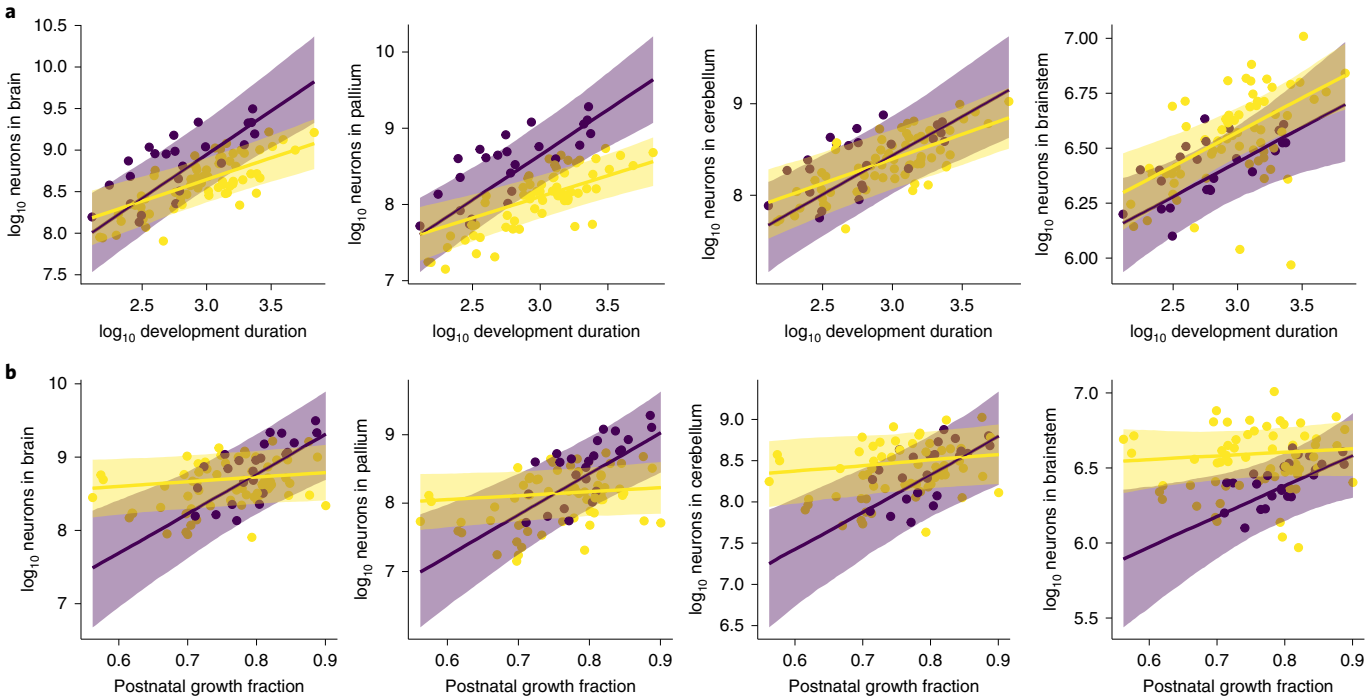

Fig. 5 | Neurons and development in species belonging to low-slope and highest slope grades. a,**b**, Neuron numbers as a function of the duration of development (embryonic stage plus postnatal growth) (**a**) and the fraction of total development time represented by the postnatal growth (**b**), for low-slope grades (yellow bar) and the highest slope grades (purple bar). Lines show the values predicted by Bayesian phylogenetic mixed models and the lower and upper bounds are the credibility intervals representing the uncertainty of the prediction. In all analyses, owls have been excluded (for analyses with the entire sample size, see Supplementary Fig. 8).

in comparative analyses of brain size. As suggested by ref. [2], this is probably legitimate when comparing brains of species with striking differences in body size, like an ostrich and a hummingbird. Yet by treating body size as a statistical nuisance, we appear to be missing important information. A larger body is often associated with greater longevity[58] and can reduce juvenile mortality risk[35], which should increase the value of learning and reduce the costs of a long development time[30,31,59]. Alternatively, the same environmental pressures that favour a slow pace of life could generate correlated selection on both cognition and body size[31]. Whether a large body facilitates selection for cognition or covaries with cognition due to either correlated selection or shared developmental processes, the consequence for the functional architecture of the brain is to link neuron numbers and cognitive performance to both absolute and relative brain size.

