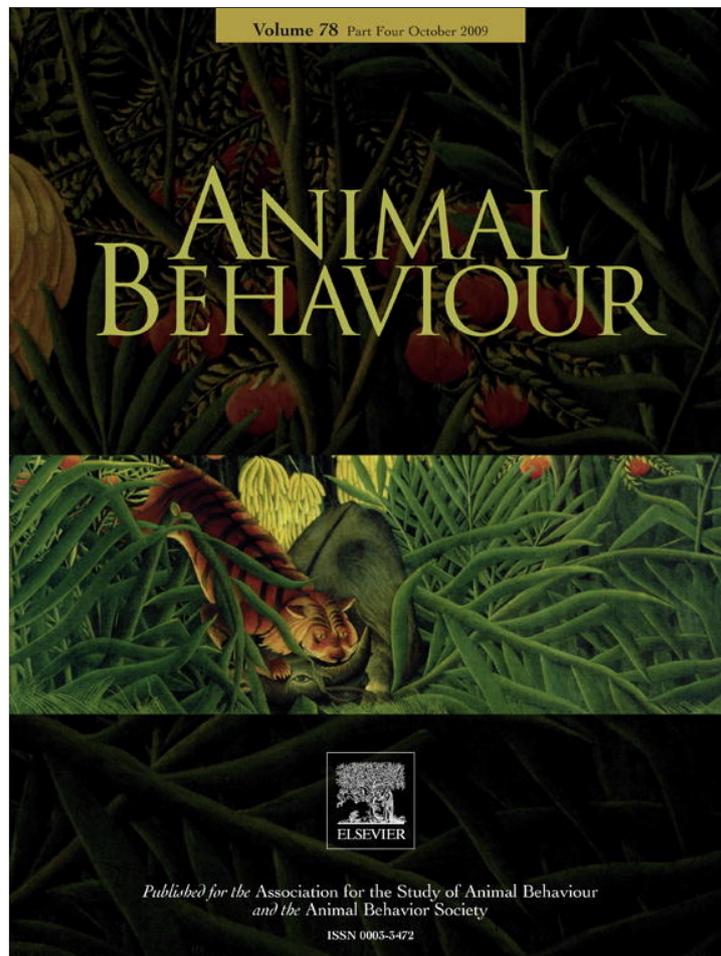


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Technical innovations drive the relationship between innovativeness and residual brain size in birds

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The hypothesis that large brains allow animals to produce novel behaviour patterns is supported by the correlation between brain size, corrected for body size, and the frequency of foraging innovations reported in the literature for both birds and primates. In birds, foraging innovations have been observed in over 800 species, and include behaviours that range from eating a novel food to using tools. Previous comparative studies have quantified innovativeness by summing all reports of innovative behaviour, regardless of the nature of the innovation. Here, we use the variety of foraging innovations recorded for birds to see which of two classic hypotheses best accounts for the relationship between innovativeness and brain size: the technical intelligence hypothesis or the opportunistic-generalism intelligence hypothesis. We classified 2182 innovation cases into 12 categories to quantify the diversity of innovations performed by each of 76 avian families. We found that families with larger brains had a greater repertoire of innovations, and that innovation diversity was a stronger predictor of residual brain size than was total number of innovations. Furthermore, the diversity of technical innovations displayed by bird families was a much better predictor of residual brain size than was the number of food type innovations, providing support for the technical intelligence hypothesis. Our results suggest that the cognitive capacity required to perform a wide variety of novel foraging techniques underpins the positive relationship between innovativeness and brain size in birds. We include a summary of innovation data for 803 species as [Supplementary Material](#).

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Some species have much larger brains than would be expected given their body size (e.g. *Corvus moneduloides*; Cnotka et al. 2008), while others have much smaller ones (e.g. *Colinus virginianus*; Striedter & Charvet 2008). Various researchers have suggested that large brains have been naturally selected because they increase an individual's capacity to process information about social companions (Dunbar 1998), prey that are numerous or difficult to track in space and time (Eisenberg & Wilson 1978), prey that are difficult to catch and handle (Milton 1988), or variable environmental conditions (Schuck-Paim et al. 2008). It has also been suggested that increased brain size allows for a larger behavioural repertoire (Changizi 2003), or one that is more flexible (Ratcliffe et al. 2006) or technically complex (Lefebvre et al. 2002). Enlarged brains might even be sexually selected if they enhance an animal's capacity to produce elaborate mate choice cues, such as bowers (Madden 2001),

or if courting signals such as song correlate positively with learning abilities in other domains (DeVoogd 2004; Boogert et al. 2008).

The presumed advantages provided by the ability to invent novel behavioural solutions have been suggested as an evolutionary force driving encephalization (Lefebvre et al. 2004, 2006; Lefebvre & Sol 2008). One approach that has proven useful in obtaining an operational measure of innovativeness is the systematic collection of field notes of previously unreported feeding behaviours. There is a strong tradition of such reports in ornithology, with entire sections of major journals (e.g. the 'behaviour notes' section of *British Birds*) being devoted to them. Since 1997, thousands of such reports (termed 'innovations': Wyles et al. 1983; Kummer & Goodall 1985) have been collated in birds (Lefebvre et al. 1997) and primates (Reader & Laland 2002), yielding robust taxonomic differences that are correlated with residual brain size. However, little is known about the psychological processes underlying innovation (Clayton 2004), and the factors underlying the relationship between innovation and brain size are unclear (Lefebvre & Bolhuis 2003; Healy & Rowe 2007).

