Big brains, enhanced cognition, and response of birds to novel environments

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The widely held hypothesis that enlarged brains have evolved as an adaptation to cope with novel or altered environmental conditions lacks firm empirical support. Here, we test this hypothesis for a major animal group (birds) by examining whether large-brained species show higher survival than small-brained species when introduced to nonnative locations. Using a global database documenting the outcome of >600 introduction events, we confirm that avian species with larger brains, relative to their body mass, tend to be more successful at establishing themselves in novel environments. Moreover, we provide evidence that larger brains help birds respond to novel conditions by enhancing their innovation propensity rather than indirectly through noncognitive mechanisms. These findings provide strong evidence for the hypothesis that enlarged brains function, and hence may have evolved, to deal with changes in the environment.

brain evolution | phenotypic flexibility | environmental change

Much of our current understanding of the evolution of large brains centers on the brain's function in cognition and information processing (1–3). Theoretical models and empirical evidence suggest that large brains can process, integrate, and store more information about the social and physical environment, enhancing the propensity of individuals to modify or invent new behaviors in potentially adaptive ways (1–17). Particularly remarkable is the recent finding that brain size is positively associated with the ability for behavioral innovation and learning in birds and mammals (5, 6, 8, 9, 16, 17). Despite this progress, it remains to be demonstrated what selective advantages large brains provide for the survival and/or reproduction of animals in the wild (8, 18).

The most widely held hypothesis is that large brains might have evolved as an adaptation to cope with novel or altered conditions (3, 15, 18–20). When faced with such situations, the ability to produce innovative behavior and store it in the repertoire through individual or social learning may have a critical effect on the survival and fitness of individuals (15, 21–24). Examples include the development of antipredatory responses against novel predators (25), the adoption of new food resources when the traditional ones become scarce (26), or the adjustment of breeding behavior to the prevailing ecological conditions (27). Thus, selection might have favored the evolution of enlarged brains because of the cognitive advantages they confer on animals to improve survival under novel or altered conditions. This idea will be termed the brain size–environmental change (BS-EC) hypothesis.

The BS-EC hypothesis is currently supported by scant empirical evidence. Most evidence is based on a statistical association between brain size and variables assumed to be associated with environmental change (4, 15, 28–34). The logic behind some of these assumptions is not always straightforward, and definitions of environmental change are sometimes vague. A strong test of the BS-EC hypothesis would require a direct measure of differential survival of species in an obvious situation where new environments are encountered and behavioral flexibility may make a life-or-death difference.

Deliberate introductions to novel environments (i.e., areas outside the natural geographic range of the species) provide such a situation (35–37). The challenges that one species must confront when exposed to a new environment are diverse and may include the discovery and adoption of novel resources, the avoidance of previously unknown enemies, or the adjustment of behavior to the new social or physical environment. Thus, success in establishing a self-sustaining population may largely depend on whether that species can rapidly cope with these new challenges through behavioral adjustments. If the BS-EC hypothesis is valid, we expect larger-brained species to have higher success than smaller-brained species at establishing themselves in areas outside their natural geographic range.

Experimental introductions of vertebrates to novel regions are in general not logistically or ethically feasible because of problems often associated with the introduction of nonindigenous species (38). An alternative is to use the rich record of past, human-mediated introductions. This approach has recently provided evidence that larger-brained, behaviorally innovative birds do attain higher success than small-brained, less innovative birds when confronted with novel environments (35, 36).

However, these previous analyses of the influence of brain size on enhanced fitness in novel environments are localized in extent, allowing little generalization, and suffer from two important methodological flaws. First, they fail to deal with the spatial and phylogenetic autocorrelation characteristic of introduction data (39, 40), whereby introduction events cannot be treated as independent data points. Such clustering structure in the data leads to correlated responses in groups of observations, violating a core assumption of standard statistical models and resulting in overestimates of the significance of the factors tested (a greater frequency of type I errors). Second, previous tests of the BS-EC hypothesis have not controlled for key factors known to affect establishment success (39, 41), notably introduction effort. The number of individuals released is the strongest correlate of introduction success in birds, yet it is nonrandomly distributed with respect to a range of characteristics for which there is evidence for an effect on establishment success, including habitat generalism, body mass, sexual dimorphism, and migratory tendency (41). Thus, previously documented correlations between these variables and establishment success may have been confounded with introduction effort. Indeed, only habitat generalism explains significant variation in bird establishment success once introduction effort has been controlled for (41). Clearly, introduction effort needs to be considered for the

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effect of brain size on introduction success to be properly understood.