Methods

Neuron numbers estimation. Our study is based on an updated database quantifying neuron numbers in the whole brain and three brain areas—the pallium (comprising the hyperpallium, mesopallium, nidopallium, entopallium, acropallium and hippocampus), the cerebellum and the brainstem (comprising the medula oblongata and midbrain tegmentum) for bird species. Information for 65 avian species was extracted from the literature[24,25]. Numbers of brain, pallial and cerebellar neurons for an additional 81 individuals representing 46 species and number of brainstem neurons for an additional 172 individuals representing 83 avian species were newly estimated using the isotropic fractionator, following experimental procedures described in ref. [24]. Briefly, animals were killed by an overdose of halothane, weighed and immediately perfused transcardially with warmed phosphate-buffered saline containing 0.1% heparin followed by cold phosphate-buffered 4% paraformaldehyde solution. The brains were immediately removed, weighted, postfixed for an additional 7–21 d and then dissected into the examined brain divisions. The cerebral hemispheres (including the olfactory bulbs) were detached from the diencephalon by a straight cut separating the subpallium from the thalamus. The cerebellum was cut off at the surface of the brainstem. The tectum (optic lobe) was bilaterally excised from the surface of the brainstem. The excised parts included most of the tectal grey, optic tectum and torus semicircularis. The remaining structures were dissected into diencephalon (rostral part) and brainstem (caudal part comprising the medula oblongata and midbrain tegmentum) along the plane connecting the posterior commissure dorsally and hypothalamus–mesencephalon boundary ventrally. The latter is visible macroscopically as a groove between the convex ventral part of the midbrain and the hypothalamus, caudally to the infundibulum and mammillary bodies. In one individual per species, one hemisphere was dissected into the pallium and the subpallium. These hemispheres were embedded in agarose and sectioned on a vibratome at 300–500 µm (depending on size of a hemisphere) in the coronal plane. Under oblique transmitted light at the stereomicroscope and with the use of a microsurgical knife (Stab Knife Straight, 5.5 mm, ref. 7516, Surgical Specialities Corporation) we manually dissected the pallium from subpallium on each section by cutting along the pallial–subpallial lamina, as defined by ref. [60].

The dissected structures were dried with a paper towel, weighed to the nearest 0.1 mg, incubated in 30% sucrose solution until they sank, then transferred into antifreeze (30% glycerol, 30% ethylene glycol, 40% phosphate buffer) and frozen for further processing. The examined brain parts were homogenized in 40 mM sodium citrate with 1% Triton X-100 using Tenbroeck tissue grinders (Wheaton) to obtain a suspension of free cell nuclei. The fluorescent DNA marker 4′,6-diamidino-2-phenylindole (DAPI) was added (0.5 mgl^{-1}) to stain the nuclei. Afterwards the homogenate was adjusted to defined volume and the mixture was kept homogenous by agitation. The total number of cells was estimated by counting at least five aliquots of 10 µl using a Neubauer improved counting chamber (BDH) with an Olympus BX51 microscope equipped with epifluorescence and appropriate filter settings; additional aliquots were counted if needed to reach the coefficient of variation among counts ≤0.10. The proportion of neurons was determined by immunocytochemical detection of the neuronal nuclear marker NeuN[61]. This neuron-specific protein was detected by an anti-NeuN mouse monoclonal antibody (clone A60, Sigma-Aldrich; dilution 1:800), which was characterized by western blotting with chick brain samples and shown to react with a protein of the same molecular weight as in mammals, indicating that it does not cross-react with other proteins in birds[62]. The binding sites of the primary antibody were revealed by Alexa Fluor 546-conjugated goat antimouse IgG (Life Technologies; dilution 1:400). An electronic haematologic counter (Alchem Grupa) was used to count the proportion of double-labelled nuclei in the Neubauer chamber. At least 500 nuclei were examined for each sample. The final dataset included information on neuron numbers for 240 specimens belonging to 111 species. For *Caloenas nicobarica* and *Eudromia formosa*, information on pallial neurons was missing and had to be imputed to

avoid comparing results with different sample sizes. We estimated these missing data by combining phylogenetic imputation with multivariate data (brain and body size and number of neurons in the entire brain, the pallium, the cerebellum and the brainstem), as implemented in the R package phytools[63]. We note that results hold whether or not these two species were included in the analyses.

Innovation data. Our innovation data were taken from ref. [41], compiled by systematically searching for reports of new behaviours in the short notes of 204 ornithology journals published between 1960 and 2020. The criterion to accept an innovation was that the report described the behaviour with key words such as 'novel', 'not noted before' and/or 'unusual'. Each innovation was classified as a resource innovation (if it involved a novel food item) or a technical innovation (if the searching and handling techniques were themselves novel regardless of whether the food type was novel or not[5]). Nocturnal clades were excluded due to the difficulty of being observed. The frequency with which a species was observed innovating in the wild was used to characterize the propensity of the species to innovate. Innovation propensity depends not only on innovative ability, however, but also on the probability that new behaviours are observed and reported. Thus, a species may have a low number of innovations not because it cannot innovate but because it is rare or secretive and hence difficult to observe and study. We tackled this issue by considering research effort in the analyses[5,11,31], using data on number of papers published per species[64]. The probability of reporting an innovation may also increase with geographic range, urbanization and island living and it can decrease with migratory behaviour[5,11,31]. Therefore, we also included these variables as covariates in the models (see below). Data were drawn from previously assembled datasets. Geographic range (number of 1° × 1° grid cells overlapping breeding/resident range), mobility (resident, nomadic, migrant and altitudinal migrant) and insularity (proportion of breeding/resident range intersecting with islands of landmass <2,000 km^2) were extracted from ref. [65], while the occurrence in urban environments was taken from ref. [11].

