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Brood Parasitism and Brain Size in Cuckoos: A Cautionary Tale on the Use of Modern Comparative Methods

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Comparative studies have yielded substantial insight into the functional relationships between the brain and behavior in birds. There are, however, important limitations to this method and problems can arise in the interpretation of the results. I use as an example, a test of whether interspecific brood parasitism is correlated with relatively smaller brains in the cuckoos and allies (Cuculiformes). Both conventional and phylogenetically based comparative statistics were used in conjunction with three alternative phylogenetic trees of the species examined. The comparisons between brood parasitism and relative brain size yielded mixed results, depending upon both the statistical method and the phylogeny employed. Although this could indicate that the evolution of interspecific brood parasitism is not related to relative brain size, the limitations of the comparative method in conjunction with the mixed results make it impossible to determine this with any certainty. The fact that different phylogenetic relationships yielded different results highlights the importance of phylogenetic relationships in assessing brain-behavior relationships. The continued use of phylogenetically based comparative methods should therefore be done cautiously, particularly with respect to interpretation of the results as the outcome may be as dependent upon the phylogeny as it is on the data itself.

Interspecific correlations of neural and behavioral variation have proven to be a useful means of assessing the function of the nervous system, particularly in birds. In recent years, there has been a proliferation of these studies, likely brought on by a greater interest in evolutionary issues in both animal behavior and the neurosciences, as well as the advent of modern comparative statistics (Harvey & Pagel, 1991). Some of these include comparisons of hippocampal formation volume and spatial behaviors (Hampton et al., 1995; Healy & Krebs, 1996, 1992; Reboreda, Clayton, & Kacelnik, 1996; Sherry et al., 1989, 1993), vocal control nuclei and song repertoire (DeVoogd et al., 1993; MacDougall-Shackleton & Ball, 1999; Szekely et al., 1996; but also see Gahr, Sonnenschein, & Wickler, 1998), and telencephalic regions and innovative behaviors (Lefebvre et al., 1998, 2001, 1997; Nicolakakis & Lefebvre, 2000; Timmermans et al., 2000) and tool use (Lefebvre et al., 2002). In all of these instances, the correlation of interspecific variation in

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behavior with similar variation in neural substrate is taken as evidence of a functional relationship between the brain region and the behavior. The interpretation of significant correlations between the brain and behavior as representative of functional relationships is predicated on the principle of proper mass as proposed by Jerison (1973). Essentially, the principle of proper mass states that the size of a brain region is proportional to the complexity of the behavior that it mediates. The correlation of behavioral abilities with the size of the neural substrate therefore provides evidence supporting the principle of proper mass.

Recently, Bolhuis and Macphail (2001) addressed a number of concerns regarding the interpretation of such comparative studies. They argued that investigating the neurobiology of learning and memory from an ecological/evolutionary perspective is inherently flawed because it assumes that memory is composed of domain-specific modules. They followed this by providing a series of examples demonstrating that comparative studies of the hippocampal formation and spatial ability and vocal control nuclei and song repertoire are inconsistent and “cannot explain the neural mechanisms of behavior in general...” (Bolhuis & Macphail, 2001, p. 432). Although it is true that neither the comparative nor the “neuroecological” approach can provide direct evidence of causal mechanisms, the extreme view of Bolhuis and Macphail (2001) ignores the potential contribution of ecological differences in shaping the evolution of the avian brain. Hampton et al. (2002), in fact, countered the critique of Bolhuis and Macphail (2001) by suggesting that is the interpretation of the results that is problematic, not the approach per se.

Although Bolhuis and Macphail (2001) are correct when they describe comparative studies as often demonstrating messy relationships and prone to subjective interpretation, an equally important aspect of comparative studies is how the use of modern comparative statistics can affect not only the interpretation of such results, but also the outcome. Whether phylogenetically based comparative methods should be used or not in interspecific comparisons has been the focus of much debate (Björklund, 1997; Harvey, 1996; Harvey, Read, & Nee, 1995a, 1995b; Price, 1997; Ricklefs & Starck, 1996; Westoby, Leishman, & Lord, 1995a, 1995b). Elsewhere, I have argued that phylogenetically based comparative methods are crucial to elucidating the correlated evolution of the brain and behavior, but not at the expense of abandoning conventional statistics (Iwaniuk & Nelson, 2001; Iwaniuk, Nelson, & Pellis, 2001; Iwaniuk, Nelson, & Whishaw, 2000; Iwaniuk, Pellis, & Whishaw, 1999a, 1999b). Several other authors have made similar arguments (Blackburn & Gaston, 1998; Price, 1997). More recently, a number of methods have been developed to test whether phylogenetically based methods should be used in interspecific comparisons (Abouheif, 1999; Blomberg, Garland, & Ives, 2003; Diniz-Filho, de Sant’Ana, & Bini, 1998; Freckleton, Harvey, & Pagel, 2002). The issue of whether phylogenetically based methods should be used or not aside, it is equally important to recognize several of the problems that can arise when modern comparative methods are employed. Recent studies by Symonds (2002) and Symonds and Elgar (2002) indicate that phylogenetic topology can have a significant effect on whether significant relationships are detected or not as well as the nature of the relationship (e.g., slopes and intercepts of allometric lines). That is, alterations in the phylogenetic relationships between species (i.e., topology) can affect the results of comparative tests.