Beside methodological issues, a key feature of the BS-EC hypothesis remains untested. The hypothesis requires not only a demonstration that larger brains enhance the ability of animals to respond to environmental changes, but also that this ability arises through enhanced cognitive skills. This premise cannot be simply assumed, because larger brains may be associated with improved motor or perceptual, rather than cognitive, abilities (30, 32, 42). Although previous evidence suggests that successful invaders have higher cognitive abilities than unsuccessful invaders (35, 36), it remains to be tested whether such cognitive differences mediate the link between brain size and the response of animals to environmental changes.

Here, we aim to address the above shortcomings with a general test of the BS-EC hypothesis for a major animal group (birds). Our first goal is to validate the key prediction, that larger brains facilitate success in novel environments, using a global database documenting the outcome of 645 introductions of 195 avian species to new locations. In testing this prediction, we use a new modeling technique that corrects for problems associated with phylogenetic and spatial nonindependence among introductions, and we control for key confounding factors that are known to affect establishment success (39, 41, 43), notably introduction effort. Having found support for the above prediction, our second goal is to examine the role of cognition in the enhanced ability of big-brained birds to respond to novel conditions. We use a recently proposed measure of cognitive ability, the propensity for innovative behaviors (6, 15, 44), to test whether enhanced cognitive skills increase fitness of birds in novel environments. Because we find support for this association, we use path analysis to validate that large brains enhance the response of animals to novel environmental conditions by enhancing cognitive skills rather than indirectly through noncognitive mechanisms.

Materials and Methods

Introduction Data. We used a previously compiled global database documenting all recorded human-mediated introductions of birds to new locations (41). In this database, the introduction of a species to a new location (an introduction event) is defined as the release of individuals of a species to either an island or a governmental state within a continental mainland that is outside the species' native range (41). Multiple releases to the same island or state were counted as one introduction to that location. We considered an introduction to be successful if it resulted in the establishment of a persistent or probably persistent population in the recipient island or state, and unsuccessful otherwise (introductions described as possible successes were ignored). From this global database, we restricted our analyses to introduction events that included information on introduction effort, measured as the total number of individuals released, because this is a major determinant of introduction success (41). Data on introduction effort were available for 646 introduction events (34% of reported bird introductions worldwide, comprising 196 species and 35 families), 243 of which were successful. Each species was introduced to a mean of 3.32 locations (SE = 0.33). Cassey *et al.* (41) have shown that introduction events with introduction effort data are a nonrandom subset of all bird introductions with respect to the region of introduction but are random with respect to the number of species per family represented. Importantly, establishment success does not differ significantly between introduction events with or without effort data.

Brain Data. We gathered data on brain mass for 1,967 species from a variety of sources (32, 45–51). We used actual brain mass, where available, but we also included cranial endocast measures

converted to mass by multiplying the reported value by the density of fresh brain tissue (1.036 g/ml) (ref. 33 and references therein). In three cases, we used telencephalon volumes reported in DeVoogd *et al.* (49) and Székely *et al.* (50); these volumes were transformed to brain mass by using regression techniques. Brain mass measurements are significantly repeatable across methods (33) and literature sources (32). When information on brain size was available from different sources, we used mean values. Information on brain mass was available for 152 of the 196 introduced species (77.5%) that we considered. For the remaining species, brain size was estimated by using the average brain mass of the closest taxonomic level (e.g., genus, which predicts 91% of the variance at the species level), which allowed us to use all species except one for this analysis. Conclusions are quantitatively similar regardless of whether we included in the analyses species with brain size estimated from close relatives.

Larger species tend to have larger brains, and this allometric effect needs to be accounted for before any comparison can properly be made (28, 34). By following previous suggestions (28, 52), we calculated the residuals of a log-log least-squares linear regression of brain mass against body mass. Variation in relative brain size among bird species is higher than within species (32), thus validating that this is a species character. The relationship between brain size and body mass was strongly positive and linear (linear regression, $R^2 = 0.88$; slope $\pm$ SE, 0.938 ± 0.008; $F_{1,1965} = 1,437.6$, $P < 0.0001$), and the residuals were uncorrelated with body mass ($R^2 < 0.00001$). Thus, these residuals (hereafter called relative brain size) may be used to test for an association between brain size (adjusted for body mass) and establishment success.