Life history data. We extracted published information on the duration of incubation (embryonic stage) and fledging periods (postnatal growth) from previously compiled datasets[11,31], updated with information from the online edition of the Handbook of Birds of the World (https://birdsoftheworld.org). Information was available for 108 species for incubation duration and 102 species for fledging duration. Postnatal growth fraction was estimated as (fledging/(incubation + fledging))$^{0.5}$, following ref. [66]. To assign species to different developmental modes, we used the classification recently proposed by ref. [67] and divided species into precocial, semi-precocial, semi-altricial, altricial and super-altricial (no super-precocial species was present in our dataset).

Modelling neurons, brains and innovations. We used Bayesian generalized linear mixed models (BGLMM) based on Markov Chain Monte Carlo (MCMC) approximations to model variation in neuron numbers and innovation propensity, as implemented in the R packages MCMCglmm[45] and BRMS[68]. To ensure that neuron numbers and brain measures were species characters, we first used intraspecific data to assess within-species consistency by means of Gaussian BGLMM, including sex as fixed effect and species as random effect (Supplementary Table 3). Consistency was estimated as the intraclass correlation coefficient (ICC), calculated by dividing the variation among species by the total variation (variation among species plus variation within species, the latter including natural variation and measurement error). The consistency attributed to shared ancestors was estimated in a similar model but incorporating a variance–covariance matrix of phylogenetic distances as a random effect. This allowed us estimating varying intercepts among species adjusted by phylogenetic dependency. Phylogenetic heritability was estimated as the fraction of total variation accounted for the phylogenetic distance between species (Supplementary Table 3).

To test whether neuron numbers affect innovation frequency, we then averaged neuron numbers for each species and used them in Gaussian phylogenetic BGLMMs to model innovation frequency (response variable). In these models, biogeographic realm[69] was included as a random effect together with the phylogenetic variance–covariance matrix to allow the integration of global information originating from different regions[31]. To control for potential confounding effects, research effort, geographic range, tolerance to urbanization, insularity and mobility were included as fixed effects.

Species-level phylogenetic BGLMMs were also used to model neuron numbers as a function of body mass, development duration (incubation and fledging) and incubation fraction. We generally used BRMS with Gaussian responses, switching to Weibull distributions when divergent transitions affected model convergence. To assess whether the relationship varied between low-slope and highest-slope grades, sensu ref. [51], we included in the models an interaction with a variable coding for these two groups. Differences between precocial and altricial species were investigated in a similar way.

The phylogenetic hypothesis was a summary tree based on 10,000 trees from one of the backbones of the complete phylogeny of birds[70] available at www.birdtree.org. We note that using the alternative phylogenetic backbone yielded similar results.

For all models, the number of MCMC iterations and the burn-in interval were chosen so as to ensure satisfactory convergence. The priors settings are described in the Code availability section. The parameters reported for fixed and random effects are the posterior mode and the 95% lower and upper credibility intervals (CI). We considered the fixed effects statistically significant when 95% CIs did not include the zero. Conditional effects plots and 95% CIs were used to visualize the relationship between predictors and response variables.

Describing neuron numbers as a function of brain size. We used regression-based random forests (RF), a type of machine-learning algorithm, to describe neuron numbers as a function of both absolute and relative brain size[71]. When modelling quantitative response variables, RF uses linear regressions to recursively partition the data by means of decision trees. Instead of selecting a best tree, however, the method does so by taking a random sample of the training data and a random selection of variables at each step[44]. For each tree in the RF, the fitted value of each terminal node is the mean of the response variable values, which is averaged over all trees to estimate the fitted values of the RF. The data not used to train the model, the out-of-bag (OOB) sample, provide a way to stabilize the error without having to sacrifice training data to use for validation. In this way, RF allows to efficiently model nonlinear relationships and deal with complex interactions between predictors while avoiding over-fitting, producing stable patterns that are more difficult to change with new data and that are less sensitive to outliers.

