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Extractive foraging behaviour in woodpeckers evolves in species that retain a large ancestral brain

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ABSTRACT

Identifying ecological factors that influence brain size evolution is a major challenge in organismal biology. The extractive foraging hypothesis proposes that large brains are more likely to evolve in taxa that extract prey items from hard-to-access substrates, but this idea has received relatively little attention. Here, we provide a comprehensive test of the extractive foraging hypothesis in woodpeckers, a family of relatively large-brained birds that contains many species that feed on wood-boring larvae extracted from trees. Our results show strong support for the extractive foraging hypothesis. First, woodpeckers that use extractive foraging have relatively larger brains compared to species that forage using other tactics. Second, our comparative analyses suggest not only that big brains are the likely ancestral phenotype among all woodpecker taxa, but also that this trait is associated with innovation in foraging behaviour. We suspect that retaining an ancestral large brain likely increases the probability that a given species evolves to become an extractive forager who eats largely wood-boring larvae, given that species that transitioned to a small brain evolved different diets. Thus, the extractive foraging hypothesis likely applies to woodpeckers because of a historical contingency (large brains) that sets the stage for behavioural innovations to better exploit ecological opportunities.

The size of the brain, in both absolute and relative terms, varies greatly among species, and decades of research have tried to explain why this variation occurs and its relation to behaviour. Most papers in this area typically focus on positive relationships between relative brain size (henceforth 'brain size') and specialized social and/or cognitive skills (Dunbar, 1998; Sol et al., 2010). The social brain hypothesis, for example, posits that relatively large brains evolve to support the cognitive demands of a complex social life characterized by living in big groups (Dunbar, 1992, 1998). However, this idea has been frequently debated and criticized because it is supported neither by studies in primates (Decasien et al., 2017), nor by work in other species such as birds (Fedorova et al., 2017) or nonprimate mammals (Finarelli & Flynn, 2009). Thus, researchers have derived conceptually broader hypotheses like the cognitive buffer hypothesis, which posits that larger brains evolve to endow species with better cognitive skills (Sol, 2009). More specifically, relatively larger brains enable the expression of behavioural innovations or the ability to respond to novel resources and risks successfully, which increases survival rates in novel and changing environments (Lefebvre et al., 2004; Overington et al., 2009; Sayol et al., 2016; Sol et al., 2005). Regardless of the extent to which either hypothesis can be shown to explain variation in relative brain size across species, it often remains unclear whether relatively larger brains evolve prior to or subsequent to the behaviour. For example, the social brain hypothesis typically assumes that behavioural changes evolve prior to changes in brain size, whereas the cognitive buffer hypothesis often assumes changes in brain size occur before any modification to behaviour (Dunbar, 1992, 1998; Sol, 2009; Sol et al., 2005). Although some work does investigate the sequence of these evolutionary events (Fristoe et al., 2017; Sayol et al., 2018; Shultz & Dunbar, 2010), the results thus far are not conclusive or equally applied across

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comparative studies, especially at lower taxonomic levels (e.g. families).

Here, we study one of the oldest hypotheses that attempts to explain the evolution of large brain size: the extractive foraging hypothesis. This idea was first posited by primatologists in the late 1970s (Gibson, 1986; Parker, 1996; Parker & Gibson, 1977, 1979), and it proposes that relatively larger brains facilitate the emergence of extractive foraging behaviour, in which individuals employ novel skills to acquire food items from locations that are otherwise difficult to access (Parker & Gibson, 1977). For many species, studying the extractive foraging hypothesis is practical because quantifying and comparing extractive foraging behaviour in a wide range of taxa is often relatively straightforward. In its simplest form, for example, one can categorize extractive foraging as present or absent, especially if foraging behaviour in the group of species in question is relatively well studied and/or understood. To some extent, the extractive foraging hypothesis could be considered a special case of the cognitive buffer hypothesis in which extractive foraging may be a behavioural mechanism by which species buffer responses to variable environments. However, the extractive foraging hypothesis is conceptually distinct from the cognitive buffer hypothesis, in that it is more specific with respect to the neural structures and sensorimotor mechanisms that might underlie the evolution of a relatively larger brain, and it only applies to specific behaviours. For instance, under the extractive foraging hypothesis, we might expect enlargement of brain regions that govern sensorimotor command and complex motor control, both of which are likely necessary to access foods embedded in different substrates using tools (e.g. twigs, stones, etc.) or anatomical structures (e.g. beaks, elongated fingers, teeth, etc.) (Gibson, 1986; Parker & Gibson, 1977). The extractive foraging hypothesis also predicts increases in the size of brain systems important for mediating cognitive function, particular learning through cultural transmission (Parker, 1996; Parker & Gibson, 1979). Yet, rigorous tests of the extractive foraging hypothesis remain scarce, as it was largely dismissed in the 1990s (Dunbar, 1992, 1998). More recent work argues that this dismissal was likely premature, in that foraging behaviour may after all be a significant factor of brain evolution across a wide range of taxa (Melin et al., 2014; Parker, 2015; Reader et al., 2011; Reader & Laland, 2002; Sterling & Povinelli, 1999).

Woodpeckers are an ideal clade in which to study the extractive foraging hypothesis. Species within this family (Picidae) express diverse foraging behaviours, including the ability to extract invertebrate prey from trees (Schuppe et al., 2021; Short, 1979). To do so, species use their beak as a drill to chip away bark and wood and thereby access ‘hidden’ food sources (Villard & Cuisin, 2004). Past work also shows that woodpeckers, compared to other birds, have especially large brains relative to body size (Fristoe et al., 2017; Lefebvre et al., 1997; Sayol et al., 2016). Many speculate these big brains are associated with feeding habits, particularly parts of the brain linked to fine motor skills and sensory command (Sultan, 2005; Winkler & Winkler, 2015). Yet, not all woodpeckers are extractive foragers (Short, 1982), suggesting that a large brain for this type of feeding is not necessary in some taxa. With all these considerations in mind, we explore whether (1) extractive foraging is associated with a relatively larger brain and (2) larger relative brain size predates or follows the emergence of extractive foraging in woodpeckers. If changes in brain size are necessary to facilitate extractive foraging, then we predict that evolution of extractive foraging will always depend on the presence of a large brain. If, however, extractive foraging drives the evolution of an enlarged brain, then the emergence of this particular trait should depend on the presence of extractive foraging. In our analyses, we also attempt to rule out the effects of other factors that might explain variation in brain size among woodpecker species, such as clutch size, fledging age, incubation period and migratory behaviour (Iwaniuk & Nelson, 2003; Jiménez-Ortega et al., 2020; Sol et al., 2010; Winkler et al., 2004).

METHODS

Morphological Data

We measured endocranial volume of woodpecker skulls from the National Museum of Natural History (USNM) in Washington, D.C., U.S.A. Following Iwaniuk and Nelson (2002), we filled each skull with lead shot (0.1 mm diameter) via the foramen magnum. Once skulls were completely full, we poured the shot into a 10 ml graduated cylinder and recorded total volume (Iwaniuk & Nelson, 2002). We converted these measures to mass by multiplying volume by the density of fresh brain tissue (1.036 g/ml; Iwaniuk & Nelson, 2002). We measured adult individuals and computed species averages when more than one individual was available.