Confounding Variables. The success of bird introductions is known to depend on the idiosyncrasies of the release event and the characteristics of the recipient community (43). Such potentially confounding factors need to be controlled for in a proper test of the relationship between relative brain size and establishment success, because they could either inflate or obscure the predicted relationships. The most important event-level effects relate to introduction effort, which is typically recorded as the number of individuals released or the number of separate release events. Both variables are highly correlated in our data ($r = 0.71$, $n = 300$), but we used the number of individuals released as the metric of effort because it is available for more introduction events (646 vs. 305). Furthermore, because some regions may be easier to invade than others, we also controlled for region-level effects by including region as a factor variable in multivariate analyses (see details below). Based on the global pattern of introductions, we recognized 13 regions as follows: New Zealand, Australia, Canada, the United States, Hawaii, the Oriental region, Oceania, Africa, South America, the West Indies, continental Europe, the British Isles, and St. Helena.

In addition to event- and region-level effects, the hypothesized link between relative brain size and establishment success may potentially be confounded by a number of species-level characteristics. As already noted, most of the variables previously argued to relate to success actually only do so because they are correlated with introduction effort (41). Moreover, previous analyses demonstrated that the association between relative brain size and establishment success is largely independent of a set of traits for which there was some evidence for an effect on establishment success (35, 36). Here, we controlled for potentially confounding traits (43) that were not previously considered: native geographic range size (range maps scanned and scaled to the area of Australia to standardize for differences in map projections; log-transformed), annual fecundity (the product of modal clutch size and average number of broods; log-transformed), dietary generalism (number of the following eight major food types included in the diet of a species: grasses and

herbs, seeds and grains, fruits and berries, pollen and nectar, vegetative material, invertebrate prey, vertebrate prey, and carrion), and habitat generalism (number of the following seven major habitat types included in a species' native range: mixed lowland forest, alpine scrub and forest, grassland, mixed scrub, marsh and wetland, cultivated and farm lands, and urban environs). In addition, we also controlled for sexual dichromatism (dichromatic if there are any differences between sexes in their color and/or pattern of ornamentation), and migratory tendency (an index of year-round occupancy of a site: 0, sedentary; 1, nomadic and/or local movements; 2, partial migrant; 3, migrant). These variables were considered because they have been recently hypothesized to be associated with relative brain size (ref. 53 and D.S. and L.L., unpublished data).

Innovation Rate. Our operational measure of cognitive capacity was the frequency of feeding innovations (5, 6). We defined a feeding innovation as any food type or feeding technique described by an observer as novel for the species (6). The frequency of feeding innovations reported in the literature has proven to be a practical index of cognitive skills in birds and primates (44). The measure shows positive correlations with other estimates of cognition, such as tool use and reversal learning, in these two taxa (44, 54) and has been examined for the possible biasing effects of nine confounding variables (16, 44). We minimized known biases in this measure by first restricting our analysis to Western Palearctic species, for which a large data set of feeding innovations are available. Our database was based on an exhaustive review of 24 European journals covering 10 countries during 1970–2002. These reviews were mostly performed by readers blind to the hypothesis. Second, we only used species with at least one recorded innovation, thus removing the possibility that some species have no recorded innovations simply because they are difficult to observe. This yielded a total of 410 innovation cases for 109 species (data available upon request). Third, we measured the research effort invested in each species (number of papers published for the species between 1993 and 2003, according to the online version of *Zoological Record*) to control for the possibility that some species yield higher innovation rates than others because they are more closely studied (16). This effect was removed from each species by calculating the residuals from a regression of innovation frequency against research effort (both log-transformed). We thus obtained a measure of innovation rate independent of research effort ($R^2 < 0.00001$). The distribution of innovation rate was left-skewed (skewness = 0.96) and not strongly correlated with research effort ($R^2 = 0.26$; slope $\pm$ SE, 0.509 ± 0.084; $F_{1,108} = 36.97$, $P < 0.0001$), which may create problems when estimating residuals. However, we obtained similar results (data not shown) by using research effort as a covariate in a regression relating innovation

frequency to establishment success, so we are confident that the residuals were estimated adequately. Finally, the role of innovation rate in mediating the link between relative brain size and establishment success was tested at the family level, avoiding the greater influence of measurement error in comparisons among close relatives (55). Innovation rate, adjusted by research effort, showed significant variation at the family level ($F_{13,94} = 2.18$, $P = 0.016$), which validates the use of family as the taxonomic level for comparisons. Mean family residual values were used in the analyses.