Here, we examine the relationship between innovation and brain size in the context of two classical hypotheses on the evolution of cognition: the technical intelligence hypothesis, which proposes that the cognitive demands of technical skills such as tool use

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underlie the evolution of increased brain size (Parker & Gibson 1977; Byrne 1997; Huber & Gajdon 2006), and the opportunistic-generalist hypothesis, which suggests that a generalist lifestyle, especially in the feeding domain, should favour an enhanced learning capacity (Daly et al. 1982; Domjan & Galef 1983; Schuck-Paim et al. 2008). Both of these hypotheses emphasize the relationship between ecological challenges and changes in brain size across taxa. We attempted to disentangle these hypotheses by assigning 2182 reports of innovative behaviour (collected from a variety of ornithological journals; see *Methods*) to one of 12 categories depending on the type of novel feeding behaviour shown. We then examined the total diversity of innovative behaviour for 76 avian families. We further examined the number and diversity of technical innovations and the number and diversity of food type innovations, and we tested the relative contribution of each of these types of innovation in explaining differences in brain size between avian families.

Adaptive correlates of size differences in the brain have been identified at two anatomical levels (summary and critical review in: Healy & Rowe 2007): specialized local centres (e.g. HVC for song; DeVogd et al. 1993; hippocampus for spatial memory; Sherry et al. 1989; Lucas et al. 2004) and broad areas controlling multiple processes (e.g. mammalian cortex, avian pallium and insect mushroom bodies; Timmermans et al. 2000; Reader & Laland 2002; Farris & Roberts 2005; Perez-Barberia et al. 2007; telencephalon: DeVogd 2004; whole brain: Sol et al. 2005, 2007; Ratcliffe et al. 2006). Given that we tested evolutionary predictions for a behaviour (innovation) that is by definition unspecialized and part of domain-general cognition (Chiappe & MacDonald 2005), we focus here on the broad level of the whole brain. Many of the assumptions required for evolutionary tests have recently been verified at these broad neuroanatomical levels: differences in the whole brain and telencephalon size are heritable (Bartley et al. 1997; Airey et al. 2000), they are associated with differences in survival (Sol et al. 2005, 2007, 2008) and they closely reflect differences in total neuron numbers (Herculano-Houzel et al. 2006, 2007). Genes affecting multiple neural networks (Green et al. 2009) and whole brain size (Evans et al. 2005; Mekel-Bobrov et al. 2005) as well as developmental schedules of embryonic neurogenesis leading to differences in the whole telencephalon (Striedter & Charvet 2008, 2009) and cortex (Chenn & Walsh 2002) have been identified. Variation in innovation rate is positively correlated with variation in tool use, reversal learning speed and, in primates, social learning (Lefebvre et al. 2004), empirically supporting Chiappe & MacDonald's (2005) logical argument that innovativeness is part of domain-general intelligence. Imaging studies reveal distributed networks of centres in many parts of the brain that are active during tasks such as tool use (Obayashi et al. 2001; Lewis 2006), reversal learning (Watanabe 2001; Cools et al. 2002) and measures of fluid intelligence (and genetic polymorphism: Bishop et al. 2008). Finally, in birds and primates, taxonomic variance in allometrically corrected whole brain size is mostly driven by changes in higher centres (Rehkämper & Zilles 1991; Rehkämper et al. 2005), suggesting that cognitive processes like innovation and learning have been important in the evolution of encephalization. For example, variance in the residual size of the primate cortex and avian pallium predicts 98% of the variance in residual size of the whole brain (Lefebvre & Sol 2008). For all these reasons, we concentrated on allometrically corrected whole brain size as the most appropriate anatomical level to test our hypotheses.

METHODS

Taxonomic Level of the Study

We focused on variation in innovative behaviour at the family level. Diversification of many avian life-history traits appears to

have occurred prior to the emergence of modern families (Bennett & Owens 2002). This is also the case for brain size, which varies most at the level of the parvorder, a divergence even deeper than the family (Lefebvre et al. 2006). It has been argued that when variance in a trait is greatest among ancient lineages, focusing on more recently diverged clades may conceal important patterns (Owens 2002), and it is therefore useful to test hypotheses at a variety of phylogenetic levels to determine when selective pressures were strongest. Studies of brain size have thus focused on both species-level (Iwaniuk & Nelson 2003; Iwaniuk & Arnold 2004) and family level (Owens 2002; Morand-Ferron et al. 2007; Sol & Price 2008) comparisons, depending on the question at hand. A primary goal of our study was to quantify the diversity of innovative behaviours for each clade. Although our innovation database was large, there are species for which we had only one innovation record. By moving to a higher taxonomic level we had a larger number and variety of innovation records per taxon, which allowed us to make meaningful comparisons between groups.

Classifying the Innovation Database

Our behavioural data were drawn from the innovation database of Lefebvre et al. (1997, 1998). This database currently contains 2182 innovation reports for 803 species in 76 families, compiled from volumes of 64 ornithology journals published between 1944 and 2002. These journals include academic serials (e.g. *Auk*, *British Birds*, *Ibis*, *Emu*) as well publications that are edited by local birding organizations (e.g. *Florida Field Naturalist*, *Nebraska Bird Review*). We excluded from our analyses taxa for which there were no innovation reports. Reports are included in the database if they contain words such as 'novel', 'opportunistic', 'first description', 'not noted before' and 'unusual' (Lefebvre et al. 1997). Although the degree to which the noted behaviour is a departure from the species' repertoire may vary, the strength of this database is that it relies on the knowledge of journal authors and editors. All of the reports, and the claim of novelty they contain, have been subject to peer review. Each innovation report contains information on the location of the observation, the species observed, and other anecdotal details of the event. We classified the innovation reports into 12 categories (Table 1). These categories emerged after extensive reading of the reports in the database by J.M.-F. and S.E.O. To avoid experimenter bias, we based our classifications strictly on the wording used in the report, using the component of the behaviour that was noted as being novel by the author of the original short note. Final classifications (J.M.-F.) were made blind to the identity of the species mentioned in the reports. Intraobserver classification was highly consistent (190 correct classifications out of 201 randomly chosen cases; 94.5%), as was interobserver classification (136 out of 150 randomly chosen cases, 93.3%). A summary of innovations for each species and family in our data set is included as *Supplementary Material*.