In this article, I illustrate the problem of multiple phylogenetic hypotheses affecting the outcome of comparative analyses by comparing relative brain size and interspecific brood parasitism in cuckoos and related species (Aves, Cuculiformes). Specifically, the results differed both quantitatively and qualitatively depending upon which of three alternative phylogenetic hypotheses were used to perform comparative analyses. This raises some concerns regarding how to use comparative methods when their use is warranted, particularly when phylogenetic information is available from multiple sources or is missing for species within the data set. I conclude by emphasizing the importance of continued research into phylogenetics and the performance of phylogeny-based comparative methods as well as the development of larger databases in assessing brain-behavior relationships in birds and other species.

The Case of Interspecific Brood Parasitism

Interspecific brood parasites are species that habitually lay their eggs in the nests of other species. The evolution of this form of parasitism and the strategies that hosts employ to avoid parasitism have been a major focus of recent research in behavioral ecology and evolutionary biology. The relationship between the parasite and the host is often viewed as an evolutionary arms race whereby the evolution of host defenses are countered by the parasite in a cycle of adaptive modifications (see reviews in Davies, 2000; Johnsgard, 1997; Rothstein & Robinson, 1998). Host adaptations include mobbing of parasites, recognition of foreign eggs, and nest abandonment. The adaptations present in a given parasite vary between species and populations, but can include thicker eggshells, mimetic colors of eggs and nestlings, vocal mimicry, rapid developmental rates, and removal of host nestlings.

Many of the adaptations present in brood parasites reflect aspects of behavioral development. For example, parasites usually lay eggs in nests that already contain eggs. Since parasitic nestlings have a better chance of survival if they hatch earlier, they must have a shorter incubation period. Alterations in the length of the incubation period are significantly correlated with adult relative brain volume (Iwaniuk, 2003; Iwaniuk & Nelson, 2003). Specifically, reducing the length of the incubation period generally results in relatively smaller adult brains. Not only is the incubation period of the parasitic species shortened, however, the hatchlings are also more advanced than that of the host's hatchlings in a number of aspects. For example, the parasitic hatchlings tend to be larger in overall size, possess relatively longer forelimbs, and have a greater degree of motor control than host hatchlings. Thus, compared to host hatchlings, the parasitic hatchlings are more precocial in both their somatic and behavioral development. These relatively precocial features of parasitic hatchlings facilitate hatching out of structurally strong eggs (Honza et al., 2001) as well as the removal of host nestlings from the nest via nest ejection or siblicide. Both of these behaviors require more complex movement patterns than that of their hosts' nestlings (Honza et al., 2001) and would not be possible without the development of advanced connections in both the central and peripheral nervous systems. Little is known, however, about differences in brain size or structure of parasitic versus nonparasitic species to assess this hypothesis.

Cuculiformes are the ideal group within which to test these hypotheses because of the great number of parasitic species as well as relatively large variability

in both brain and body size. The parasitic species also possess a wider range of host adaptations than other taxa, thus providing the opportunity to compare different parasitic strategies within one group. Based upon the preceding discussion of developmental differences between parasitic and nonparasitic birds in general, I expected that parasitic cuculiforms would possess smaller brains, relative to body size, than nonparasitic cuculiforms.

Methods

Brain volumes were measured from 174 specimens representing 28 species of cuculiforms. Both the endocranial volumes of skeletal specimens and brain masses of dead birds collected in the field were used (Table 1). Details of the methods of measuring endocranial volumes and brain masses are provided in Iwaniuk and Nelson (2002, 2001). Where both sexes were measured, the values for each sex were averaged and the mean of the two sexes taken as the species value.

Two methods of scoring brood parasitism were employed to test for correlations with relative brain size. Firstly, species were simply scored as parasitic or nonparasitic regardless of the frequency with which parasitism occurs (Table 1). This scoring system, therefore, does not provide information on whether a species exhibits obligatory or facultative parasitism, nor any information on cuckoo nestling behavior or the degree of host specialization. Variation in these aspects of brood parasitism could be correlated with relative brain size, so the parasitism scoring method of Krüger and Davies (2002) was also employed. Their method of scoring brood parasitism incorporates information on the degree of host specificity, behavior of cuckoo nestlings (eg. whether they eject host nestlings or not) and whether the parasitism is obligatory or facultative by ranking brood parasitism on scale of 0 to 3.3 (Table 1). Thus, species with a 0 are nonparasites, 1 and 2 are facultative parasites, and 3 are obligatory parasites. Within the rank of 3, species are then divided into three subranks depending on the criteria outlined above (see details in Krüger & Davies, 2002).