Analyses. Relative brain size is not randomly distributed with respect to the regions of introduction [estimate $\pm$ SE, 0.324 ± 0.160, $Z = 2.03$, $P = 0.021$; see Cassey *et al.* (41) for details on the method]. Introductions of large-brained species were more frequent in the Oriental region and less frequent in Canada and the United States, compared with the remaining regions. If large-brained species tend to have been introduced to regions that are easier to invade, then we could erroneously conclude that enhanced brains facilitate establishment in novel locations. To account for the clustering of introduction events by region and for the clustering of species according to taxonomic hierarchy, we used the GLIMMIX (SAS Institute, Cary, NC) macro (56) to fit generalized linear mixed models. Generalized linear mixed models take the clustered structures of data into account when carrying out statistical analyses to provide estimates of SE corrected for the resulting nonindependence (56, 57). We modeled the likely nonindependence of introductions of closely related species by assuming a common positive correlation between introduction outcomes for species within nested taxonomic groups (species, genera, families, and orders) but a zero correlation between introduction outcomes involving species in different groups (a variance components model). Clustering of introduction events within regions was similarly modeled. The remaining variables (relative brain size, introduction effort, and species-level characteristics) were included as fixed effects. Success was modeled by specifying a binomial error distribution and logit link function, with introduction outcome (establishment success or failure) as the response variable. We first fitted a model that included all fixed effects as explanatory variables. We then simplified this model by backward selection to identify a minimal adequate model that retained only significant variables.

Most of the variation in relative brain size resides at higher taxonomic levels (37, 58), which can been interpreted as extensive diversification in brain size early in the avian radiation (59). Thus, it is relevant to consider how variation in relative brain size relates to variation in establishment success at higher taxonomic levels, such as among families. We estimated the magnitude of family-level differences in establishment success by using the random effect coefficients obtained from a generalized linear mixed model that included taxonomy and region as random

Table 1. Fixed and random effects in a minimum adequate generalized linear mixed model explaining variation in bird establishment success while controlling for geographical region and taxonomic levels

Effect	Estimate	SE	Type III, F	Z	P
Fixed					
Propagule size	0.973	0.134	52.83		< 0.0001
Habitat generalism	0.625	0.146	18.28		< 0.0001
Relative brain size	0.526	0.185	8.08		0.0047
Random					
Orders	0.266	0.289		0.92	0.1785
Families within orders	—	—		—	—
Species within families	0.846	0.286		2.96	0.0015
Region	0.739	0.442		1.67	0.0472

The minimum adequate model was obtained by backward selection, removing nonsignificant fixed effects.
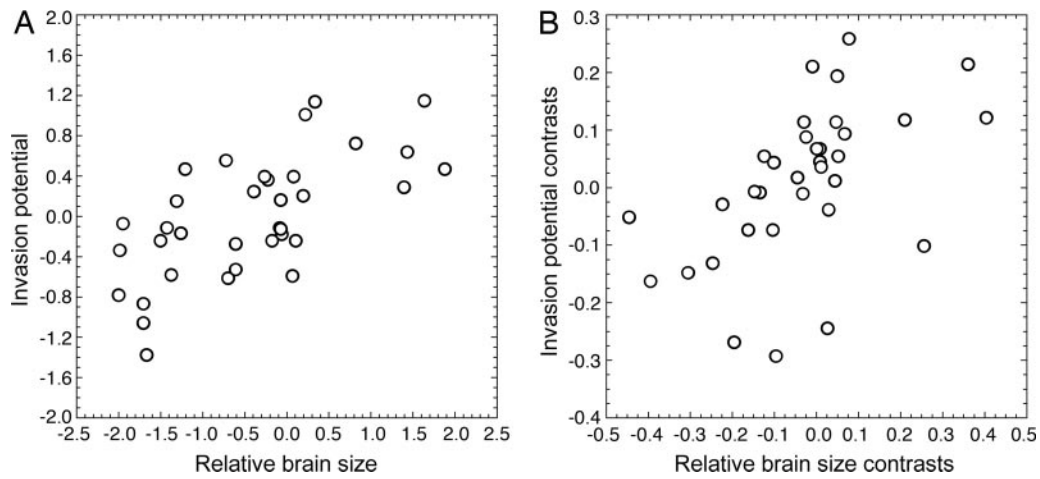
Fig. 1 Relationship between mean relative brain size and invasion potential for worldwide avian families. The relationship is shown without (*A*) and with (*B*) control for phylogenetic effects by using independent contrast analysis.