To tease apart the technical and opportunistic-generalist hypotheses, we classified all reports as 'technical' or 'food type' innovations. Technical innovations were obtained by lumping cases in categories 4–11: novel technique, novel technique in an anthropogenic context, novel parasitic behaviour, novel commensal behaviour, novel mutualistic behaviour, novel proto-tool behaviour, novel true tool behaviour and novel caching behaviour. These categories refer to reports where the author described the foraging technique itself as novel, regardless of whether the food type was novel or not (e.g. Cetti's warbler, *Cettia cetti*, catching insects in mid-air like a flycatcher; Hill 1993). Food type innovations involved a novel food item, but no departure from the usual foraging techniques of the species (e.g. Wilson's storm-petrels, *Oceanites oceanicus*, feeding on decaying whale fat;

Table 1

Each of the innovation reports from our database was classified into one of the 12 categories as listed below; an example is given for each category

Innovation category	Example	Source
(1) Novel food item: species observed eating a food item that had not previously been recorded in its diet	Killdeer, <i>Charadrius vociferous</i> , preying on live frog	Schardien & Jackson 1982
(2) Novel food item taken in opportunistic manner: as in category (1), but a change in the environment preceding the event was noted	Purple finch, <i>Carpodacus purpureus</i> , feeding on an ant swarm	Harlow 1971
(3) Novel anthropogenic food item	Bonaparte's gull, <i>Larus philadelphia</i> , feeding on walnut meal	Frohling 1967
(4) Novel foraging technique in an urban environment	House sparrow, <i>Passer domesticus</i> , using automatic sensor to open bus station door	Breitwisch & Breitwisch 1991
(5) Novel predatory technique	Northwestern crows, <i>Corvus caurinus</i> , fishing for sandlance by digging in the sand at low tide	Robinette & Ha 1997
(6) Novel parasitic technique	Galapagos mockingbird, <i>Nesomimus parvulus</i> , pecks food from sea lion's mouth	Trimble 1976
(7) Novel commensal foraging	Cattle egret, <i>Bubulcus ibis</i> , feeding in association with a black bear	Smith 1985
(8) Novel mutualistic foraging	Great egret, <i>Ardea alba</i> , using leap-frog prey-flushing technique with Cattle egret, <i>Bubulcus ibis</i>	Wiese & Crawford 1974
(9) Novel proto-tool use*	Herring gull, <i>Larus argentatus</i> , catching small rabbits and killing them by dropping them on rocks or drowning them	Young 1987
(10) Novel true tool use*	Green jays, <i>Cynaocorax yncas</i> , using twigs as probes and levers	Gayou 1982
(11) Novel caching technique	Gila woodpecker, <i>Melanerpes uropygialis</i> , a nonstoring species, stores acorns	MacRoberts & MacRoberts 1985
(12) Unusual habitat or time of day	Lapwings, <i>Vanellus vanellus</i> , feeding in an estuary	Mason & MacDonald 1999

* True tool use included cases where the tool item was held in the bird's bill or feet, and proto-tool use included cases where the tool item was not detached from the substrate, following Parker & Gibson (1977).

Payne et al. 1983). This included categories 1, 2 and 3: novel food item, novel food item taken in an opportunistic manner and novel anthropogenic item.

Innovations in category 12 (unusual habitat or time of day) were excluded from this analysis.

To correct our measures for the fact that more intensely studied species inevitably have more innovation reports, we regressed each of the log-transformed innovation measures against log-transformed research effort. Research effort is defined as the number of scientific papers published on a given taxon according to Zoological Records' web index (1978–2004). This index covers all the types of journals from which our innovation database is collated. There is a strong relationship between the frequency of innovation reports and research effort in our data set ($R^2 = 0.75$). Previous work (Nicolakakis & Lefebvre 2000; Morand-Ferron et al. 2007) has also shown that research effort is highly correlated with species number per taxon and taxonomic distribution of photos in birding magazines ($R^2 = 0.688–0.889$). Because of these correlations, regressing innovation frequency or diversity against research effort also controls for speciosity and differential interest by birdwatchers. We used the Studentized residuals of the innovation-research effort regressions as the predictor variables in the models with residual brain size as the response variable.

Brain Size Information

We had data for brains of 1714 species from 76 families, which comprised both directly measured brain mass and endocranial volumes converted to mass (as described in Mlikovsky 1989a, b, c; 1990; DeVoogd et al. 1993; Székely et al. 1996; Garamszegi et al. 2002; Iwaniuk & Nelson 2002; Iwaniuk 2003; Sol et al. 2005). These data represent mean values of male and female specimens. To remove the allometric effect of body size on brain mass (Bennett & Harvey 1985), we averaged brain volumes and body masses within each family and calculated the residuals from a log–log linear regression of the mean body size and brain size of species for each family. We used the mean brain and body values for each family in our calculation of residual brain size, not the mean of residuals calculated on each species' brain and body, because some families were more speciose than others, and this could bias the slope of the regression line.