We obtained brain volume data from 401 specimens, representing 97 extant woodpecker species (≈4 individuals/species, with a range of 1–10 individuals/species). We complemented this data set with additional information from the literature (Fedorova et al., 2017), bringing our total to 119 species (out of ≈221 total, see Supplementary Data). Fedorova et al. (2017) measured endocranial volume using an identical technique, and we verified that measurements collected from species represented in both data sets were highly correlated ($r^2 = 0.991$, $t_{43} = 50.578$, $P < 0.001$). For each taxon, we averaged body mass data from specimen tags at the USNM, previously published books and research papers (Dunning, 1992; Montoya et al., 2018; Short, 1982; Winkler et al., 1995). Finally, we included brain size and mass data on three Indicatoridae species as an outgroup (Corfield et al., 2013).

To disentangle the possible effects of the woodpecker's diet on the evolution of cranial size versus the brain size, we also tested for possible effects on constitutive elements of the skull, including cranial and rostrum size. As such, we measured (1) skull length (distance between culmen base and foramen magnum) and (2) rostrum size (distance between culmen base and beak tip) for each specimen using Mitutoyo digital callipers (0.1 mm precision). This analysis was based on evidence that dietary niche as well as the physical properties of the diet (i.e. liquid versus solid; hardness versus softness, etc.) shape the evolution of cranial morphology across vertebrates (Felice et al., 2019; Klaczko et al., 2016; Santana et al., 2012). Additionally, we recognize that skull size could be highly correlated with brain size estimates using our methodological approach. Consequently, any potential correlation between brain size and extractive foraging could result from an enlarged cranial vault as opposed to a large brain.

Behavioural Data

We collected information on feeding and nesting behaviour from published accounts in the *Handbook of the Birds of the World* (hereafter: HBW) (del Hoyo et al., 2002). Woodpeckers (including subfamilies: Picumninae and Picinae) have varied diets; however, we focused on whether birds feed on wood-boring larvae as their primary diet, since this food item requires vigorous extractive foraging (Wiebe et al., 2006; Winkler & Winkler, 2015). Following the standardized protocol outlined in the EltonTraits 1.0 (Wilman et al., 2014) to classify diet, and used to study the evolution of foraging (Felice et al., 2019; Pigot et al., 2020), we considered extractive foragers as taxa described in the HBW that eat ‘mainly’, ‘mostly’, ‘greatly’, ‘principally’ and ‘especially’ wood-boring larvae (score of ≥6; Wilman et al., 2014, $N = 29$ species). Species that did not include wood-boring larvae in the diet description or that were described in the account as ‘occasional’ or ‘sometimes’ eaters of wood-boring larvae were considered as nonextractive foragers (score of 1–2; Wilman et al., 2014, $N = 86$ species).

Next, to separate the possible effects of drilling behaviour from the effects of an innovative foraging strategy on the evolution of the brain size, we tested whether species' nesting behaviour was related to brain size. This analysis was based on evidence that nest excavation requires levels of drilling similar to those of foraging (Schuppe et al., 2021). We classified each species according to its nesting strategy, given that many woodpeckers excavate nests in trees or snags. Again, we obtained this information through published accounts (HBW) of woodpecker behaviour (del Hoyo et al., 2002). If a species' nest cavity was primarily excavated, we classified it as an excavator ($N = 99$ species) regardless of the substrate in which the nest was built. If the species used a nest cavity that came from a natural cavity, burrow, another species' cavity or an artificial existing cavity (nestbox), we classified the species as nonexcavator ($N = 12$ species).

Last, given that some studies show a relationship between brain size and different life history traits and/or migratory behaviour (Isler & van Schaik, 2006; Iwaniuk & Nelson, 2003; Jiménez-Ortega et al., 2020; Sol et al., 2010; Winkler et al., 2004), we included minimum clutch size, incubation period, fledging age and migration as additional predictors of relative brain size. We collected data for minimum clutch size ($N = 92$), incubation period ($N = 51$), fledging age ($N = 49$) and migratory behaviour as a binary trait ($N = 119$) through published accounts of woodpecker behaviour in the HBW (del Hoyo et al., 2002).

Statistical Approach

Analyses were performed in R version 3.6.3 (R Core Team, 2022), using comparative methods that account for the shared ancestry (nondependence) of the data points (species). As such, we based our analyses on a woodpecker phylogeny (Miles et al., 2020) that combines two recent well-resolved phylogenies for this clade (Dufort, 2016; Shakya et al., 2017).

We first tested whether extractive foraging or the nesting strategy predict species differences in relative brain size, cranium size and rostrum size. Given the correlation between each of our response variables (brain size, cranium size and rostrum size) and body size, we estimated the residuals of a log–log least square linear regression with body mass for each of these variables. We then used these residuals to run separate phylogenetic generalized least squares (PGLS) models for each response variable (to maximize sample size) using the package ‘caper’ (Orme et al., 2018), where we allowed the phylogenetic signal in the residuals (Pagel's λ; Pagel, 1999) to be optimized to its maximum likelihood. Our results are reported as relative brain size, relative cranium size and relative rostrum size. As a validation analysis and to better describe the bivariate relationship between each of our response variables and our predictors, we also ran PGLS analysis between body size and brain size, cranium size and rostrum size. In these models, we included either foraging behaviour or nesting behaviour as a covariate, which allowed us to test whether such an allocation variable altered the intercept of the scaling relationship between body size and brain size (see Supplementary material). Finally, to assess whether there were any effects of life history traits on brain size, we tested how clutch size, incubation period, fledging age and migration predicted species differences in measures of brain size. As such, we ran PGLS models between body mass and brain size, using either clutch size, incubation period, fledging age or migration as a covariate. All analyses used a significance level of $P < 0.05$.

Evolutionary Modelling

After establishing a relationship between brain size and foraging behaviour (see Results), we next sought to explore how each of these traits evolved across these species' phylogenetic history. As a first step in this process, we ran analyses to estimate the probability of different trait states at the different ancestral nodes within the broader woodpecker phylogeny (Harmon et al., 2008). For foraging behaviour, this was straightforward because the data were already categorical; however, our brain size data were continuous. Although we recognize that certain ancestral state reconstructions can be done with continuous variables (Revell & Harmon, 2022), our brain size data needed to be categorized to run the discrete trait models outlined below. Several other studies of brain size evolution have categorized brain size data into discrete categories using residuals of a log–log regression with body mass, where positive residuals are assigned to the large brain size group and negative residuals are assigned to the small brain size group (Fristoe et al., 2017; Kotrschal et al., 2013; Sol et al., 2010). However, this approach can be problematic when species have values too close to the regression line or when variation within species is high. Therefore, to avoid these issues in our binarization procedure, we categorized brain size data using a *k*-means clustering algorithm. *K*-means clustering is a commonly deployed unsupervised machine learning algorithm that unbiasedly assigns continuous variables into defined clusters (Steinley, 2006). Accordingly, this algorithm aims to partition n observations into k groups, where individual observations are assigned to respective categories (‘clusters’) so that the degree of association between two observations is maximal if they belong to the same cluster and minimal otherwise. Mathematical details of *k*-means clustering models are described elsewhere (Hartigan & Wong, 1979), but note the approach is a widely used clustering technique in the field of animal behaviour (Scacco et al., 2019; Valletta et al., 2017; Zhang et al., 2015) and evolutionary biology, particularly in studies that use the resulting binarized data in phylogenetic comparative analysis to understand trait evolution among taxa (Abzhanov et al., 2006; Fabbri et al., 2017; Riede et al., 2016).