We modelled neuron numbers (response variable) as a function of relative and absolute brain size (predictors) with the R package randomForest[72]. Following the protocol suggested by others[44], we ran 500 trees twice and compared the stability of the results (correlation > 0.97 in all cases). Deviations between the fitted and observed values were used to compute a 'pseudo' R^2. Bivariate partial dependence (marginal effects) plots for the last tree in the forest, once the model had converged, were used to visualize the covariation of neuron numbers with absolute and relative brain size while univariate plots were used to visualize the influence of each predictor separately.

To be included together with absolute brain size in the RF, we estimated relative brain size by means of the normalized scaled brain index[73] (NSBI). This approach uses the equation of allometric growth to adjust the brain size of species to that which they would have if all had the same body size, making the values directly comparable:

$$\mathrm{NSBI} = Y_i \left[\frac{X_0}{X_i}\right]^b$$

where b is the allometric exponent, Y_i and X_i are, respectively, brain size and body size for the individual i and X_0 is the ancestral body size used to scale all species to the same size. We estimated the allometric exponent b on the basis of a log-log phylogenetic Gaussian BGLMMs of absolute brain size against body mass. To this purpose, we used a previously assembled dataset of brain mass (g) and volume (ml)[74], updated with information on brain mass from the specimens used to estimate neuron numbers (see above) and with new endocast measures of specimens from museums in Europe and North America ($n = 114$ specimens). Volumes were obtained by means of the endocast method and converted to mass by multiplying by the density of brain tissue (1.036 g ml^{-1}) (ref. [74]). We only used specimens of known body mass, yielding information for 10,523 specimens belonging to 1,976 species. To scale all species to the same size, we used the body mass of the presumed ancestor of current birds (2,400 g), as suggested by ref. [75]. In our dataset, for example, the greater adjutant (*Leptoptilos dubius*) has the largest brain (~34 g) of the 1,976 species from our dataset but this mainly reflects that it is a large bird (~7,400 g). Using the above normalization technique to scale the brain, the NSBI of the greater adjutant (*L. dubius*)—estimated around 6.29—brings the species down to the 300th position of the ranking.

The NSBI is equivalent to the residual approach used in previous studies and hence presumes that species share the same brain:body allometric equation. However, there is evidence that the allometric exponent can exhibit some differences across lineages[51]. Consequently, we used a second NSBI ($\mathrm{NSBI}_{\mathrm{grades}}$) based on an allometric exponent b estimated excluding clades that have been found to exhibit substantial grade shifts in brain:body allometries (*Anseriformes* and *Neoaves*)[51]. This exponent represents the scaling relationship of birds before some lineages experienced grade shifts (Fig. 1) and it is remarkably close to that estimated with the entire dataset (Supplementary Fig. 9). Thus, in the main text we present the results based on the $\mathrm{NSBI}_{\mathrm{grades}}$, which better fit to the proposed theoretical framework (Fig. 1).

Ethics statement. The experimental procedures were approved by the Institutional Animal Care and Use Committee at Charles University in Prague, Ministry of Culture (permit no. 47987/2013) and Ministry of the Environment of the Czech Republic (permit no. 53404/ENV/13-2299/630/13).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data used in the analyses of this paper are archived in zenodo (https://doi.org/10.5281/zenodo.6460346).

Code availability

The R code used for the analyses of this paper are archived in zenodo (https://doi.org/10.5281/zenodo.6460346).