To confirm that our results were not due to error introduced by combining data from multiple sources (Healy & Rowe 2007), we repeated all of our analyses using a subset of the data taken from a single source collected by the same individual using the same method, measurement of endocranial volume (Iwaniuk 2003). Brain size measures obtained with this method yielded 0.99 correlations with data on fresh brains (Iwaniuk & Nelson 2002) and were not influenced by potential errors related to freezing, dessication or perfusion that can affect fresh brains (Healy & Rowe 2007). Conclusions were identical whether we used the restricted endocast data (1197 species) or the larger data set (1714 species). To use the broadest possible sample of species and families, we present results only from our larger data set.

Phylogenetic Information

Our models did not always reveal a strong phylogenetic signal. When this occurs, there is ongoing debate as to whether phylogenetic correction may actually render analyses too conservative and lead to type II error (Kunin 2008). Indeed, when we performed analyses without phylogenetic corrections, effect sizes were much larger. Nevertheless, we took evolutionary history into account by constructing a phylogenetic tree in Mesquite (Maddison & Maddison 2009) for the 76 families in our study using the branch lengths based on DNA–DNA hybridization in Sibley & Ahlquist (1990). The phylogenetic hypothesis of Sibley & Ahlquist continues to be used in comparative studies of birds because it provides the most complete tree available in which a single technique is used to determine the relationships between species. However, more recent studies (Barker et al. 2004; Davis 2008; Hackett et al. 2008) suggest that some of the higher-level relationships presented in Sibley & Ahlquist may not be robust. On the other hand, these studies did not provide enough information to reliably place all of the species and families in our data set. We therefore modified our phylogenetic hypothesis based on several major changes suggested by the phylogenomic study of bird groups by Hackett et al. (2008): placement of Psittaciformes as a sister group to Passeriformes; Falconidae as sister to these two, and Piciformes nested within Ciconiiformes. We repeated all of our analyses using this modified tree (with proportional branch lengths) to reflect these changes; our conclusions were again identical when we used the Sibley &

Ahlquist phylogeny and the one that incorporated the recent changes suggested by Hackett et al (2008). Our results were unchanged when we repeated our analyses with this revised phylogeny, consistent with the fact that the phylogenetic signal in the data was weak. We therefore report only the analyses based on Sibley & Ahlquist (1990).

Confounding Variables

We included several variables that may confound the relationship between innovation and brain size. Juvenile development mode is strongly associated with brain size, with altricial species having relatively larger brains than precocial species (Iwaniuk & Nelson 2003). We also included habitat and diet generalism, which could influence the number and diversity of innovations recorded for a family. We took these measures from Bennett & Owens (2002), where habitat generalism was quantified using a three-category scale, with higher numbers indicating a greater diversity of breeding habitats used. The feeding generalism scale was the opposite, with higher numbers indicating greater specialization. Juvenile development was recorded as precocial, semiprecocial, semialtricial or altricial. Family level values were calculated using the mode of all species within the family for which relevant data were available (see Owens et al. 1999; Bennett & Owens 2002).

Statistical Analyses

We used phylogenetic generalized least squares (PGLS) to estimate the strength of the phylogenetic signal (λ) in the data from the 76 bird families in our database. Lambda may vary from 0 (phylogenetic independence) to 1 (traits evolve according to Brownian motion on the given phylogeny; Freckleton et al. 2002). PGLS fits a statistical model to the data using generalized least squares, while altering the covariance structure of the error terms to reflect the phylogenetic distance between families. We ran all models in R 2.8.1 (R Development Core Team 2008), using the Analysis of Phylogenetics and Evolution (APE) package (Paradis et al. 2004) and codes kindly provided by R. Freckleton and R. P. Duncan. We checked the diagnostic plots of each model for curvature, non-normality of errors, heteroscedasticity and outliers (Crawley 2007).

In each of our PGLS models, we treated residual brain size (corrected for body size) as the response variable, and innovation rate (corrected for research effort; see below) as the predictor variable. We used this model structure to facilitate comparison between model fits, not to imply causality. In comparing models, we examined (1) the total amount of variance in brain size explained by the model (R^2); (2) the significance of each innovation measure as a predictor of residual brain size (P value) and (3) the model fit (Akaike's Information Criterion, AIC). AIC is a measure of the penalized log-likelihood of the model, and a smaller AIC indicates a better model fit (Crawley 2007). We ran our analyses using residual brain size as the response variable rather than brain size with body size included as an independent variable, because our aim was to understand how different measures of innovation contribute to the relationship between innovation and residual brain size across families. This information is harder to extract when brain size is the response variable and body size is included as a predictor. However, residual analyses may lead to over-conservative results and thus an inflation of type II error (Darlington & Smulders 2001). We therefore ran all of our analyses with brain size (log-transformed) as the response variable and body size (log-transformed) included as one of the predictor variables. All of our results were consistent with those presented here, though the P values were lower for our predictor variables in some cases when body size was included as predictor. We present all of our results

using residual brain size, because this facilitates comparison between measures.

RESULTS

Taxonomic Distribution of Innovation Categories and Diversity

Of the 2182 reported cases of innovation included in the database, the most common type of innovation was eating a novel food item (category 1; Fig. 1); 58 of 76 families (76%) had at least one innovation report of this type. The least common type of innovation was novel true tool use (category 10) which was observed in only seven families (9%). Innovation diversity ranged from 1 to 12 categories per family (median = 4). Fourteen families (18%) innovated in only one of our categories, most often with novel food type innovations (category 1; e.g. Coccyzidae (cuckoos), Otidae (bustards) and Gaviidae (loons)). Families showing the most diverse innovation repertoires were Corvidae (corvids), Accipitridae (birds of prey), Muscicapidae (flycatchers) and Laridae (gulls) with 12, 12, 11 and 11 innovation categories, respectively (see Supplementary Material for a summary of innovations for each species and family).