For our study, we classified brain size in one of two clusters: large or small. This form of binning allowed us to run discrete trait models that uncover the order in which brain size and foraging behaviour evolve relative to each other (see below). Importantly, we verified the robustness of this categorization approach using bootstrap sampling. We began our bootstrapping procedure by highlighting all the species for which we had brain size measurements of more than two individuals (77 species). We then created a series of bootstrap iterations in which we sampled (with replacement) brain size measures of each species, ensuring the same number of observations per species as in the original data set (i.e. first iteration: 3 observations (A, B, C); second iteration (A, A, C), third iteration (A, B, B), etc.). This allowed us to compute a mean brain size value for the different species with each iteration, and then re-enter this value into a ‘new’ clustering event. After performing this exercise 100 times, we could determine the percentage of times that a given species was classified in the same cluster to create a consistency measure. In total, 93.5% of the species (72 out of 77) were classified to the same cluster in more than 70% of the bootstrap iterations (Supplementary Fig. S1, and we therefore classified a species as having a small or big brain size according to this 70% cutoff (Supplementary Table S1). Our results (presented below) were effectively the same when we included only species with >70% consistence measure, compared to when we ran our analyses with all the taxa for which we had any measure of brain size consistency.

Next, we used ancestral state reconstructions to model how relative brain size and foraging strategy likely evolved over time. In doing so, we used the ‘fitDiscrete’ function in ‘geiger’ to estimate the best model of trait evolution for our categorical estimates of brain size and foraging behaviour (Harmon et al., 2008). We tested three different continuous time Markov models of trait evolution that assumed one of the following models: (1) equal transition rates (ER), (2) all rates different (ARD) or (3) symmetrical model (SYM). The best-fitting model for each trait was chosen based on Akaike information criterion scores corrected for small samples (AICc), with ER describing categorical brain size and ARD describing foraging behaviour (Supplementary Table S2). With this information, we ran an ancestral state reconstruction for each trait using the ‘ace’ function in the ‘ape’ package (Paradis et al., 2004).

Discrete Trait Modelling

We investigated the evolutionary timeline that describes the relationship between woodpecker brain size and feeding behaviour with discrete trait modelling and transition rate analysis in BayesTraits version 3 (Pagel, 1994; Pagel et al., 2004; Pagel & Meade, 2006). First, we tested for coevolution between the traits using a maximum likelihood framework. We used the ‘Discrete: Independent’ function to fit a null model, which assumes that two traits are evolving in an independent fashion (in other words, transition rates between states for one trait are unaffected by the state of the other). The alternative model was fitted in the ‘Discrete: Dependent’ module. This model adopts different transition rates for each trait depending on the state of the second trait; therefore, in this model, we have up to eight different transition rates (versus four transition rates in the independent model). We fitted additional models in this continuous line from independency to full dependency by testing intermediate models of correlated evolution. For these series of alternative models, we allowed one transition rate (gain or loss in a trait) to adopt a different value given that the other trait was present or absent. We then tested whether each alternative model (correlated evolution) was better at explaining our data than the null model (independent evolution) using a likelihood ratio test. This test uses a chi-square distribution with degrees of freedom equal to the difference in the number of parameters between the two models.

After testing for coevolution between traits, we assessed the magnitude and direction of these relationships through time. Accordingly, we used reversible-jump Markov chain Monte Carlo (rjMCMC) to estimate transition rate posteriors from the dependent model of evolution. Reversible-jump analyses estimate the posterior probability of all possible model configurations along with individual parameter values (Pagel & Meade, 2006). This algorithm allows one to assess the strength of evidence that two transition rates are different or not, by comparing the relative sampling frequency of models in which the two transition types were constrained to be zero (Z), the same (1,1 or 0,0) or different (1,0 or 0,1). To conform to the independent model of evolution, the probability of pairs of transition rates must be equal (1,1 or 0,0). By contrast, to conform to the dependent model of evolution, these transition rates must be assigned to different rate classes (1,0 or 0,1) or one of the two must be assigned to the zero bin (Z).

We ran the rjMCMC analysis three times to ensure chain convergence and to assess the consistency of our results using a hyperprior with gamma distribution. Each chain ran for 10 million iterations and after a 100 000-generation burn-in, we concatenated the posterior sample using a thinning interval of 10 000 samples. We validated our inference by checking that the chain moved quickly between models of low and high likelihood and reached a stationary distribution (mean log likelihood: 107.64 ± 1.37; Supplementary Fig. S2). We verified that chains were mixing (acceptance rate ≈0.28), and we then evaluated the posterior distribution and trace of harmonic mean of log likelihoods. We assumed convergence when this distribution was approximately normal and the likelihood traces did not show large jumps across runs. Models visited by the Markov chain were ranked in order of their posterior probability (Supplementary Table S3). For all diagnostic analyses, we used the software Tracer version 1.7.1 (Rambaut et al., 2018).

We visualized these results by plotting the distribution of each rate across the posterior distribution. We also computed posterior rate difference samples ($\Delta q = q_{\text{trait present}} - q_{\text{trait absent}}$); accordingly, $\Delta q > 0$ reflects a higher transition rate when a second trait is present, whereas $\Delta q < 0$ indicates a lower rate when the second trait is absent. We summarized the Δq sample and calculated the posterior percentage difference rate as the proportion of samples where $q_{\text{trait present}} < q_{\text{trait absent}}$.

Discrete trait modelling can be prone to type I error (Pagel, 1994; Pagel & Meade, 2006), in which significant associations between pair of traits are driven by a few independent phylogenetic transitions (Maddison & FitzJohn, 2015). One way to address such phylogenetic pseudoreplication is by visually evaluating the number of independent evolutionary transition coincidences between the traits of interest across a phylogeny (Clark et al., 2018; Fristoe et al., 2017). We found a pattern of coincident origins of brain size and extractive foraging replicated across at least 14 clades (see Results), which is sufficient to provide reasonable confidence that associations from our discrete trait analysis are unlikely spurious or the result of the problematic ‘Darwin's scenario’ or ‘unreplicated bursts’ (Maddison & FitzJohn, 2015).