effects and introduction effort as a fixed effect. These coefficients, hereafter called invasion potential (60), provide a relative measure of the ability of each family to establish itself in a novel location having controlled for region and introduction effort effects and may subsequently be used as the response variable in regression models (61). Invasion potential was normally distributed (Shapiro–Wilk $W = 0.98$, $P = 0.93$), and we tested for a relationship between this variable and brain size by using least-squares regression. For this family-level analysis, relative brain size was calculated as the average residual (from the regression of brain size on body mass) per family by using the 1,967 species for which brain mass data were available. We repeated this analysis, controlling for similarities among families due to common ancestry by using phylogenetically independent contrasts (62) (PIC hereafter), by using Sibley and Ahlquist's family-level phylogeny with branch lengths estimated by using genetic distances (63). PIC values were calculated by using the program COMPARE 4.4. (http://compare.bio.indiana.edu) and analyzed by using regressions forced through the origin. The contrasts were satisfactorily standardized as indicated by a plot of the absolute value of the contrasts of each variable against their standard deviation (64).

Finally, we used path analysis to untangle the causal relationships between relative brain size, innovation rate, and invasion

potential at the family level (65). We tested two path models (see *Results and Discussion*). The first is a causal chain model that predicts that the effect of relative brain size on invasion potential is entirely due to the effect of brain size on innovation propensity. The second path model also sees the effect of relative brain size on invasion potential as indirectly caused by its influence on innovation propensity but in addition recognizes the possibility that brain size may have an effect for other reasons. The BS-EC hypothesis predicts that the indirect effect of brain on invasion potential mediated by innovation propensity is stronger than the direct effect. The contrary would suggest either that cognition is little involved in the relationship between brain size and invasion potential, or that innovation propensity is not the cognitive ability involved in that link.

Results and Discussion

Establishment success was higher for species with larger brains, relative to their body size, than for those with smaller brains (estimate ± SE, 0.483 ± 0.130; $F_{1,445} = 13.72$, $P = 0.0002$; $n = 645$ introductions of 195 species) when both taxonomic and regional autocorrelations were accounted for. This relationship was not due to the confounding effect of other factors that influence establishment. Relative brain size remained significantly associated with establishment success when all of the significant confounding
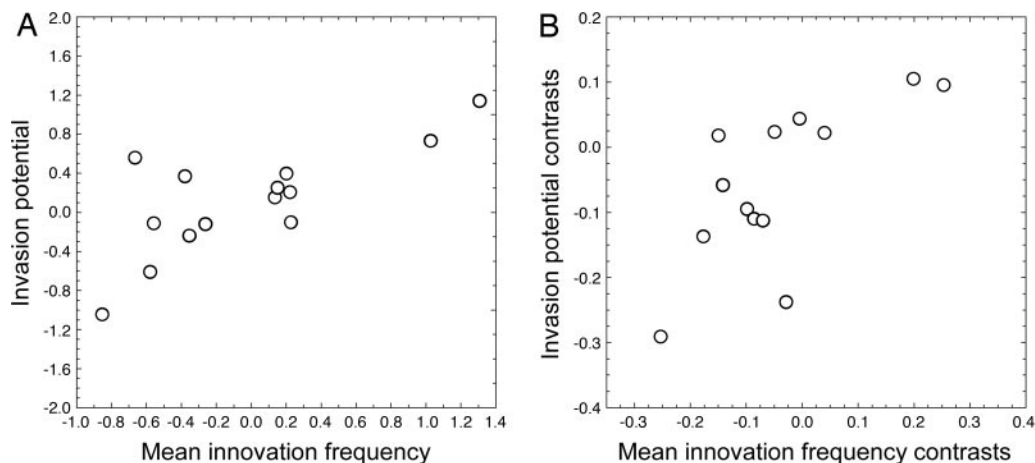
Fig. 2 Relationship between mean feeding innovation propensity and invasion potential for Palearctic avian families. The relationship is shown without (*A*) and with (*B*) control for phylogenetic effects by using independent contrast analysis..

effects were included in the same model. The minimal adequate model showed that increased introduction effort and increased habitat generalism also favored establishment success (Table 1), consistent with previous findings (41).