Received: 31 July 2021; Accepted: 19 May 2022;
Published online: 11 July 2022

References

1. Shultz, S. & Dunbar, R. Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proc. Natl Acad. Sci. USA* **107**, 21582–21586 (2010).
2. Jerison, H. J. Animal intelligence as encephalization. *Phil. Trans. R. Soc. Lond. B* **308**, 21–35 (1985).
3. Roth, G. & Dicke, U. Evolution of the brain and intelligence. *Trends Cogn. Sci.* **9**, 250–257 (2005).
4. Lefebvre, L., Whitle, P., Lascaris, E. & Finkelstein, A. Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549–560 (1997).
5. Overington, S. E., Morand-Ferron, J., Boogert, N. J. & Lefebvre, L. Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Anim. Behav.* **78**, 1001–1010 (2009).
6. Reader, S. M., Hager, Y. & Laland, K. N. The evolution of primate general and cultural intelligence. *Phil. Trans. R. Soc. B* **366**, 1017–1027 (2011).
7. Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E. M. & Holekamp, K. E. Brain size predicts problem-solving ability in mammalian carnivores. *Proc Natl Acad. Sci. USA* **113**, 2532–2537 (2016).
8. Reader, S. M. & Laland, K. N. Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**, 4436–4441 (2002).
9. Fristoe, T. S., Iwaniuk, A. N. & Botero, C. A. Big brains stabilize populations and facilitate colonization of variable habitats in birds. *Nat. Ecol. Evol.* **1**, 1706–1715 (2017).
10. van Woerden, J. T., van Schaik, C. P. & Isler, K. Effects of seasonality on brain size evolution: evidence from Strepsirrhine primates. *Am. Nat.* **176**, 758–767 (2010).
11. Ducatez, S., Sol, D., Sayol, F. & Lefebvre, L. Behavioural plasticity is associated with reduced extinction risk in birds. *Nat. Ecol. Evol.* **4**, 788–793 (2020).
12. Herculano-Houzel, S. Brains matter, bodies maybe not: the case for examining neuron numbers irrespective of body size. *Ann. NY Acad. Sci.* **1225**, 191–199 (2011).
13. Logan, C. J. et al. Beyond brain size: uncovering the neural correlates of behavioral and cognitive specialization. *Comp. Cogn. Behav. Rev.* **13**, 55–89 (2018).
14. Jerison, H. *Evolution of the Brain and Intelligence* (Academic Press, 1973).
15. Herculano-Houzel, S. Numbers of neurons as biological correlates of cognitive capability. *Curr. Opin. Behav. Sci.* **16**, 1–7 (2017).
16. Van Schaik, C. P., Triki, Z., Bshary, R. & Heldstab, S. A. A farewell to the encephalization quotient: a new brain size measure for comparative primate cognition. *Brain Behav. Evol.* **96**, 1–12 (2021).
17. Striedter, G. F. *Principles of Brain Evolution* (Sinauer Associates, 2005).
18. MacLean, E. L. et al. The evolution of self-control. *Proc. Natl Acad. Sci. USA* **111**, E2140–E2148 (2014).
19. Matějů, J. et al. Absolute, not relative brain size correlates with sociality in ground squirrels. *Proc. R. Soc. B* **283**, 20152725 (2016).
20. Deaner, R. O., Isler, K., Burkart, J. & Van Schaik, C. Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain Behav. Evol.* **70**, 115–124 (2007).
21. Smaers, J. B., Dechmann, D. K. N., Goswami, A., Soligo, C. & Safi, K. Comparative analyses of evolutionary rates reveal different pathways to encephalization in bats, carnivorans, and primates. *Proc. Natl Acad. Sci. USA* **109**, 18006–18011 (2012).
22. Smaers, J. B. et al. The evolution of mammalian brain size. *Sci. Adv.* **7**, eabe2101 (2021).
23. Němec, P. & Osten, P. The evolution of brain structure captured in stereotyped cell count and cell type distributions. *Curr. Opin. Neurobiol.* **60**, 176–183 (2020).
24. Olkowicz, S. et al. Birds have primate-like numbers of neurons in the forebrain. *Proc. Natl Acad. Sci. USA* **113**, 7255–7260 (2016).
25. Kverková, K. et al. The evolution of brain neuron numbers in amniotes. *Proc. Natl Acad. Sci. USA* **119**, e2121624119 (2022).
26. Iwaniuk, A. N. & Hurd, P. L. The evolution of cerebrotypes in birds. *Brain Behav. Evol.* **65**, 215–230 (2005).
27. Timmermans, S., Lefebvre, L., Boire, D. & Basu, P. Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. *Brain Behav. Evol.* **56**, 196–203 (2000).
28. Sayol, F., Lefebvre, L. & Sol, D. Relative brain size and its relation with the associative pallium in birds. *Brain Behav. Evol.* **87**, 69–77 (2016).
29. Healy, K. et al. Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. B* **281**, 20140298 (2014).
30. Deaner, R. O., Barton, R. A. & van Schaik, C. P. in *Primate Life Histories and Socioecology* (eds Kappeler, P. M. & Pereira, M. E.) 233–265 (Univ. of Chicago Press, 2003).
31. Sol, D., Sayol, F., Ducatez, S. & Lefebvre, L. The life-history basis of behavioural innovations. *Phil. Trans. R. Soc. B* **371**, 20150187 (2016).
32. Dukas, R. Evolutionary biology of animal cognition. *Ann. Rev. Ecol. Evol. Syst.* **35**, 347–374 (2004).
33. Ricklefs, R. E. The cognitive face of life histories. *Wilson Bull.* **116**, 119–133 (2004).
34. Martin, T. E., Oteyza, J. C., Boyce, A. J., Lloyd, P. & Ton, R. Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. *Am. Nat.* **186**, 223–236 (2015).
35. Unzeta, M., Martin, T. E. & Sol, D. Daily nest predation rates decrease with body size in passerine birds. *Am. Nat.* **196**, 743–754 (2020).
36. Charvet, C. J. & Striedter, G. F. Developmental modes and developmental mechanisms can channel brain evolution. *Front. Neuroanat.* **5**, 4 (2011).
37. Finlay, B. L. & Darlington, R. B. Linked regularities in the development and evolution of mammalian brains. *Science* **268**, 1578–1584 (1995).
38. Herculano-Houzel, S. Isotropic fractionator: a simple, rapid method for the quantification of total cell and neuron numbers in the brain. *J. Neurosci.* **25**, 2518–2521 (2005).
39. Massen, J. J. M. et al. Brain size and neuron numbers drive differences in yawn duration across mammals and birds. *Commun. Biol.* **4**, 1–10 (2021).
40. Ramsey, G., Bastian, M. L. & Schaik, C. Van Animal innovation defined and operationalized. *Behav. Brain Sci.* **30**, 393–437 (2007).
41. Lefebvre, L. A global database of feeding innovations in birds. *Wilson J. Ornithol.* **132**, 803–809 (2021).
42. Barton, R. A. Embodied cognitive evolution and the cerebellum. *Phil. Trans. R. Soc. B* **367**, 2097–2107 (2012).
43. Gutiérrez-Ibáñez, C., Iwaniuk, A. N. & Wylie, D. R. Parrots have evolved a primate-like telencephalic–midbrain–cerebellar circuit. *Sci. Rep.* **8**, 9960 (2018).
44. Brieuc, M. S. O. O., Waters, C. D., Drinan, D. P. & Naish, K. A. A practical introduction to random forest for genetic association studies in ecology and evolution. *Mol. Ecol. Res.* **18**, 755–766 (2018).
45. Hadfield, J. D. & Nakagawa, S. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J. Evol. Biol.* **23**, 494–508 (2010).
46. Güntürkün, O., Ströckens, F., Scarf, D. & Colombo, M. Apes, feathered apes, and pigeons: differences and similarities. *Curr. Opin. Behav. Sci.* **16**, 35–40 (2017).
47. Ströckens, F. et al. High associative neuron numbers could drive cognitive performance in corvid species. *J. Comp. Neurol.* **530**, 1588–1605 (2022).
48. Shanahan, M., Bingman, V. P., Shimizu, T., Wild, M. & Güntürkün, O. Large-scale network organisation in the avian forebrain: a connectivity matrix and theoretical analysis. *Front. Comput. Neurosci.* **7**, 89 (2013).
49. Emery, N. J. Cognitive ornithology: the evolution of avian intelligence. *Phil. Trans. R. Soc. B* **361**, 23–43 (2006).
50. Lambert, M. L., Jacobs, I., Osvath, M. & von Bayern, A. M. P. Birds of a feather? Parrot and corvid cognition compared. *Behaviour* **156**, 505–594 (2019).
51. Ksepka, D. T. et al. Tempo and pattern of avian brain size evolution. *Curr. Biol.* **30**, 2026–2036 (2020).
52. Herculano-Houzel, S., Manger, P. R. & Kaas, J. H. Brain scaling in mammalian evolution as a consequence of concerted and mosaic changes in numbers of neurons and average neuronal cell size. *Front. Neuroanat.* **8**, 77 (2014).
53. Smaers, J. B., Mongle, C. S., Safi, K. & Dechmann, D. K. N. Allometry, evolution and development of neocortex size in mammals. *Prog. Brain Res.* **250**, 83–107 (2019).
54. Cárdenas, A. & Borrell, V. Molecular and cellular evolution of corticogenesis in amniotes. *Cell Mol. Life Sci.* **77**, 435–1460 (2020).
55. García-Moreno, F. & Molnár, Z. Variations of telencephalic development that paved the way for neocortical evolution. *Prog. Neurobiol.* **194**, 101865 (2020).
56. Charvet, C. J. & Striedter, G. F. Developmental basis for telencephalon expansion in waterfowl: enlargement prior to neurogenesis. *Proc. R. Soc. B* **276**, 3421–3427 (2009).
57. Striedter, G. F. & Charvet, C. J. Developmental origins of species differences in telencephalon and tectum size: morphometric comparisons between a parakeet (*Melopsittacus undulatus*) and a quail (*Colinus virgianus*). *J. Comp. Neurol.* **507**, 1663–1675 (2008).
58. Sibly, R. M. & Brown, J. H. Effects of body size and lifestyle on evolution of mammal life histories. *Proc. Natl Acad. Sci. USA* **104**, 17707–17712 (2007).