RESULTS

Brain Size and Behaviour

We found no major differences in body size between woodpeckers that use extractive foraging or extractive nesting versus those that do not (extractive foraging: $F_{1,114} = 5.073$, $P = 0.2178$; nesting: $F_{1,111} = 0.0768$, $P = 0.8911$). However, we find that woodpeckers that use extractive foraging tactics to acquire wood-boring larvae had significantly larger brains compared to species that use other foraging tactics ($F_{2,114} = 176.3$, $P = 0.005$, $\lambda = 1$; Fig. 1a). Importantly, even though the relationship between brain size and cranium size was linear, positive and significant ($t_{94} = 21.094$, $R^2 = 0.823$, $P < 0.001$), the effect of extractive foraging did not extend to measures of cranium size (head size) ($F_{1,95} = 1.94$, $P = 0.166$, $\lambda = 0.99$; Fig. 1b) or rostrum length ($F_{1,95} = 0.016$, $P = 0.8982$, $\lambda = 0.93$; Fig. 1c). In a second analysis of these data, we ran PGLS models to test scaling relationships between each of our response variables and body size, while including foraging behaviour as a covariate. As expected, we found a significant positive correlation between body size and all response variables (brain size: $F_{2,113} = 17.21$, $P < 0.001$; cranium size: $F_{2,91} = 21.75$, $P < 0.001$; rostrum size: $F_{2,91} = 20.43$, $P < 0.001$; Fig. 1d, e, f). Importantly, for the model in which our response variable was brain size, we found that extractive foragers had a significantly higher intercept than nonextractive foragers ($F_{2,113} = 2.97$, $P = 0.0035$; Fig. 1d, Supplementary Table S4), yet the slopes of the scaling relationship between these two groups were statistically indistinguishable from each other ($F_{2,113} = 1.439$, $P = 0.232$; Fig. 1d). We did not see any differences in the intercept values between extractive and nonextractive foragers in the context of cranium size

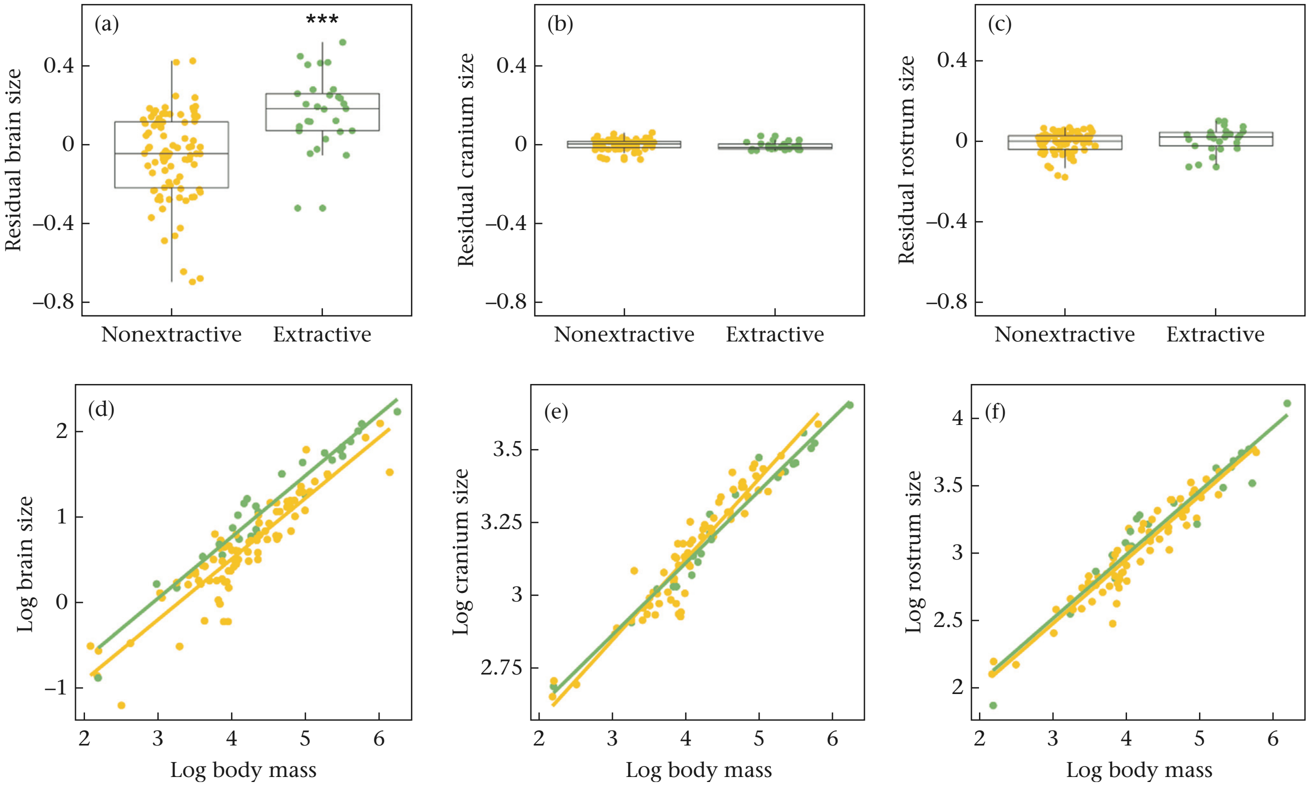

Figure 1. Box plots of residual (a) brain, (b) cranium and (c) rostrum size and foraging behaviour. Foraging behaviour was binarized (see Methods) into nonextractive/extractive categories, while residuals for dependent variables were obtained via phylogenetic regression analyses with body mass (see Methods). Lower and upper hinges correspond to the first and third quartiles (25th and 75th percentiles); middle lines represent median values, whereas upper/lower whiskers extend to the largest/lowest value 1.5× interquartile range. Asterisks denote significance in phylogenetic generalized least squares (PGLS) models ($P < 0.001$). (d, e, f) Relationship between morphological traits and body mass using foraging as a covariate. For the statistics, please refer to Supplementary Tables S1–S3. Yellow represents nonextractive species; green represents extractive species.

($F_{2,91} = 0.886$, $P = 0.377$) or rostrum size ($F_{2,91} = -0.179$, $P = 0.857$) (Fig. 1e, f, Supplementary Tables S5–S6).

We found no evidence of an association between species' nest excavation behaviour and brain size ($F_{1,108} = 1.77$, $P = 0.186$, $\lambda = 1$; Fig. 2a), cranium size ($F_{1,93} = 0.86$, $P = 0.355$, $\lambda = 0.98$; Fig. 2b) or rostrum size ($F_{1,93} = 0.012$, $P = 0.912$, $\lambda = 0.94$; Fig. 2c). Similarly, when we tested the scaling relationship between brain size and body size with nesting behaviour as a covariate, we found a significant positive relationship between these variables (brain size: $F_{2,107} = 17.95$, $P < 0.001$; cranium size: $F_{2,89} = 22.38$, $P<0.001$; rostrum size: $F_{2,89} = 20.76$, $P < 0.001$; Fig. 2d, e, f). Yet, our models also revealed no difference in the intercept values between species that excavate nests and species that do not (brain: $F_{2,107} = 1.264$, $P = 0.208$; cranium: $F_{2,89} = -0.805$, $P = 0.422$; rostrum: $F_{2,89} = -1.171$, $P = 0.244$; Fig. 2d, e, f, Supplementary Tables S7–S9). Our results therefore align with our initial predictions that correlated evolution occurs exclusively between woodpecker brain size and extractive foraging behaviour.