Innovation Rate versus Innovation Diversity

Although both innovation measures were significantly associated with residual brain size, innovation diversity (Fig. 2) was a slightly better predictor of residual brain size than was the total number of innovations (both corrected for research effort; Table 2): residual innovation diversity explained 8.67 % of the variance in residual brain size, while residual innovation rate explained 7.28 % (models 1 and 2; Table 2).

The relationship between innovation diversity and residual brain size did not seem to be due to a potential type I error in innovation classification: when we excluded cases where a family scored in a category because of a single innovation report in that category (which reduced the innovation diversity score by 1 for $N = 24$ families, by 2 for $N = 30$ families, by 3 for $N = 4$ families, by 4 for $N = 8$ families, by 5 for $N = 2$ families and by 6 for $N = 1$ family), the relationship between innovation diversity and residual brain size remained significant ($F_{2,76} = 9.567$, $P = 0.015$).

We repeated these analyses of total number of innovations and innovation diversity including three potentially confounding variables for the 55 families for which we had data. Juvenile development mode was a strong predictor of residual brain size across families. Habitat generalism was not a significant predictor in any analyses, while diet generalism was close to the traditional

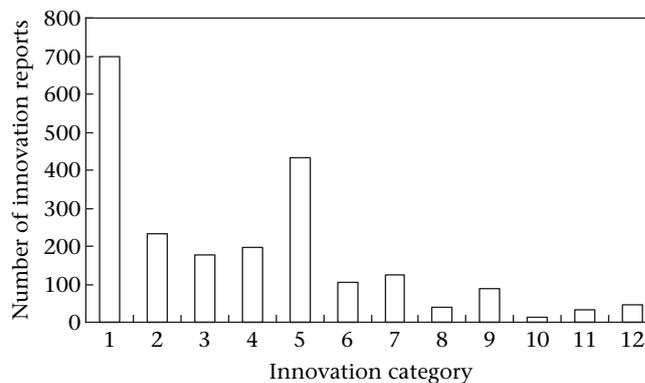


Figure 1. Breakdown of the 2182 innovations into 12 categories (1–12).

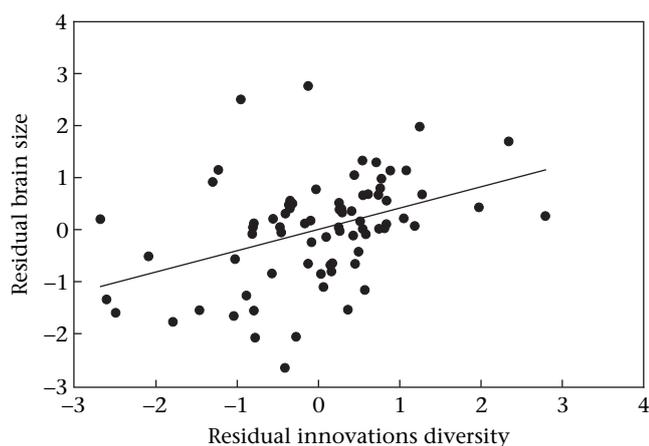


Figure 2. Residual brain size plotted against innovation diversity (corrected for research effort) for the 76 families included in the innovation database.

threshold for significance in some cases (Table 3). The inclusion of these variables did not negate the relationship between total number of innovations and residual brain size, or innovation diversity and residual brain size, which remained strong even when the data set was reduced to 55 families (models 4 and 5; Table 3).

Technical Innovations and Food Type Innovations

Both the number of technical innovations (categories 4–11, corrected for research effort) and the number of food type innovations per family (categories 1, 2 and 3, corrected for research effort) were significantly associated with residual brain size (models 3 and 4; Table 2). However, the number of technical innovations per family explained much more of the variance in residual brain size (10.22%) than did the number of food type innovations (2.99%; models 3 and 4; Table 2), despite the fact that food type innovations made up 50.8% of the innovation reports in our database. Moreover, in a multivariate model including both variables, only the number of technical innovations significantly predicted residual brain size (both variables corrected for research effort; food type innovations: $F_{3,76} = 0.008$, $P = 0.994$; technical innovations: $F_{3,76} = 2.43$, $P = 0.017$). The diversity of technical innovations (i.e. number of technical innovation categories) was associated with larger residual brain size ($F_{2,76} = 11.42$, $P = 0.001$; model 5; Table 2, Fig. 3) and was the measure that explained the greatest proportion of variance in residual brain size (13.36%). The diversity of food type innovations was not significantly associated with residual brain size ($F_{2,76} = 0.05$, $P = 0.82$; model 6; Table 2).

We repeated all of these analyses for 55 families with the inclusion of potentially confounding variables: juvenile development mode, as well as habitat and food generalism. In all analyses, juvenile development mode was a strong predictor of residual

brain size, while habitat generalism was not (Table 3). Diet generalism was a significant predictor when included in the analysis of number of food type innovations (model 12; Table 3), and was not significant in other analyses (models 9, 10 and 11; Table 3). The inclusion of these variables weakened the relationship between the diversity of food type innovations and residual brain size, such that it failed to reach significance at the 0.05 level (model 12; Table 3). However, the number and diversity of technical innovations remained significant predictors of residual brain size in all analyses, even in this data set of only 55 families. These models explained 25–40% of the variance in residual brain size across families (Table 3). Figure 4 illustrates the taxonomic distribution of the diversity of technical innovations in our sample.