To analyze the binary score of parasitic/nonparasitic and relative brain size, ANCOVAs were employed. Prior to all analyses, both brain volumes and body masses were log-transformed. Using brood parasitism, body mass, and their interaction as covariates of brain volume, a conventional ANCOVA was performed. To incorporate phylogenetic information, phylogeny-corrected critical F values (Garland et al., 1993) were calculated using programs in the Phenotypic Diversity Analysis Programs (PDAP) software package (available upon request from T. Garland, Jr.). First, a phylogenetic tree was constructed and brain volumes and body masses for each species entered using the PDTREE program. In many cases where this approach is employed, only a single phylogenetic tree is available (e.g., Pellis & Iwaniuk, 2002). However, there is considerable debate concerning the evolutionary relationships within the Cuculiformes and therefore three alternative phylogenetic trees were employed. The first of these (Hughes, 2000) is based on osteological characters and indicates a single origin of brood parasitism (Figure 1). The second tree is based on DNA sequencing of both cytochrome b and ND2 (Johnson, Goodman, & Lanyon, 2000) and indicates either two independent gains of brood parasitism (one in the Cuculinae and one in the Coccyzinae) or a single origin and subsequent loss in the squirrel cuckoo (*Piaya cayana*; Figure 1). The third by Aragón et al. (1999) suggests multiple independent origins of brood parasitism, in a number of different Cuculinae genera (Figure 1). PDSIMUL then uses Monte Carlo simulations of the traits along the phylogeny to create a phylogeny-corrected F distribution that can be used to calculate phylogeny-corrected critical F values (Garland et al., 1993). For each phylogeny, 1000 of these simulations were performed utilizing both gradual and speciation models of evolutionary change. These two models differ in that evolutionary changes in a trait in a gradual model occur along the branch lengths whereas in a speciation model, evolutionary changes in a trait occur at the nodes (i.e., speciation events). Since I had no a priori reason to assume either model applied to relative brain size evolution, both were employed. Also, to ensure that the simulated values are biologically realistic for the species examined, the upper and lower limits of brain volume and body mass were set just above and below those of the largest (*Scythrops novaehollandiae*) and smallest (*Chrysococcyx minutillus*) species measured (Table 1). Lastly, PDANOVA was used to calculate the phylogeny-corrected critical F values based upon the simulated data.

To analyse the relation between relative brain size and brood parasitism using Krüger and Davies' (2002) scoring system, a multiple regression model of species values and independent contrasts was employed using brain size as the dependent variable. As with the above, brain volumes and

Table 1

Sample Size, Brain Volume (ml) and Body Mass (g) of the 28 Parasitic and Nonparasitic Cuculiform Species Analysed.

Family	Species		<i>n</i>	Brain Volume	Body Mass	Brood Parasitism	Parasitism Score
Centropidae	Lesser coucal	<i>Centropus bengalensis</i>	9	2.27	117.1	No	0.0
	Pheasant coucal	<i>Centropus phasianus</i>	10	4.12	518.8	No	0.0
Coccyzidae	Yellow-billed cuckoo	<i>Coccyzus americanus</i>	10	1.17	64.0	Yes	2.0
	Black-billed cuckoo	<i>Coccyzus erythrophthalmus</i>	6	1.01	50.5	Yes	2.0
	Squirrel cuckoo	<i>Piaya cayana</i>	8	1.84	104.0	No	0.0
	Jamaican lizard-cuckoo	<i>Saurothera vetula</i>	10	2.00	99.3	No	0.0
Crotophagidae	Smooth-billed ani	<i>Crotophaga ani</i>	10	1.56	100.2	No	0.0
	Guira cuckoo	<i>Guira guira</i>	5	1.92	146.6	No	0.0
Cuculidae	Chestnut-breasted cuckoo	<i>Cacomantis castanneiventris</i>	2	0.95	31.0	Yes	3.3
	Fan-tailed cuckoo	<i>Cacomantis flabelliformis</i>	3	1.09	49.9	Yes	3.3
	Brush cuckoo	<i>Cacomantis variolosus</i>	5	0.97	37.8	Yes	3.3
	Yellowbill	<i>Ceuthmochares aereus</i>	3	1.33	63.8	No	0.0
	Horsfield's bronze-cuckoo	<i>Chrysococcyx basalis</i>	8	0.62	22.6	Yes	3.3
	Dideric cuckoo	<i>Chrysococcyx caprius</i>	5	0.77	32.0	Yes	3.3
	Shining bronze-cuckoo	<i>Chrysococcyx lucidus</i>	11	0.69	22.2	Yes	3.3
	Little bronze-cuckoo	<i>Chrysococcyx minutillus</i>	1	0.58	15.5	Yes	3.3
	Black-eared cuckoo	<i>Chrysococcyx osculans</i>	1	0.73	28.0	Yes	3.2
	Great spotted cuckoo	<i>Clamator glandarius</i>	5	1.90	153.5	Yes	3.3
	Common cuckoo	<i>Cuculus canorus</i>	10	1.57	113.0	Yes	3.3
	Pallid cuckoo	<i>Cuculus pallidus</i>	5	1.43	81.6	Yes	3.3
	Oriental cuckoo	<i>Cuculus saturatus</i>	6	1.58	99.9	Yes	3.3
	Common koel	<i>Eudynamys scolopacea</i>	7	2.46	232.7	Yes	3.3
	Long-tailed koel	<i>Eudynamys taitensis</i>	2	2.00	117.3	Yes	3.3
	Chestnut-breasted Malkoha	<i>Phaenicophaeus curvirostris</i>	4	2.92	126.0	No	0.0
	Red-crested Malkoha	<i>Phaenicophaeus superciliosus</i>	3	2.51	102.3	No	0.0
Green-billed Malkoha	<i>Phaenicophaeus tristis</i>	3	2.30	124.0	No	0.0	
Channel-billed cuckoo	<i>Scythrops novaehollandiae</i>				Yes	3.1	
Neomorphidae	Greater Roadrunner	<i>Geococcyx californianus</i>	9	3.49	302.7	No	0.0

Note. Parasitism score was determined using the system of Krüger & Davies (2002) and taxonomy follows Monroe & Sibley (1997).