Finally, we found no evidence of an association between brain size and any of the life history variables we analysed, including: clutch size ($F_{2,89} = 134.5$, $P = 0.2593$, $\lambda = 0.845$), incubation period ($F_{2,48} = 102.9$, $P = 0.3061$, $\lambda = 0.99$), fledging age ($F_{2,46} = 107.3$, $P = 0.07175$, $\lambda = 1$) and migratory behaviour ($F_{2,116} = 129.5$, $P = 0.5529$, $\lambda = 0.9$).

Ancestral State Reconstruction

Our ancestral state reconstruction of relative brain size and extractive foraging behaviour maps out the possible tempo in which these traits likely diversified (Fig. 3). The most ancestral node of the Picidae phylogeny, comprising the wrynecks (*Jynx* sp., subfamily Jynginae), likely had a relatively small brain (probability: >0.80). In the piculets (Picumninae), species exhibit a mixed pattern with high probabilities for both small and large brain sizes scattered across the clade. However, the common ancestor of 'true woodpeckers' (Picinae) likely had a large brain (probability: ≈96%) that was retained by many clades that arose thereafter (probability: >0.90). Despite the relatively large brain of the ancestor of all Picinae, we found several independent transitions to small brains within extant lineages of the true woodpeckers (e.g. Melanerpini, Pici; Fig. 3).

As expected, based on the behaviour and ecology of the wrynecks (del Hoyo et al., 2002), extractive foraging was likely absent at the base of the Picidae, and thus gained by more recent ancestors of the lineage (Picinae probability: ≈0.69). Notably, extractive foraging was subsequently lost at the base of the Picini tribe, likely evolving independently in both *Dryocopus* and *Colaptes*. Conversely, an extractive foraging strategy was retained in the Campephilini and Melanerpini tribes, and then lost in the ancestors of the genera *Sphyrapicus* and *Melanerpes* (Fig. 3). From these ancestral state reconstructions, both traits show evidence of repeated gains and losses, as opposed to existing in a state of evolutionary stasis. Lastly, our results suggest a coincident origin of extractive foraging in the lineages that retained a large brain.

Correlated Evolution

Building on our ancestral state reconstructions, we next used discrete trait modelling to test for evidence of correlated

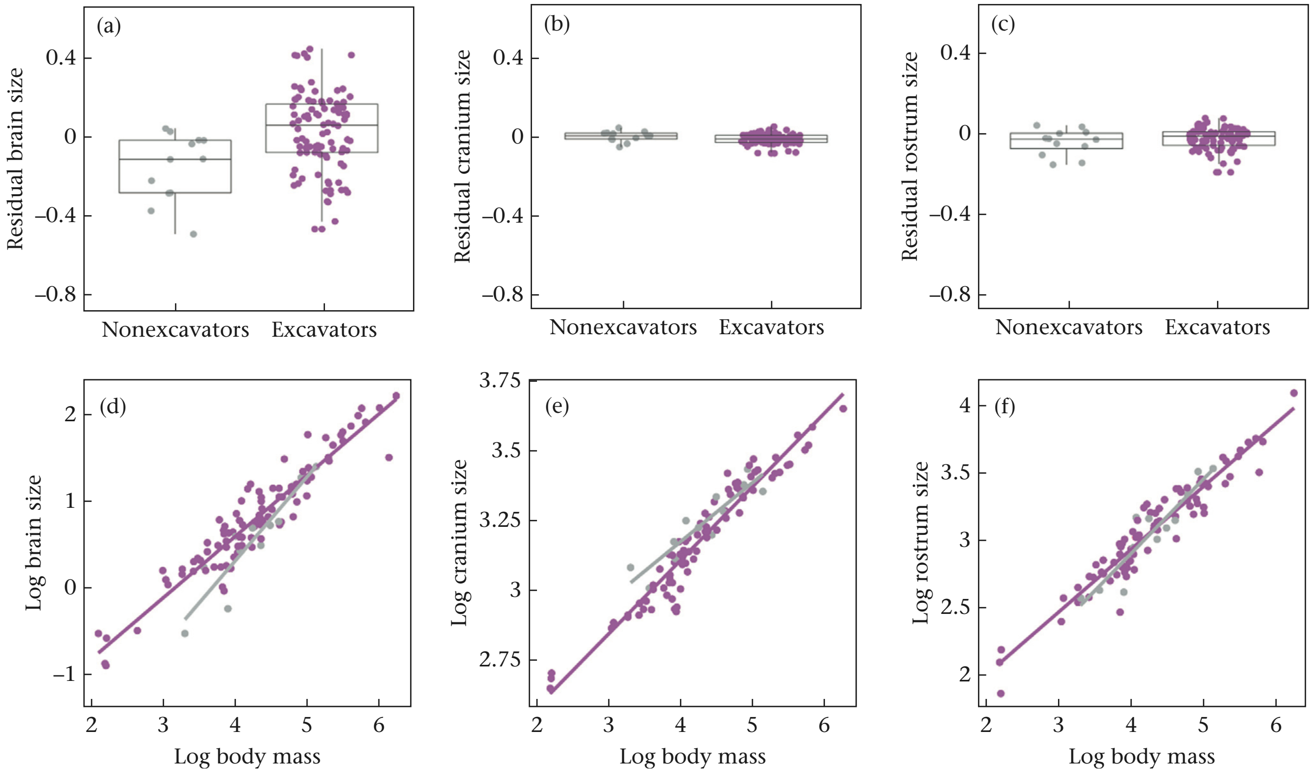

Figure 2. Box plots of residual (a) brain, (b) cranium and (c) rostrum size and nesting behaviour. Nesting behaviour was binarized by assigning species to nonexcavator/excavator category depending on whether they excavate their own nesting cavity. Residuals for each dependent variable were obtained by running a phylogenetic regression analysis with body mass. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles), the middle line represents the median and the upper/lower whiskers extend from the hinge to the largest/lowest value 1.5 × interquartile range (IQR) from the hinge (where IQR is the distance between the first and third quartiles). Relationship between body mass and (d) brain size, (e) cranium size and (f) rostrum size using nesting as a covariate. For the statistics, please refer to Supplementary Tables S6–S8. Grey represents nonexcavator species; purple represents excavator species.

coevolution between relative brain size and extractive foraging. A model where these two traits evolved in a fully dependent manner gained higher support than models in which each trait evolved independently ($\mathrm{LL}_{\mathrm{D(dependent)}} = -96.12$, $\mathrm{LL}_{\mathrm{I(independent)}} = -101.77$; $\mathrm{LRT} = 11.29$, $df = 4$, $P < 0.05$). The probability of evolving (or losing) extractive foraging behaviour to feed on wood-boring larvae was therefore correlated with a species' relative brain size.