The above results confirm and generalize previous findings that birds with larger brains are better able to invade novel locations (35, 36). This result also is supported by our analysis at the family level. At this taxonomic level, there is a significant positive relationship between relative brain size and invasion potential ($R^2 = 43\%$, $t_{33} = 5.07$, $P < 0.0001$; Fig. 1A), a relationship that held when phylogenetic nonindependence was controlled for by using independent contrasts ($R^2 = 26\%$, $t_{33} = 3.39$, $P = 0.001$; Fig. 1B). Relative brain size is more closely associated with invasion potential at the family level than at the level of introduction events. It is commonly found in comparative analyses that a pattern is stronger at higher taxonomic levels (55) because of a greater signal-to-noise ratio in comparisons between less closely related taxa, making it easier to detect real trends. In our case, much of the variation in brain size resides at the family level (59). This high variation is likely to have further facilitated the detection of clear patterns, emphasizing the utility of adopting a hierarchical approach (66) in future analyses of brain evolution.

Having found support for the prediction that larger brains facilitate success in novel environments, we next examined the role of cognition in this link. In agreement with previous studies (5, 6), innovation propensity was positively related to relative brain size among avian families ($R^2 = 52\%$; 0643 ± 0.177; $F_{1,12} = 13.23$, $P = 0.003$; PIC, $R^2 = 39\%$; 0.693 ± 0.248; $F_{1,12} = 7.82$, $P = 0.016$). Moreover, as the BS-EC hypothesis predicts, innovation propensity also was positively associated with invasion potential ($R^2 = 56\%$; $F_{1,12} = 15.10$, $P = 0.002$; PIC, $R^2 = 55\%$; $F_{1,12} = 15.01$, $P = 0.002$; Fig. 2).

Finally, we used path analysis to test the prediction that large brains enhance the response of animals to novel environmental conditions by innovation propensity rather than indirectly through noncognitive mechanisms. A path model in which the effect of relative brain size on invasion potential is entirely attributed to its effect on innovation propensity (Fig. 3 *Upper*) explained almost all of the variation explained by the regression model (92.9%). The alternative path model, where relative brain size has both direct and indirect positive effects on invasion potential (Fig. 3 *Lower*), explained slightly more of the variation (98.2%) but was largely consistent with the first model: The direct effect of relative brain size on invasion potential (0.19) is smaller than the indirect effects associated with innovation propensity (0.72 × 0.60 = 0.432). Thus, assuming that innovation rate is an accurate measure of cognitive ability, large brains appear primarily to help birds respond to novel conditions by enhancing their cognitive skills rather than by other mechanisms.

Our findings support the hypothesis that large or elaborated brains function, and hence may have evolved, to deal with changes in the environment. Environmental uncertainty and
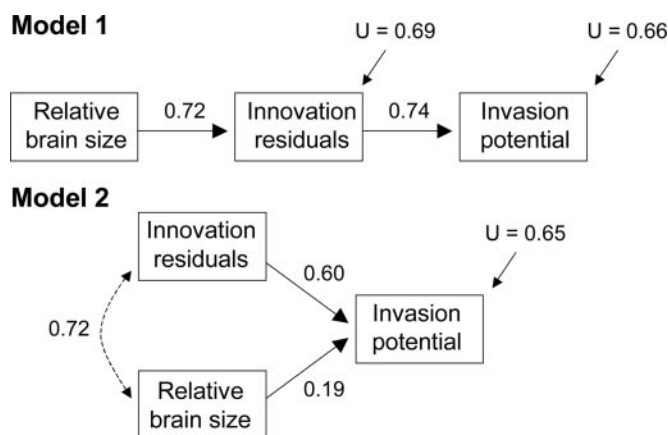
Fig. 3 Path diagram depicting two causal models for the relationship between relative brain size, residual innovation propensity (i.e., corrected for research effort), and invasion potential for Palearctic avian families.

behavioral complexity are central in many of the social and ecological hypotheses proposed to explain the evolution of large brains (7, 10). However, different hypotheses tend to focus on different aspects of complexity and change (18). The "extractive foraging" hypothesis (67) emphasizes the benefits of larger brains for the need to learn how to access hard-to-eat foods, often with the use of tools. The "resource variation" hypothesis emphasizes the importance of enlarged brains to track changes in the spatial or temporal distribution of food. The "social intelligence" hypotheses focus more on the benefits of large brains in dealing with changes in the social environment (4, 8, 17, 68). Finally, the "positive feedback" hypothesis proposes that it is the tendency of large-brained animals to discover and explore novel conditions that expose them to changes in the environment (18). Yet, all these hypotheses are essentially based on the same principle, that enlarged brains enhance the cognitive skills necessary to respond to changes in the environment, and thus may be integrated into the more general BS-EC hypothesis. The selective pressure to deal with novel or altered circumstances may have been a powerful evolutionary force for increasing the size of the brain.

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