body masses were log-transformed prior to analysis. Again, the results for both conventional and phylogenetic approaches are provided. In the former, body mass, the Krüger and Davies' (2002) score and the interaction between the two were used as covariates of brain volume. In the latter, the same statistical approach applied, but instead of species values, independent contrasts (Felsenstein, 1985; Harvey & Pagel, 1991) were calculated for each of the three phylogenies. Independent contrasts is the most frequently performed and statistically robust comparative method available (Diaz-Uriarte & Garland, 1998, 1996; Garland & Ives, 2000; Garland, Harvey, & Ives, 1992; Martins & Garland, 1991; Martins & Hansen, 1996; Martins, Diniz-Filho, & Housworth, 2002). Briefly, it involves comparing traits at nodes throughout a phylogeny and scaling the comparisons by the branch lengths. These were calculated in the PDTREE program of the PDAP software package using actual branch lengths from the three phylogenies (Aragon et al. 1999; Hughes, 2000; Johnson et al., 2000). Adequate standardization of the contrasts was checked and the multiple regression model was forced through the origin following Garland, Harvey, and Ives (1992).

Results

In all instances, the phylogeny-corrected F values exceeded those of the conventional F values for the effect of brood parasitism, but not the interaction between brood parasitism and body mass (Table 2). That is, the intercepts of the lines were significantly different, but the slopes were not (Figure 2). This means that parasitic species have relatively smaller brains than nonparasitic species.

When compared against the phylogeny-corrected F values, a significant effect of brood parasitism was only present using the Aragon et al. (1999) phylogeny and not the other two phylogenies (Table 2). In other words, two of the phylogenies yielded no significant difference in relative brain volume (Hughes, 2000; Johnson et al., 2000), but one phylogeny supported the original observation that parasitic species have relatively smaller brains than nonparasitic species. Thus, the ANCOVAs using a binary coding system of brood parasitism yielded ambiguous results, despite the smaller relative brain size of brood parasites that is apparent in the scatterplot (Figure 2).

Multiple regressions using the alternative scoring system of Krüger and Davies (2002) produced similarly mixed results. The analyses of species data yielded a significant effect of the parasitism score, $F(1, 26) = 10.71, p < 0.01$, but not the interaction between the parasitism score and body mass, $F(1, 26) = 0.28, p = 0.60$. That is, relative brain size decreases with an increasing brood parasitism score. Independent contrasts analyses also yielded a significant effect of the parasitism score using the Aragon et al. (1999) that suggested the same relationship between parasitism and relative brain size. This was not, however, corroborated by independent contrasts analyses using the other two phylogenies (Table 3). Thus, both sets of analyses yield ambiguous results.

Discussion

Are Brood Parasitism and Relative Brain Size Correlated?

Although the analyses of species data did support the prediction that parasitic species would have relatively smaller brains, the incorporation of phylogenetic information yielded mixed results. Thus, it remains unclear whether there is a difference in relative brain size between parasitic and nonparasitic cuculiforms. There are at least two reasons why the results may have been mixed.