To explore this coevolution more thoroughly, we estimated the stepwise evolution that brain size and foraging behaviour likely followed (i.e. order in which the traits were gained/lost). In our analysis of the distribution of the rjMCMC posterior sample, we found a total of 312 models visited by the chain, with 10 models accounting for 90% of the samples obtained (Supplementary Table S3). Therefore, by analysing the most visited models by the MCMC, we could look at a representative sample of the most probable pathway of evolution. Among this group, we found that most (>99%) had at least one transition rate for which the mean posterior distribution peaked at zero, suggesting that the given transition rate had a low probability of occurrence (Supplementary Table S3). Transition rates associated with the emergence of extractive foraging behaviour in species with a small brain are a perfect example because the rate of gain was itself indistinguishable from zero (0) (Fig. 4a). This result makes sense in the context of our ancestral state reconstructions, where it is clear that ≈one species of the Picumninae subfamily (out of 119 total species analysed) has a small brain and is an extractive forager (Fig. 3).

The model with the highest visits in the MCMC showed that the transition rate from nonextractive to extractive foraging was always higher when a big brain was retained, rather than when a species transitioned to a small brain ($\Delta q = -0.386$, 97.7% of the iterations) (Table 1, Fig. 4a). Additionally, the probability of losing extractive foraging behaviour was more likely when a big brain was retained, compared to when a small brain was retained ($\Delta q = -0.096$) (Table 1, Fig. 4b). Again, this effect was largely expected because the probability of gaining extractive foraging with a small brain was almost zero (98% of the iterations, see above). In stark contrast, transitions in brain size were independent of feeding behaviour, such that there were not differences in the probability of gaining ($\Delta q = 0.056$) or losing ($\Delta q = 0.023$) a big brain in the presence or absence of extractive feeding (Table 1, Fig. 4c, d). Together these results support a coevolutionary dependency between brain size and foraging, such that extractive foraging depends on relative brain size, but not the other way around (see a likely evolutionary pathway in Fig. 4e).

DISCUSSION

The evolution of foraging behaviour largely depends on two features: (1) traits (morphological and/or physiological) that support food acquisition and (2) neural systems that support prey capture and foraging. Most of our knowledge about mechanisms of foraging and its evolution come from the former category (Navalón et al., 2019; Santana et al., 2012), whereas substantially less is

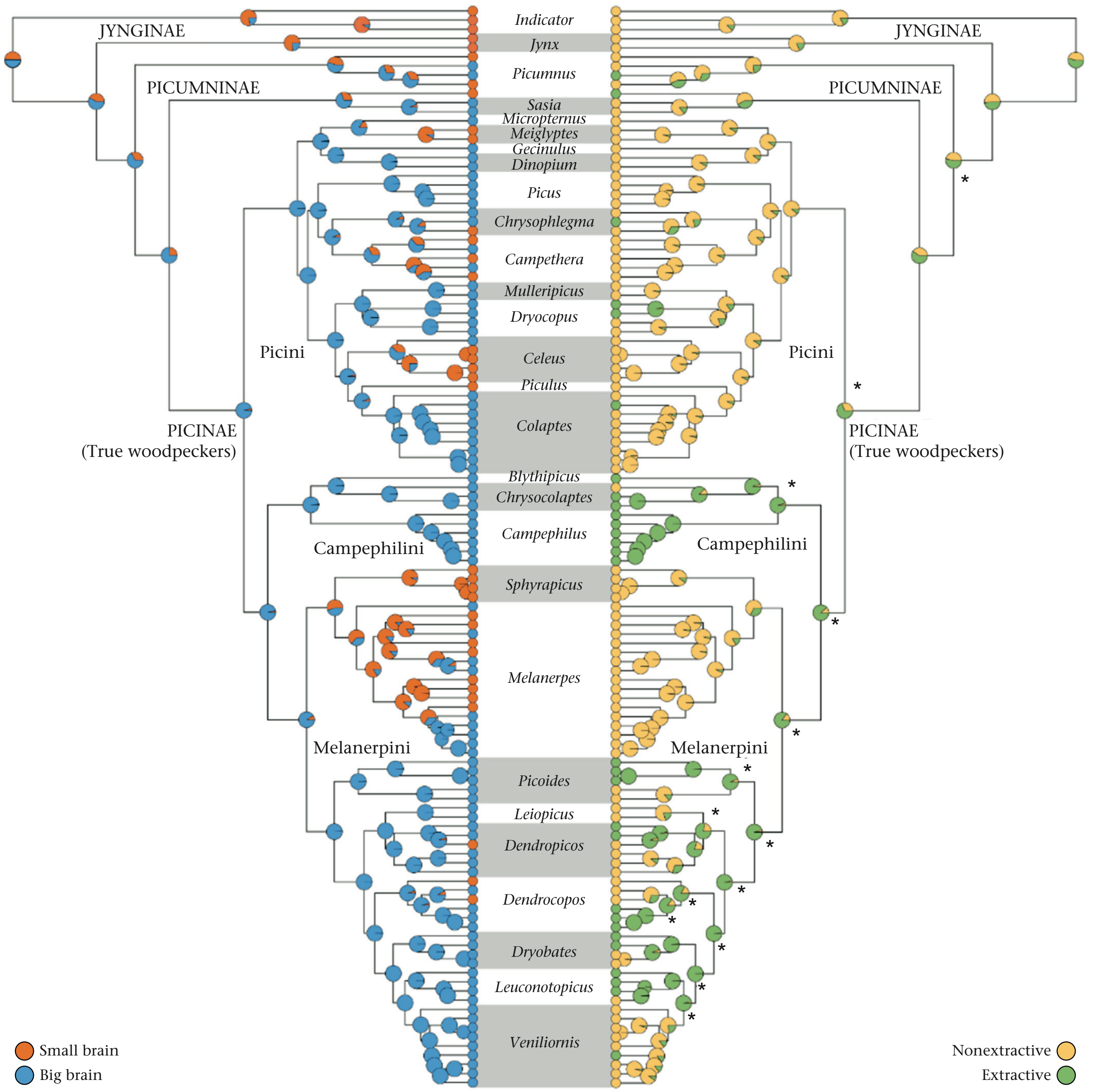

Figure 3. Ancestral state reconstruction of brain size (left) and extractive foraging strategy (right) in woodpeckers. Names in all capital letters represent subfamilies and names with initial capital letters represent tribes in the ancestral nodes. Genera are described at the tips (in italic). Pies at ancestral nodes represents probabilities of each state for the given trait. Asterisks in ancestral nodes of foraging behaviour depict clades with co-distribution of traits (big brain was retained and extractive foraging strategy was acquired). Note that big brain and nonextractive foraging behaviour are the likely ancestral states for true woodpeckers (Picidae).

understood about how the brain evolves alongside novel foraging skills. In woodpeckers, we show that evolution of extractive foraging behaviour is correlated with relatively larger brains. Further analyses that map out how these two traits emerge reveal that ancestors of contemporary woodpeckers likely had large brains, while the retention of this trait appears to precede the emergence of extractive foraging. At the same time, our results suggest that extractive foraging is unlikely to arise in lineages that have transitioned to a small brain. Brain size evolution therefore seems to guide the process of behavioural innovation by creating opportunities for phenotypic change, or by cutting off such opportunities altogether.