DISCUSSION

In this study, we teased apart several factors that contribute to the positive relationship between innovation rate and residual brain size, and reached two major conclusions.

First, we found that brain size was positively correlated with both the total number of innovations and the diversity of innovations for a given family. This demonstrates that the positive relationship between innovation and residual brain size is not driven by only a few families repeating similar innovations that are observed multiple times, but instead represents a strong relationship between expansion of the behavioural repertoire and brain size.

Second, we found that technical innovations were the best predictor of residual brain size. Overall, the number of novel feeding techniques observed in a given family explained more of the variance in brain size than did the number of food type innovations, and the diversity of technical innovations performed by a given family explained the greatest proportion of variance in brain size of all of the innovation measures used in our analyses.

Previous work has highlighted the relationship between enlarged brain size and technical skills such as tool use in birds (Lefebvre et al. 2002; Cnotka et al. 2008). Our results support and expand the technical intelligence hypothesis, suggesting that increased brain size allows individuals to use innovation to modify their technical skills. In this study, we did not restrict our definition of technical skills to tool use. Instead, we included a range of behaviours in which individuals used novel techniques to capture food items (e.g. activating an automatic sensor to open a door, bait-fishing and kleptoparasitism; Table 1). It has been argued that tool use, defined as using an object that is detached from the self and the substrate (Parker & Gibson 1977), may be less common in birds than would be expected because the beak may function as a readily available 'Swiss-Army knife' (Huber & Gajdon 2006). Indeed, non-tool-using species of birds are able to solve complex physical tasks in laboratory settings (Tebich et al. 2007), and even tool-using species may only use tools when the ecological conditions are appropriate (Tebich et al. 2002). Our broader definition of

Table 2
PGLS models of residual brain size (corrected for body size) as a function of different innovation measures

Model	Predictor variable*	Slope±SE	λ	df	F	P	R ²	AIC
1	Innovation diversity	0.258±0.10	1	2, 76	7.03	0.010	0.087	196.16
2	Total number of innovations	0.230±0.10	1	2, 76	5.81	0.018	0.073	197.31
3	Number of technical innovations (categories 4, 5, 6, 7, 8, 9, 10, 11)	0.262±0.09	1	2, 76	8.43	0.005	0.102	194.86
4	Number of food type innovations (categories 1, 2, 3)	0.149±0.10	1	2, 76	2.28	0.135	0.030	200.75
5	Diversity of technical innovations	0.296±0.09	1	2, 76	11.42	0.001	0.134	192.15
6	Diversity of food type innovations	-0.025±0.11	1	2, 76	0.05	0.824	<0.001	203.01

* Corrected for research effort.

Table 3
PGLS models of residual brain size (corrected for body size) as a function of different innovation measures with confounding variables included

Model	Term	Values for each term individually				Values for model as a whole						
		Estimate	SE	T	P†	Slope±SE	λ	df	F	P	R ²	AIC
7	Total number of innovations	0.353	0.129	2.73	0.009**	-2.03±0.720	0	5, 55	7.98	<0.001	0.390	153.93
	Juvenile development mode	0.507	0.123	4.11	<0.001***							
	Habitat generalism	0.373	0.221	1.69	0.097							
	Feeding generalism	-0.250	0.186	-1.34	0.186							
8	Innovation diversity	0.307	0.133	2.31	0.025*	-1.62±0.832	1	5, 55	5.36	<0.001	0.300	153.90
	Juvenile development mode	0.481	0.169	2.85	0.006**							
	Habitat generalism	0.272	0.229	1.19	0.240							
	Feeding generalism	-0.323	0.169	-1.90	0.063							
9	Number of technical innovations	0.354	0.119	2.97	0.005**	1.81±0.754	0	5, 55	8.45	<0.001	0.404	152.66
	Juvenile development mode	0.506	0.121	4.16	<0.001***							
	Habitat generalism	0.364	0.218	1.67	0.101							
	Feeding generalism	-0.245	0.183	-1.34	0.187							
10	Number of food type innovations	0.265	0.128	2.06	0.044	-2.14±0.752	0	5, 55	6.82	<0.001	0.353	157.11
	Juvenile development mode	0.571	0.124	4.57	<0.001***							
	Habitat generalism	0.344	0.227	1.52	0.136							
	Feeding generalism	-0.265	0.193	-1.37	0.176							
11	Diversity of technical innovations	0.347	0.127	2.73	0.009**	-1.70±0.818	1	5, 55	6.06	<0.001	0.326	151.80
	Juvenile development mode	0.458	0.166	2.74	0.008**							
	Habitat generalism	0.226	0.221	1.02	0.311							
	Feeding generalism	-0.212	0.174	-1.21	0.229							
12	Diversity of food type innovations	0.115	0.146	0.790	0.432	-1.68±0.888	1	5, 55	3.84	0.009	0.250	150.39
	Juvenile development mode	0.604	0.179	3.38	0.001**							
	Habitat generalism	0.191	0.236	0.808	0.422							
	Feeding generalism	-0.371	0.177	-2.09	0.041*							

† Variable was a significant predictor of residual brain size at: * $\alpha < 0.05$; ** $\alpha < 0.01$; *** $\alpha < 0.001$.

technical intelligence may therefore be more generally applicable for studies of cognition in birds.