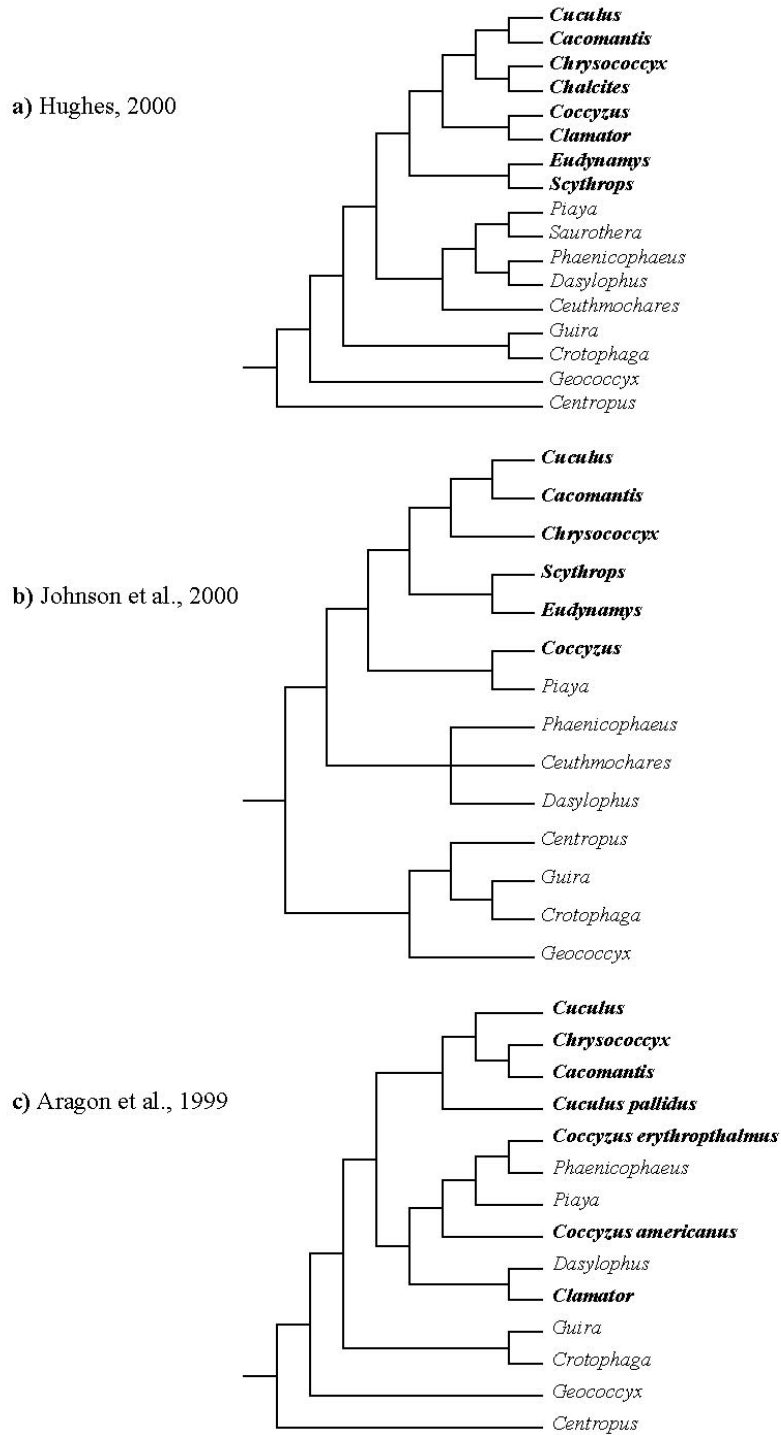


Figure 1. Three alternative phylogenetic trees of cuculiforms (Cuculiformes) are shown as follows: **a)** Hughes (2000), **b)** Johnson et al. (2000) and **c)** Aragon et al. (1999). Parasitic genera are shown in bold italics and nonparasitic genera in italics. Also note that *Chalcites* refers to the Australian species of *Chrysococcyx* (*basalis*, *lucidus*, *minutillus* and *osculans* in Table 1) and *Dasylophus* refers to the Red-crested Malkoha (*Phaenicophaeus superciliosus*) in Table 1.

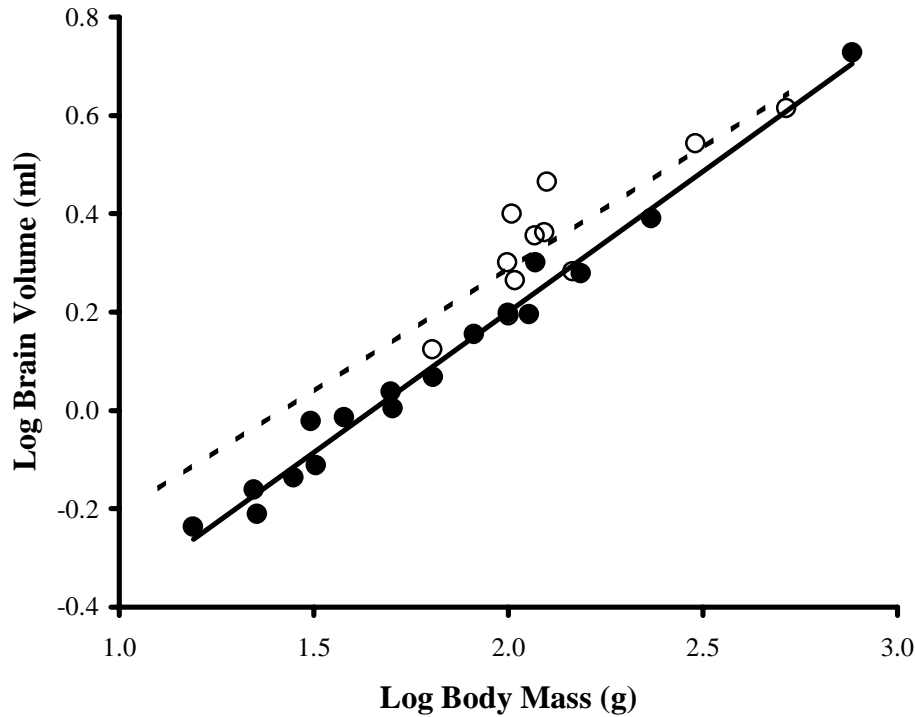


Figure 2. A scatterplot of log-transformed brain volume (ml) against log-transformed body mass (g) for the 28 cuculiforms measured is shown. Brood parasitic species are indicated by the filled circles and nonparasitic species by the open circles. Linear least-squares regression lines for the parasitic (solid) and nonparasitic (dotted) species are also shown.

Firstly, the comparative statistics used may have been too conservative. Although the use of phylogenetically-based statistics substantially reduces the chance of a type II error (Garland et al., 1992, 1993; Harvey & Pagel, 1991; Martins & Garland, 1991), there have been suggestions that it may increase the chance of type I errors under certain conditions. For example, if changes in a trait do not evolve via a Brownian motion model, significant relationships may not be recognized (Diaz-Uriarte & Garland, 1998, 1996; Diniz-Filho & Tôrres, 2002; Martins, 1996; Martins et al., 2002). Similarly, adaptive radiations can also affect the validity of some comparative tests (Harvey & Rambaut, 2001; Price, 1997). In this instance, the problem may lie in the number of times a trait has arisen within the phylogeny. The only phylogeny that provided a significant result was also the phylogeny that presented the greatest number of evolutionary changes in brood parasitism (Figure 1). In contrast, the highest critical F was calculated using Hughes (2000) phylogeny, which indicated a single origin. This problem is then compounded by phylogenetic uncertainty, which can result in large deviations in contrast values if species are not placed adjacent to true sister taxa (Symonds, 2002). Clearly, there are some significant issues affecting the use of phylogeny-based statistics that require resolution if they continue to be used (see below).