Evidence for the Extractive Foraging Hypothesis

Our data provide strong support for the extractive foraging hypothesis. First, we found a positive association between relative brain size and extractive foraging across the entire woodpecker clade. Meanwhile, we found no association between extractive foraging behaviour and cranium size or rostrum size. Had we

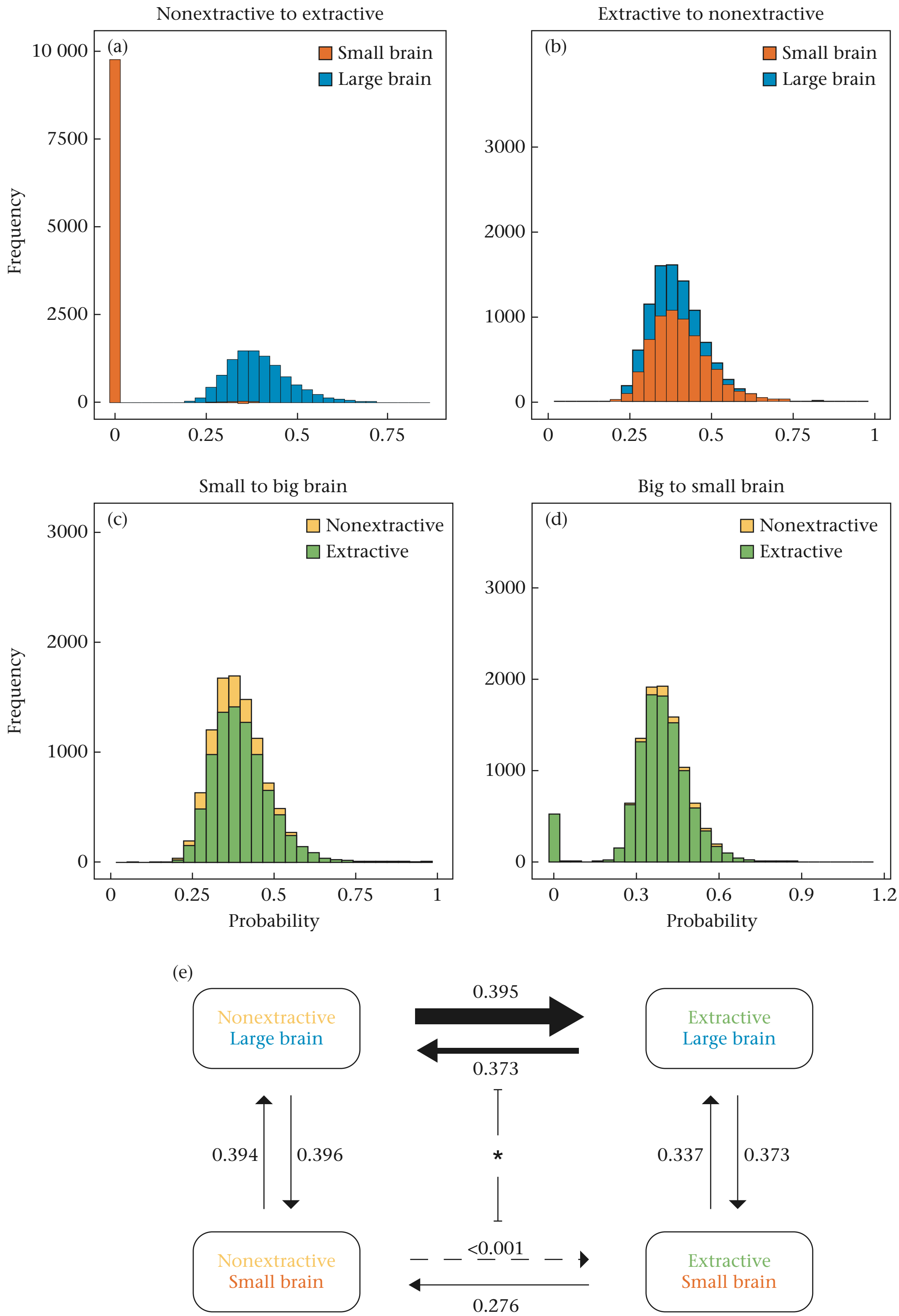

Figure 4. Posterior distribution probabilities of transition rates obtained from discrete trait modelling using rjMCMC, with different transition scenarios depicted in (a)–(d) (see Methods for details). (e) Proposed evolutionary pathway for brain size and extractive foraging. Arrows represent the direction of the transition rate probabilities (based on the posterior distributions, see (a)–(d)). With arrow thickness reflecting transition rate difference when comparing rates using arrows pointing in the same direction, up–down and left–right. An asterisk denotes a significant difference between transition rates.

Table 1

Statistical summary of discrete trait models evaluating the probabilities of the transition rates between brain size and extractive foraging

Trait	Transition	Log likelihood$_{\text{(null hypothesis)}}$	Log likelihood$_{\text{(alternative hypothesis)}}$	LRT	*P*	rjMCMC rate comparison	Δq (%)
Brain	$0\rightarrow1$	−108.412	−104.507	7.809	0.003	*q*12/*q*34	0.056 (1.07)
Brain	$1\rightarrow0$	−108.412	−104.498	7.827	0.003	*q*21/*q*43	0.023 (0.14)
Extractive foraging	$0\rightarrow1$	−108.412	−104.635	7.554	0.003	*q*13/***q*24**	**−0.386 (97.75)**
Extractive foraging	$1\rightarrow0$	−108.412	−102.304	12.215	0.000	*q*31/*q*42	−0.096 (34.09)

LRT: likelihood ratio test; rjMCMC: reversible-jump Markov chain Monte Carlo. Bold denotes the only transition rate comparison that had a high percentage difference in the posterior distribution. $\Delta q > 0$ reflects a higher transition rate when a second trait was present, whereas $\Delta q < 0$ indicates a lower rate when the second trait was absent. The posterior percentage difference rate is calculated as the proportion of samples where $q_{\text{trait present}} < q_{\text{trait absent}}$.

uncovered a significant effect for either of these two variables, then our data would have suggested that selection for extractive foraging was associated with not only a larger brain (as measured by endocranial cavity), but also a broader evolutionary increase in skull and/or rostrum size (Marroig & Cheverud, 2005; Santana et al., 2012). Rather, our results collectively suggest that extractive foraging is more likely to depend on the evolution of relatively larger brains, while skull and rostrum size remain more similar among taxa, at least with respect to how they scale to body size. Other factors that can be related to the evolution of the cranium and rostrum size are the eye size and the head and jaw musculature (Brooke et al., 1999; Lowie et al., 2022).

We also found no relationship between brain size and the nest excavation strategy, which we would have expected if selection for drilling behaviour depended on relative brain size. This logic is predicated on evidence that nest excavation requires significant amounts of drilling into trees, potentially even more than foraging. Thus, a big brain does not appear to confer an ability to vigorously or violently drill, but instead likely facilitates extractive foraging by providing the necessary sensorimotor abilities and/or cognitive skills that are required to obtain food embedded into woody substrates (Gibson, 1986; Parker & Gibson, 1977). Functionally, this idea makes sense for several reasons: (1) woodpeckers likely need extensive motor and sensorimotor machinery to control complex bill movements and the barbed and extensible tongue they use for extractive feeding (Villard & Cuisin, 2004); (2) woodpeckers might rely on some degree of tactile and auditory systems to detect prey embedded underneath the bark of a tree (Sterling & McCreless, 2007); (3) there might be important learning components that underlie the woodpeckers' ability to successfully extract food (Gajdon & Winkler, 2015). This last point is especially important, with birds potentially needing to discover how to recognize trees that contain abundant wood-boring larvae, as well as how to find these larvae. Indeed, the food extraction process could vary depending on tree type, prey type and/or season.