59. Uomini, N., Fairlie, J., Gray, R. D. & Griesser, M. Extended parenting and the evolution of cognition. *Phil. Trans. R. Soc. Lond. B* **375**, 20190495 (2020).
60. Reiner, A. et al. Revised nomenclature for avian telencephalon and some related brainstem nuclei. *J. Comp. Neurol.* **473**, 377–414 (2004).
61. Mullen, R. J., Buck, C. R. & Smith, A. M. NeuN, a neuronal specific nuclear protein in vertebrates. *Development* **116**, 201–211 (1992).
62. Mezey, S. et al. Postnatal changes in the distribution and density of neuronal nuclei and doublecortin antigens in domestic chicks (*Gallus domesticus*). *J. Comp. Neurol.* **520**, 100–116 (2012).
63. Revell, L. J. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223 (2012).
64. Ducatez, S. & Lefebvre, L. Patterns of research effort in birds. *PLoS ONE* **9**, e89955 (2014).
65. Sheard, C. et al. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nat. Commun.* **11**, 2463 (2020).
66. Cooney, C. R. et al. Ecology and allometry predict the evolution of avian developmental durations. *Nat. Commun.* **11**, 2383 (2020).
67. Botelho, J. F. & Faunes, M. The evolution of developmental modes in the new avian phylogenetic tree. *Evol. Dev.* **17**, 221–223 (2015).
68. Bürkner, P.-C. Brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).
69. Pigot, A. L. et al. Macroevolutionary convergence connects morphological form to ecological function in birds. *Nat. Ecol. Evol.* **4**, 230–239 (2020).
70. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
71. Berk, R. A. *Statistical Learning from a Regression Perspective* (Springer International, 2017).
72. Liaw, A. & Wiener, M. Classification and regression by randomForest. *R News* **2**, 18–22 (2002).
73. Lleonart, J., Salat, J. & Torres, G. J. Removing allometric effects of body size in morphological analysis. *J. Theor. Biol.* **205**, 85–93 (2000).
74. Sayol, F., Downing, P. A., Iwaniuk, A. N., Maspons, J. & Sol, D. Predictable evolution towards larger brains in birds colonizing oceanic islands. *Nat. Commun.* **9**, 2820 (2018).
75. Torres, C. R., Norell, M. A. & Clarke, J. A. Bird neurocranial and body mass evolution across the end-Cretaceous mass extinction: the avian brain shape left other dinosaurs behind. *Sci. Adv.* **7**, eabg7099 (2021).