Table 2
The F Values Calculated in ANCOVAs Using Brood Parasitism and Body Mass as Covariates of Brain Volume.

Phylogeny	Slope	Intercept
Hughes, 2000 (df = 26)		
Gradual	8.35	26.26
Speciational	8.60	25.53
Conventional	4.26	4.24
Calculated	0.92	13.13
Johnson et al., 2000 (df = 24)		
Gradual	6.79	14.71
Speciational	8.08	23.11
Conventional	4.28	4.26
Calculated	1.06	10.35
Aragon et al., 1999 (df = 22)		
Gradual	6.99	12.06
Speciational	6.70	12.35
Conventional	4.32	4.28
Calculated	0.82	12.93

Note. All F values are tested at $\alpha = 0.05$. Note that the only calculated F value to exceed the phylogeny-corrected F values was that for the intercepts in the Aragon et al. (1999) phylogeny. The degrees of freedom of each comparison is shown in brackets.

Table 3.
Results of Multiple Regression Models of Brain Volume Contrasts Using Body Mass Contrasts and Contrasts of the Brood Parasitism Scoring System of Krüger and Davies (2002) as Independent Variables.

Analysis Type	F	P
Hughes, 2000 Contrasts (df = 25)		
Parasitism Score	0.18	0.67
Parasitism Score x Body Mass	0.08	0.78
Johnson et al., 2000 Contrasts (df = 23)		
Parasitism Score	0.01	0.94
Parasitism Score x Body Mass	2.34	0.14
Aragon et al., 1999 Contrasts (df = 21)		
Parasitism Score	4.53	0.04
Parasitism Score x Body Mass	3.23	0.09

Secondly, parasitism may not be correlated with a significant change in relative brain size. A cursory examination of parasitic species of two other distantly related taxa, however, yields mixed results despite possessing similar adaptations to the cuckoos. Two parasitic cowbird species (*Molothrus ater* and *Scaphidura oryzivora*) are not significant outliers compared with other New World blackbirds

(Icterini; Figure 3a). In contrast, the paradise whydah (*Vidua paradisaea*) does appear to have a noticeably smaller brain relative to its body size than other estrildine finches (Figure 3b). A direct comparison between the paradise whydah and a species with a similar brain volume (approximately 0.63 ml), the diamond firetail (*Stagonopleura guttata*), reveals that the whydah possesses a larger body mass (22.2 g) than the firetail (19 g). Unfortunately, information on brain size for other interspecific brood parasites, such as the black-headed duck (*Heteronetta atricapilla*), cuckoo finch (*Anomalospiza imberbis*) and the honeyguides (Indicatoridae, Piciformes), could not be obtained for further comparisons of parasitic and nonparasitic species that could yield less ambiguous results.

It should be emphasised that the lack of correlation between overall brain size and brood parasitism does not necessarily indicate a lack of correlated evolution between the brain and brood parasitism. Since brain regions can change in size independently of one another, it is likely that changes in the size of individual brain regions are correlated with brood parasitism. In the cowbirds, parasitic species possess significantly larger hippocampal formations relative to both their body mass and their telencephalic volume than the nonparasitic bay-winged cowbird (*Molothrus badius*; Reboreda et al., 1996) as well as other icterines (*Agelaius phoeniceus* and *Quiscalus quisicala*; Sherry et al., 1993). Furthermore, there are sex differences in the size of the hippocampal formation that are related to whether the male accompanies the female while she is parasitizing host nests (*Molothrus rufoaxillaris*) or not (*M. bonariensis*; Reboreda et al., 1996). Thus, variation in some brain regions does appear to be correlated with brood parasitism, but whether the same relationship applies to cuckoos remains unknown, as it was not possible to collect fresh brains of any cuculiform species for volumetric analyses.

Apart from the hippocampal formation, there are several other important aspects of neuroanatomy that may be related to a parasitic lifestyle. For example, as discussed previously, hatchling cuckoos are more precocial than the hosts' hatchlings. Given that relative brain size and development are correlated in birds (Bennett & Harvey, 1985; Iwaniuk, 2003; Iwaniuk & Nelson, 2003; Nealen & Ricklefs, 2001; Starck & Ricklefs, 1998; Sutter, 1951), the brains of hatchling cuckoos likely differ in both relative size and structure from that of the host's hatchlings. Specifically, hatchling cuckoos could be expected to have relatively larger brains than host hatchlings (Starck & Ricklefs, 1998; Sutter, 1951) with larger telencephala and larger paleostriatal areas within the telencephalon (Iwaniuk, 2003). In addition, the aforementioned ability of some cuckoo hatchlings to eject host nestlings from the nest could reflect more advanced development of the cerebellum, motor areas of the telencephalon and the peripheral nervous system. Perhaps the most intriguing aspect of cuckoo nestling behavior is the ability of several species to mimic host nestlings (McLean & Waas 1991; Payne & Payne, 1998; Redondo & Arias de Reyna, 1988). What makes this behavior intriguing is that the similarity in begging calls between the cuckoo and host nestlings is not innate. Instead, the cuckoo nestling appears to learn the begging calls of its nestmates early in its development. In most instances, the similarity in note structure between the cuckoo and host nestlings is moderate to slight (Payne & Payne, 1998), whereas they are highly similar in temporal structure (Butchart et al., 2003; Payne & Payne, 1998). Regardless of how well the cuckoo chicks mimic, it is clear that the cuckoo chicks do learn some aspects of the begging calls of the host chicks. Similar types of vocal learning are associated with the evolution of brain nuclei that are specific to vocal learning, pro-

duction and perception (Gahr, 2000; Jarvis et al., 2000; Nottebohm, 1999), so it is reasonable to predict that some neural adaptation(s) may be present in cuckoo chicks that modulate and/or control their ability to mimic. Further research into this phenomenon in cuckoos could therefore yield insight into the evolution of vocal learning and the neuroanatomical structures associated with it.