Although technical innovations explain a greater proportion of variance in residual brain size than do food type innovations,

larger-brained families also had a greater number of food type innovations than smaller-brained families. In addition, feeding generalism emerged as a significant predictor of residual brain size in some analyses. Taken together, this suggests that larger-brained

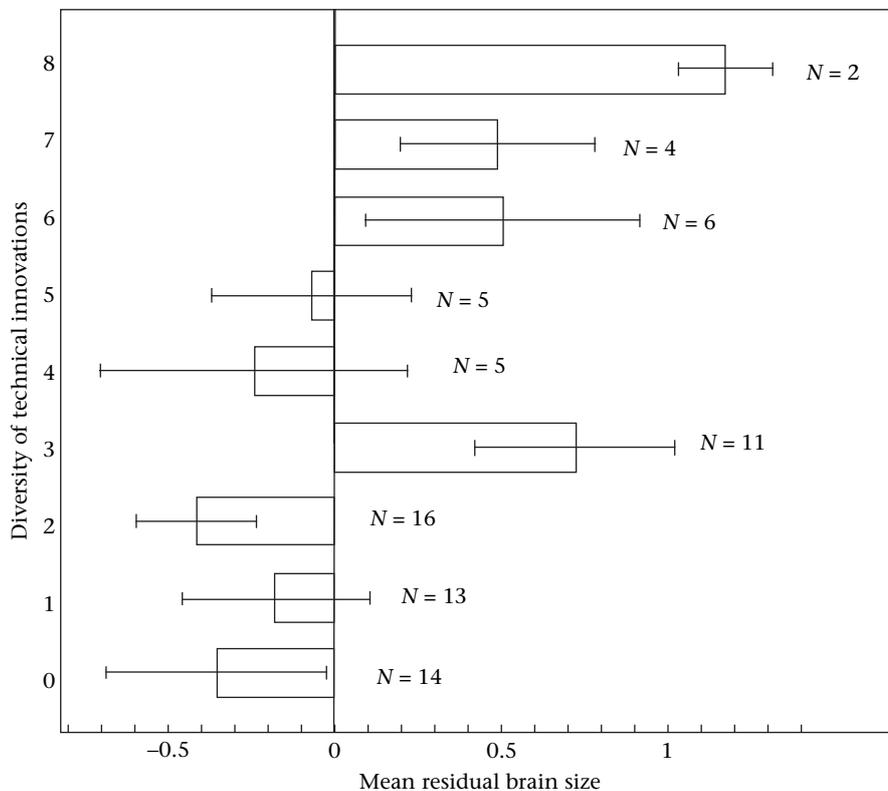


Figure 3. Mean ± SE residual brain size of families for each score of diversity of technical innovations, from 0 (no technical innovations recorded) to 8 (at least one innovation for each of the 8 technical innovation categories). The number of families (N) with each score is given to the right of each bar.