Acknowledgements

This research was funded by MINECO (PID2020-119514GB-I00 to D.S.), the Czech Science Foundation (18-15020 to P.N.), the Grant Agency of Charles University (1438217 to M.K.) and the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie postdoctoral fellowship (grant agreement no. 838998 to F.S.). F.S. and J.G.P. were supported by the postdoctoral fellowship program Beatriu de Pinós (2020 BP 00067 and 2020 BP 00147, Government of Catalonia). We thank A. Iwaniuk, S. Reader, S. Ducatez and J. Morand-Ferron for discussions and the R team and package contributors for facilitating analytical tools. We also thank J. Louys for facilitating bird silhouettes. This paper is dedicated to J. Morand-Ferron.

Author contributions

L.L. and F.S. proposed the study. D.S., L.L., F.S. and P.N. conceived the study. D.S. and T.E.M. elaborated the life history framework. P.N., S.O., L.M., M.K., Y.Z. and C.O. collected the neuro-anatomical data, L.L. the innovation data and J.G.P., F.S. and E.C. the endocast data. D.S. designed and conducted the analyses, with contributions from F.S., L.L., P.N. and T.E.M. D.S. wrote the manuscript and all authors edited and approved it.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-022-01815-x.

Correspondence and requests for materials should be addressed to Daniel Sol, Louis Lefebvre or Pavel Němec.

Peer review information *Nature Ecology & Evolution* thanks Onur Güntürkün, Cristian Gutierrez-Ibanez and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

nature portfolio

Corresponding author(s): Daniel Sol, Louis Lefebvre and Pavel Nemec

Last updated by author(s): Apr 14, 2022

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed
☐	☒ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒ The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒ A description of all covariates tested
☐	☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒ For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☐	☒ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Most data comes from a literature review, except those of neuron numbers that includes some measures specially taken for the study.
Data analysis	All analyses have been conducted by means of the open source R.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The data and R-code used in the analyses of this paper are archived in Zenoto (DOI: 10.5281/zenoto.6460346)