Unfortunately, sufficiently detailed descriptions of the behavioral ontogeny or neural development of any cuculiform is currently wanting. Assessing whether there are developmental differences between the young of parasitic and nonparasitic species is hampered by variability in the growth rates of parasitic chicks depending upon the host species (Kleven et al., 1999). That is, the growth rate of cuckoo chicks increases with the body mass of the host species. Despite fledging at approximately the same age, fledgling cuckoo chicks raised by larger parents have significantly larger body masses (Kleven et al., 1999). Thus, any interspecific comparison of growth rates or behavioral ontogeny would require either a controlled ratio of parasite to host body mass or as wide a selection of hosts as possible for each parasite as well as the use of morphological (Butler & Juurlink 1987) and behavioral (Nice 1962, 1943) developmental staging techniques. Given the secretive nature of many cuculiforms, this will be a difficult task to accomplish.

Problems Associated With the Comparative Method

As demonstrated by the results presented above, both the implementation and interpretation of the results of comparative analyses are not always straightforward. Although relative brain size is a crude measure (as discussed above); a similar scenario could have ensued had relative brain size been replaced with hippocampal formation, septum, neostriatum or any other brain region. For that matter, it could just as readily apply to a comparison of demographic, ecological, morphological or behavioral variation and interspecific brood parasitism.

Most phylogenetically based comparative methods rely heavily upon two assumptions: Phylogenetic relationships are known and evolutionary changes in a trait occur according to a Brownian motion model (Harvey & Pagel, 1991). Phylogenetic accuracy has often been suspected of affecting the use of all phylogenetically based methods (Ryan 1996), but the actual effects of inaccuracy have remained relatively unexplored. A recent study by Symonds (2002), however, demonstrates the potential severity of topological errors on the performance of independent contrasts analysis. Errors at the tips of the phylogeny can have a greater effect on the calculation of independent contrasts than errors deep within the phylogeny. Thus, relationships between species within clades have a greater effect than relationships between families, orders, etc. This does raise concerns regarding the ability of these methods to test for grade effects and specific hypotheses. Equally troubling is the difference in independent contrasts calculated from molecular versus morphological phylogenies (Symonds & Elgar, 2002). At present, there is little that can be done to alleviate this problem, but it clearly requires closer scrutiny if the use of independent contrasts is to persist.