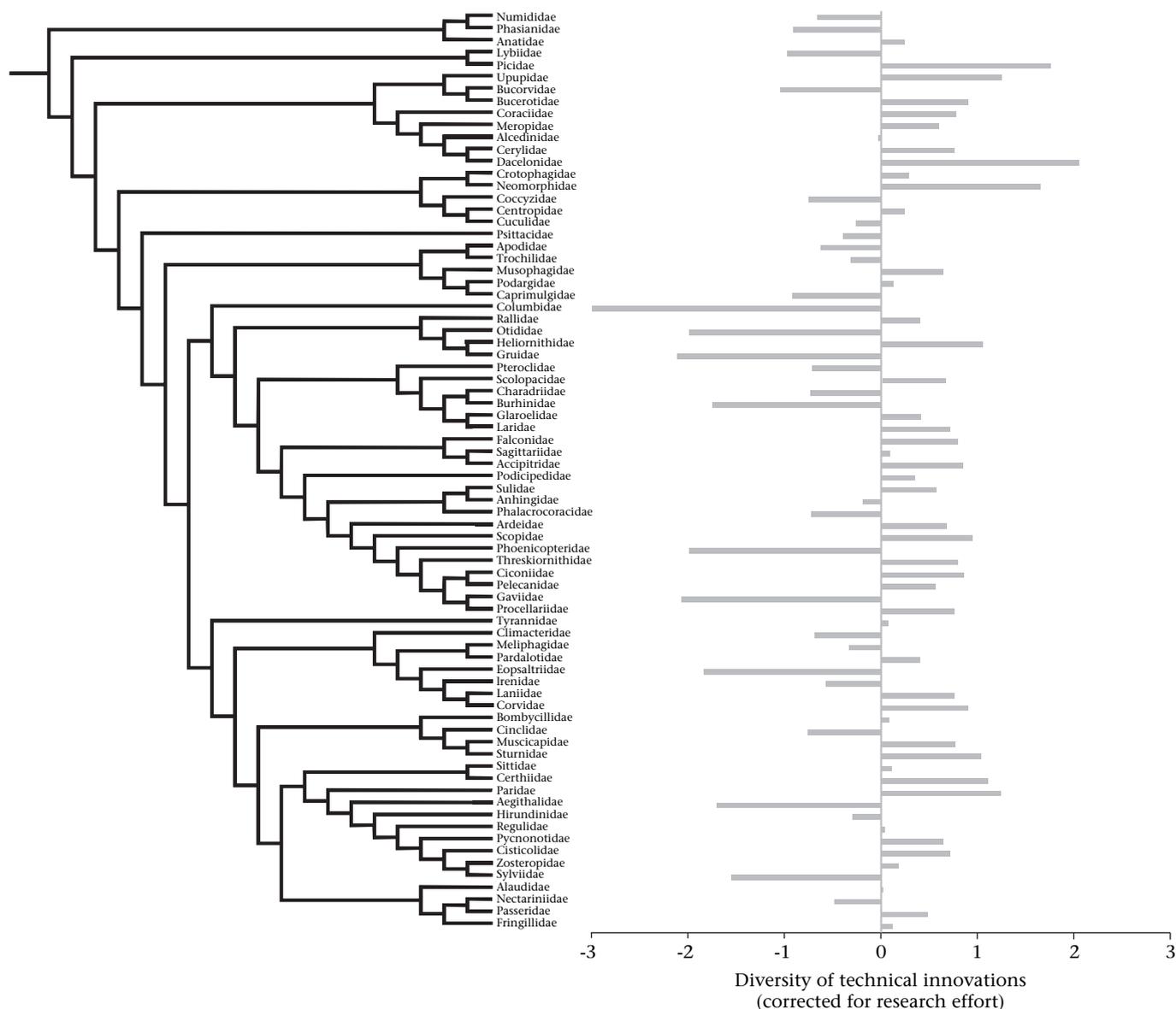


Figure 4. Residual diversity of technical innovations (number of technical innovation categories, corrected for research effort) for 76 avian families. Phylogenetic tree from Sibley & Ahlquist (1990).

families tend to eat a wider variety of foods, which may appear to support the opportunistic-generalist hypothesis. The ability to innovate is thought to allow individuals to adjust their behaviour as environmental conditions change, such as when introduced to new habitats (Sol et al. 2005). In this case, a willingness to sample new foods and the ability to learn about the palatability of these new food items may be important. For example, newly invading populations of house sparrows, *Passer domesticus*, are less fearful of novelty than are established populations (Martin & Fitzgerald 2005). However, in a multivariate model including technical and food type innovations, the number of food type innovations was not a significant predictor of residual brain size. Furthermore, the diversity of food type innovations was not significantly associated with brain size. The weak relationship between food type innovations and residual brain size suggests that the opportunistic-generalist hypothesis for the evolution of large brains does not provide a sufficient explanation for the variation in brain size in birds. Although larger-brained, innovative species may be more

likely to incorporate novel foods into their diets, and although this ability may be ecologically important, our results suggest that the relationship between innovativeness and brain size is primarily driven by technical innovations.

Little is known about the psychological processes underlying animal innovation (Clayton 2004), or whether innovation is a 'unitary phenomenon' (Reader & Laland 2003). In a recent theoretical paper, Ramsey et al. (2007) suggested that innovations may range from being 'weak' to 'strong'. The authors separated weak from strong innovations based on frequency (strong innovations should be more rare), novelty (strong innovations should be more novel) and the amount of cognition involved (strong innovations should require more cognition). While this may be intuitively appealing, these measures are difficult to operationalize across taxa (Giraldeau et al. 2007). For example, to compare the novelty of two innovative behaviours, one would have to dissect the behaviour into its motor and psychological components and compare these components with existing behavioural patterns. The behaviours

described in foraging innovation reports may indeed vary in the degree to which they are true departures from the species repertoire. For example a great tit, *Parus major*, opening a milk bottle (Fisher & Hinde 1949) might apply an existing behavioural pattern to a novel object (Sherry & Galef 1984), whereas a European blackbird, *Turdus merula*, using a twig to push off snow (Priddey 1977) may be using an entirely different set of motor skills than those used during other types of foraging. Using our innovation categories, we obtained an operational definition of different types of innovation based on the wording in the original reports, and found that our distinction was supported by another measure of cognition, brain size. Our results suggest that innovations involving novel techniques require a greater cognitive capacity than do nontechnical innovations. This is consistent with studies of problem-solving ability in captive birds, wherein large-brained birds are able to spontaneously solve novel tasks that may require very specific technical skills unlike those they use in the wild (Webster & Lefebvre 2001; Heinrich & Bugnyar 2005; Biondi et al. 2008). However, our results are merely suggestive, and more studies of the processes involved in innovation are needed.

Our results demonstrate that larger-brained species perform a wider variety of innovative behaviour, but we can only speculate on the factors driving this relationship. Selection for increased behavioural flexibility may have driven accompanying changes in brain size. Alternatively, selection for large brain size, driven by another unexamined factor, may be accompanied by an increase in behavioural flexibility. That is, innovativeness may be a 'spandrel', a by-product of selection for other cognitive abilities (Gould & Lewontin 1979). Measures of cognition are often correlated with one another (Lefebvre et al. 2004), suggesting that selection may act on some measure of general intelligence rather than on innovativeness per se. Furthermore, the performance of novel behaviour patterns probably depends not only on the 'innovativeness' of the species, but also on morphology and motor abilities, habitat, as well as other environmental and social variables. In this study, we have attempted to capture some of this variation by including confounding variables in our final analyses. These analyses suggest that the ability to expand the behavioural repertoire is correlated with increased brain size. The next step should be to use experimental approaches to better understand the psychological and neural processes underlying the production of novel behaviour patterns (Clayton 2004), and to determine whether these processes are distinct from those involved in other forms of learning.

Recent comparative studies of brain size have operationalized behavioural flexibility in two ways. Some studies have considered the variety of behaviour within a species' repertoire, such as the number of foraging modes used by bats (Ratcliffe et al. 2006), or the number of different behaviours recorded in an ethogram for mammals (Changizi 2003). Others, including the present study, focus on the degree to which a given species deviates from its behavioural repertoire through innovation (Lefebvre et al. 1997, 1998; Garamszegi et al. 2007; Sol et al. 2007). The results of these studies, in combination with our own, suggest that large brains are associated with increased diversity and plasticity of behaviour in animals.

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Supplementary Material

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