The association we report between large brain size and extractive foraging is also consistent with current thinking about the energetics of brain size. Eating wood-boring larvae or other wood-boring insects likely offsets the high metabolic demand of maintaining an especially large brain relative to body size (Rutz et al., 2010). These ‘costs’ are not trivial, as neural tissue is one of the most metabolically expensive tissues in the body (Aiello & Wheeler, 1995; Isler & van Schaik, 2006). Thus, if having a big brain is adaptive, then selection should also concomitantly evolve appropriate supportive strategies (otherwise selection would presumably favour a smaller brain). Because larval prey items have ≈23–66% protein content (Kouřimská & Adámková, 2016) and ≈40% lipid content, they likely make an ideal food source that is available year-round to help fuel a larger brain.

Finally, our data add to the ongoing discussion on the correlated evolution of brain size and diet in vertebrates. Past work suggests that larger brains may be related to a species' ability to consume a wider variety of food items because the ability to locate and process such foods is presumably greater for generalists than nongeneralists (Harvey & Krebs, 1990). Although Overington et al. (2011) found no relationship between brain size and diet generalism in birds, subsequent studies using larger data sets support previous findings: dietary generalism, or a broader diet, is associated with relative larger brains (Ducatez et al., 2015; Sayol et al., 2016). To some extent, we observed the opposite effect in our analyses, as generalist woodpeckers were classified as nonextractive foragers and had smaller brains. We did not analyse diet specifically and cannot rule out the possibility that generalism and brain size are correlated in woodpeckers. That said, we also stress that the occurrence of broad patterns across all species does not mean the same pattern applies within individual clades. For example, environmental variation is positively associated with relative brain size across all birds but not within all avian orders (Sayol et al., 2016). The correlation between dietary generalism and brain size may exhibit similar variability. Looking at the relationship between diet and brain size in other taxa like primates, also suggests that this relationship is complex, with some studies finding a direct link between these variables (Chambers et al., 2021; Decasien et al., 2017) and other studies finding that such a relationship may be explained by alternative factors (Powell et al., 2017). Therefore, additional work will be needed to investigate how diet and brain size are associated with each other.

Stepwise Evolution of Brain Size and Extractive Foraging

Equally important is that we show a putative evolutionary order of changes that explain the extractive foraging hypothesis. Our ancestral state reconstructions, for instance, suggest that large brains were the most likely ancestral phenotype of true woodpeckers (Picinae, Fig. 3), and thus extant species with large brain likely retained this trait throughout time. In this way, we might think of the large brains of woodpeckers as an example of an evolutionarily static trait that is conserved and only changes in response to major shifts in selective regime (Burt, 2001). This point is clarified by looking at woodpecker species that transitioned to smaller brains, an evolutionary change that coincides with behaviours unrelated to extractive foraging. For example, several *Melanerpes* woodpeckers have smaller brains and socially organize into large, long-lasting groups (Fedorova et al., 2017). Sociality may provide benefits of cooperation without the competitive social elements, potentially resulting in decreased computational processing requirements and a smaller brain (Dunbar, 1998; Shultz et al., 2011). Other species in which natural histories could have influenced how brain size evolves include wrynecks (*Jynx*) and sapsuckers (*Sphyrapicus*). Some of these species are migratory (del Hoyo et al., 2002) and, similar to other migratory species, have small brains that may be attributed to the energetic and developmental costs associated with a highly mobile life cycle (Sol et al., 2010; Winkler et al., 2004).

In contrast to brain size, extractive foraging behaviour has likely been gained more recently several times across the woodpecker phylogeny, occurring in the Picumninae and Picinae subfamilies but then disappearing in several genera within the Picini and Melanerpini tribes (Fig. 3). This pattern reveals the evolutionary lability of foraging behaviour, much like we see in primates (Reader et al., 2011), as well as the propensity for behavioural change favoured by an enlarged brain. We also found evidence in the phylogeny that extractive foraging in extant species arose where a large brain was retained (Fig. 3). This finding was confirmed by our discrete trait modelling, which showed that an extractive diet was more likely to be gained (or lost) in species that retained a big brain. By contrast, for species that transitioned to a small brain, the probability of gaining extractive foraging behaviour was mostly zero (Fig. 4). Taken together, these data therefore suggest that an enlarged brain favours evolutionary innovations in foraging behaviour, such as the extractive foraging strategy used to find larvae embedded within trees. In this way, we might think of brain size evolution in woodpeckers not as a result of behavioural drive, but instead a prerequisite for emergence of behavioural innovation (Mayr, 1974).

Procedural Constraint as an Effect on How Behavioural Evolution Unfolds

Finally, our study reveals how historical contingencies associated with organismal design might fundamentally impact how behavioural repertoires evolve in the future. For example, we found that many of the deepest nodes within the woodpecker phylogeny were characterized as likely to represent species that had large brains but did not necessarily rely on extractive foraging to feed. This result suggests that the origin of the large woodpecker brain was probably not linked to foraging behaviour. Indeed, the factors that explain where this large brain comes from in this clade suggest that it corresponds to a general reduction in body size of the first woodpecker species to emerge (Ksepka et al., 2020); however, it might be the case that large brains emerged through a complex suite of selective forces that have since dissipated (Gould & Lewontin, 1979; Gould & Vrba, 1982). Regardless of these considerations, our data do still help show how past evolution of the organismal form can potentially create a landscape that promotes (or extinguishes) future opportunities for the diversification of the behavioural repertoire (Blount et al., 2018).

Others have similarly pointed to the effects of such ‘procedural constraint’ on behavioural design, highlighting the idea that certain traits can arise through a canalized order of operations that may or may not depend on morphological and physiological variables (Miles et al., 2020). Such procedural constraint has even been alluded to in the context of extractive foraging in New Caledonian crows, *Corvus moneduloides* (Cnotka et al., 2008; Rutz et al., 2010), striped possums, *Dactylopsila trivirgata* (Rawlins & Handasyde, 2002), and aye-ayes, *Daubentonia madagascariensis* (Sterling & McCreless, 2007; Sterling & Povinelli, 1999). Contingencies and the way they affect how new traits arise is an important part of understanding the adaptation and diversification of behavioural traits in the natural world. This is especially true with respect to neurobiological design and our general efforts to understand how the brain influences the organic evolution of animal systems.

Author Contributions

M.J.F. and G.C.P. designed the study, G.C.P. collected data and performed the analyses, A.I. provided guidance in the method to collect brain size data, G.C.P. and M.J.F. wrote the manuscript and all authors contributed substantially to revisions.

Data Availability

The raw morphological and behavioural data supporting the results are provided as Supplementary material.

Declaration of Interest

None.

Acknowledgments

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2023.02.003.

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