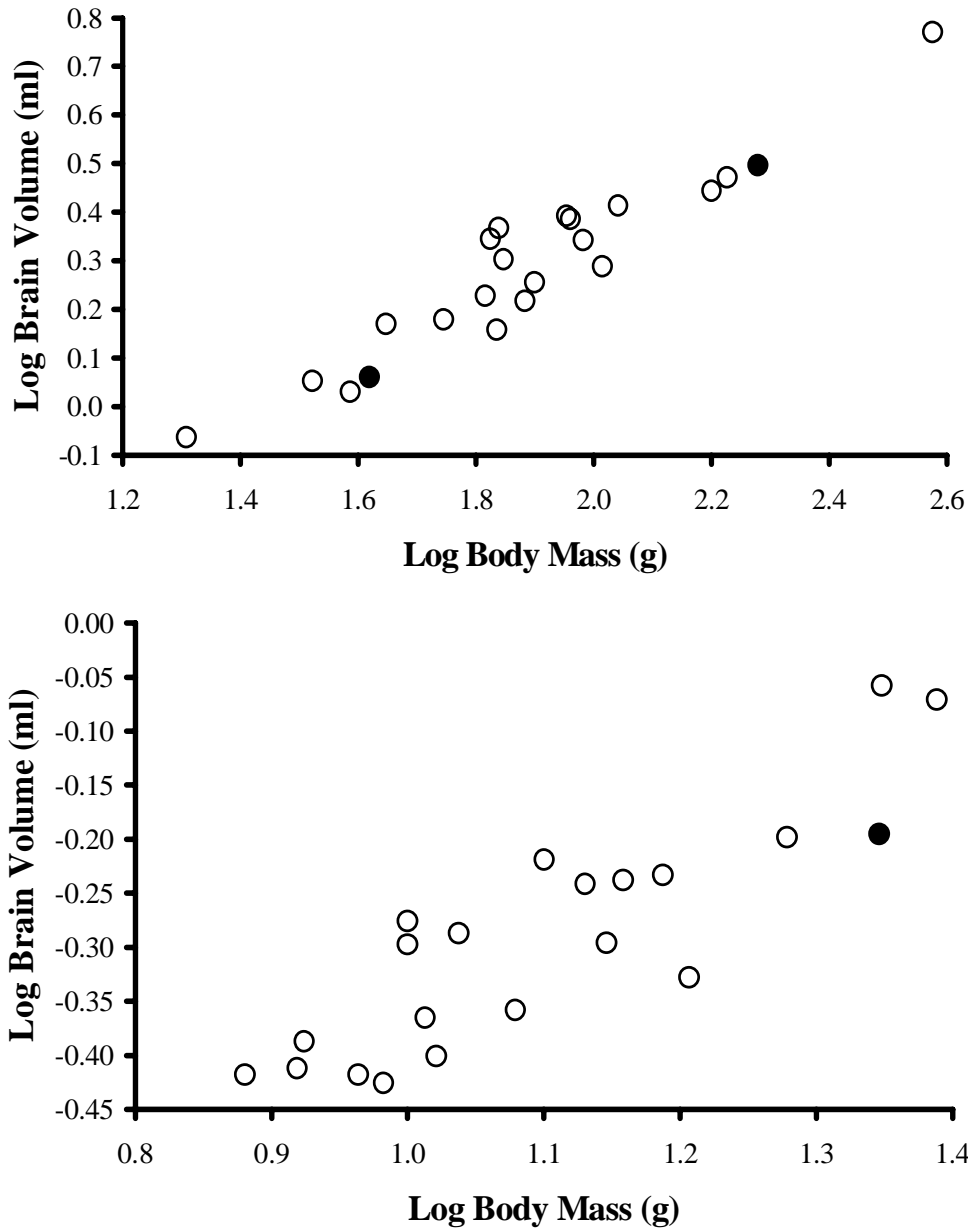


Figure 3. A scatterplot of log-transformed brain volume (ml) against log-transformed body mass (g) is shown for: **a)** New World blackbirds, orioles and cowbirds (Icterinae; 22 species); and **b)** estrildine finches (Estrildinae; 22 species; all data from Iwaniuk, 2003). The parasitic species are represented by the filled circles whereas the nonparasitic species are the open circles.

Deviations from Brownian motion models of evolutionary change are also cause for concern. Brownian motion describes evolutionary changes in a trait that are normally distributed at any time point with variation proportional to the interval between time points and the values are independent of the original character state (Martins & Hansen, 1996). It therefore describes characters responding to genetic drift, selection that fluctuates in direction, or stabilizing selection around an optimum value that evolves according to Brownian motion (Felsenstein, 1985; Hansen,

1997; Hansen & Martins, 1996). Although branch lengths can be mathematically transformed (e.g., logistic, power transformations) to account for different models of evolutionary change (Diaz-Uriarte & Garland 1998, 1996; Garland et al., 1992), these are not always successful (Diaz-Uriarte & Garland 1998, 1996; Diniz-Filho & Tôrres, 2002; Harvey & Rambaut, 2000; Martins et al., 2002). This is particularly true for adaptive radiations where branch lengths are functionally zero (Harvey & Rambaut, 2000; Price, 1997). While there is no reason to assume that brain size or structure has evolved via other patterns of change, there is similarly no reason to assume that they have evolved via a Brownian motion model. The recently developed methods of testing for phylogenetic signal (Abouheif, 1999; Blomberg et al., 2003; Diniz-Filho et al., 1998; Freckleton et al., 2002) could be used to assess whether the Brownian motion model applies to the evolution of differences in avian brain size and structure. This is unlikely to resolve which phylogeny should be used, however, as different models of evolutionary change could be present in each one of them, but only one (or alternatively none) of the phylogenies reflects the true relationships.

The serious nature of these problems begs the question: should phylogeny-based methods continue to be used? Given that skews in data (e.g., Iwaniuk et al., 1999b) and highly inflated type II errors (Martins & Garland, 1991) occur when phylogenetic information is ignored, I would suggest that they should continue to be used. They should not, however, be used exclusively and should always be used in conjunction with conventional statistical techniques (i.e., species as independent data points). Consistent results obtained across statistical methods can then be used to judge whether correlations are real or not. This is why multiple methods were employed throughout this study and should continue to be used, despite the strict use of only one method by many researchers (e.g., Barton & Harvey, 2000; Finlay, Darlington, & Nicastro, 2001). Alternatively, the use of the aforementioned methods of testing for phylogenetic signal can be used to assess whether independent contrasts or other methods should be employed.

Even if multiple methods are used, there is still the potential for mixed results as presented above. It is at this stage that interpretation becomes even more crucial. In this sense, both Bolhuis and Macphail (2001) and Hampton et al. (2002) are correct in their assertion that it is interpretation and not methodology that is the problem. I have attempted to approach this issue by suggesting possible reasons for the mixed results without addressing whether the correlation is present or not simply because there is insufficient information to make that determination. However, if a significant correlation was present, it is important to emphasize that this describes a correlation effect and not a causal one. This is perhaps the most significant drawback of the comparative method, that only correlations or relationships can be detected or tested and not causation (see Bolhuis & Macphail, 2001). In many instances, the correlations may yield insight into causal mechanisms, but this is not always the case. This should not detract from the potential importance of comparative studies in behavioral neuroscience as they have provided significant insight into the function of brain regions (e.g., hippocampal formation). It is, however, important to realize this limitation when attempting to extrapolate comparatively based correlations to causal mechanisms.

Conclusion

The ambiguous results of this case study represent a prime example of the problems encountered when comparing neural and behavioral variation in any taxon. Paucity of data, uncertainty of phylogenetic relationships, and deviations from Brownian motion models of evolutionary change may all combine to cause ambiguous results. From the perspective of avian functional neuroanatomy, the only solution to these shortcomings is to continuously add to existing databases by systematically collecting data on a wider range of species. This must, however, be combined with further research into phylogenetically based comparative methods if independent contrasts and other methods are to continue to be used. Together, these approaches may enable more robust analyses and more consistent results.

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