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The study uses a comparative framework to investigate the relationship between innovativeness, brain size and neuron numbers in birds.
Research sample	To analyses neuron numbers, sample size includes information gathered for 111 avian species both from the literature or directly measured. Specifically, the dataset of the numbers of brain, pallial and cerebellar neurons was updated with additional information for 81 individuals representing 46 species and number of brainstem neurons for additional 172 individuals representing 83 avian species were newly estimated using the isotropic fractionator, following well-established procedures. To analyze innovations, we used a dataset of published data on feeding innovations including > 4400 observations.
Sampling strategy	Sampling effort was mostly defined by data availability in the literature, but data are representative of the main avian orders.
Data collection	Most data were available from previous studies, updated with additional data gathered from the literature or measured by one of the teams (see above). The criteria was to use all data available, based on exhaustive searches in google scholar and web of knowledge.
Timing and spatial scale	Timing and spatial scale is not particularly relevant for the present study, but the data used is the most recent available and represents all major orders.
Data exclusions	No data have been excluded from the analyses.
Reproducibility	The study does not involve experimental approaches, but the variables used have been verified to be species characters (i.e. to be consistent despite the existence of variation within species). Previous publications from our team have shown that the relationship between innovativeness and different measures of the brain (excluding neuron numbers, for which this manuscript is the first test) is robust at several taxonomic and anatomical levels, as well as with different phylogenies.
Randomization	We used data extracted from previous studies, which is therefore non-random. However, we have dealt with potential biases in a number of ways. Innovation propensity, for example, depends not only on innovative ability but also on the probability that new behaviors are observed and reported. Thus, a species may have a low number of innovations not because it cannot innovate but because it is rare or secretive, and hence difficult to observe and study. We tackled this issue by considering research effort in the analyses. First, we restricted the analyses of innovations to species with >50 published papers in the Web of knowledge. Second, we included research effort as co-variate in the models to deal with any remaining effect of research effort on innovation propensity. The probability of reporting an innovation may also increase with geographic range, urban use and island living, and it decreases with migratory behavior. Therefore, we also included these variables as covariates in the models. The same rationale has applied to all the analyses.
Blinding	Data used come from different sources and were assembled independently. Blinding is one of the biases that have been checked for the innovation data.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☐	☒ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Antibodies

Antibodies used: anti-NeuN mouse monoclonal antibody (clone A60, Sigma-Aldrich)

Validation: The antibody was characterized by Western blotting with chick brain samples and shown to react with a protein of the same molecular weight as in mammals, indicating that it does not cross-react with other proteins in birds.
Reference: Mezey, S. et al. Postnatal changes in the distribution and density of neuronal nuclei and doublecortin antigens in domestic chicks (Gallus domesticus). J Comp Neurol 520, 100–116, 2012.

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals: Study did not involve laboratory animals.

Wild animals: Altogether we used data for 111 avian species. Neuron numbers for 28 species were extracted from the literature (Olkowicz et al. Birds have primate-like numbers of neurons in the forebrain. Proc Natl Acad Sci USA 113, 7255–7260, 2016), data for additional 37 species were gathered within the scope of another, so far unpublished study (data deposited at https://figshare.com/s/e5cc85d028bcbe313ca6). Representatives of the following 46 species were newly gathered and examined: Alectoris rufa (M,2F), Callipepla californica (M), Francolinus francolinus (F,M), Numida meleagris (2M,F), Phasianus colchicus (2M,F), Tetrao tetrix (M,F), Lophonetta specularioides (M,F), Chenonetta jubata (M), Dendrocygna arcuate (M, F), Mergellus albellus (M,F), Oxyura vittata (M,M), Anas clypeata (M,F), Anser cygnoides (M,F), Anas bahamensis (M), Aix galericulata (2M,2F), Branta canadensis (2M,F), Chauna torquata (F), Tadorna ferruginea (2M,F), Cereopsis novaehollandiae (M,F), Anas Formosa (M,F), Anas penelope (M,F), Cairina moschata (M,F),Otus scops (M,F), Aegolius funereus (F), Ninox novaehollandiae (2M), Surnia ulula (M), Strix nebulosa (F), Circus pygargus (M), Circus aeruginosus (2M), Milvus migran (M), Milvus milvus (F), Accipiter gentilis (M,F), Falco sparverius (M,F), Falco vespertinus (2M), Falco peregrinus (F), Cariama cristata (F), Caloenas nicobarica (M), Ducula luctuosa (F), Gallicolumba luzonica (2M), Columbina passerine (M,F), Treron vernans (M,F), Oena capensis (M), Ptilinopus melanospila (M,F), Columba guinea (2M,F), Chalcophaps indica (M,F), Phaps chalcoptera (M,F). All birds were sexually mature or at least had adult-like size and plumage coloration. We determined the sex of all animals upon dissection; sex of the examined individual is indicated in parentheses. Birds were purchased from breeders, local hunters, obtained from zoos (animals that would be euthanized for other reasons) and animal rescue centers (injured animals with a low chance of recovery), a small minority of birds were wild-caught in Czech Republic (Permissions No. 00212/C S/13 and 446/13).

Field-collected samples: Birds collected in the field were euthanized by an overdose of halothane.

Ethics oversight: All experimental procedures were approved by the Institutional Animal Care and Use Committee at Charles University in Prague (UKPRF/28830/2021), Ministry of Culture (Permit No. 47987/2013) and Ministry of the Environment of the Czech Republic (Permit No. 53404/ENV/13-2299/630/13).

Note that full information on the approval of the study protocol must also be provided in the manuscript.