## **ORIGINAL ARTICLE**

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# Is the link between forebrain size and feeding innovations caused by confounding variables? A study of Australian and North American birds

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Abstract The short notes of ornithology journals feature new and unusual feeding behaviours, which, when systematically collated, could provide a quantitative estimate of behavioural flexibility in different bird groups. Previous studies suggest that taxonomic variation in the frequency of new behaviours (innovations) is correlated with variation in relative forebrain size. Recent work on primates shows, however, that observer bias can affect innovation frequency. We assess this possibility in birds via three estimates in North America and Australia: the number of full-length papers in academic journals, the frequency of photographs in birding magazines and a questionnaire on reporting bias given to ornithologists at a meeting. We also look at sampling effects due to single journal sources by doing a split-half analysis of our North American database (The Wilson Bulletin vs. six other journals) and adding three new Australian journals to the one we had used previously. In multiple regressions that also included species number per taxon, none of the potential biases could account for the correlation between forebrain size and innovation frequency. Species number was the best predictor of full-length paper frequency, which was the best predictor of photograph numbers. Ornithologists are not preferentially interested in innovative, large-brained taxa, suggesting that the correlation between innovations and neural substrate size is not a spurious effect of the biases examined here.

**Keywords** Feeding innovations · Relative forebrain size · Confounding variables · Birds

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## Introduction

When birds display behaviours that deviate from their species' norm, ornithologists routinely report this in the short notes section of avian journals. Most often, the notes record sightings of a species outside its known range, but the second most frequent category concerns feeding innovations, i.e. unusual, rare or unreported food types and foraging techniques. The frequency with which a taxon appears in these notes could yield a quantitative estimate of its feeding flexibility. All other things being equal, birds that have a broader diet (generalists), respond more quickly to new feeding possibilities (opportunists) and show innovative solutions to feeding problems should be featured in more notes. A larger neural substrate for processing and integrating information could be associated with innovative feeding (Wyles et al. 1983). Short note frequency, corrected for species number, is correlated with relative size of the forebrain across avian taxa (Lefebvre et al. 1997, 1998), in particular that of the hyperstriatum ventrale, the telencephalic equivalent of the mammalian neocortex (Timmermans et al. 2000).

Reader and Laland (1999) have reported a similar association between innovation rate and relative size of the neocortex in primates. In correcting for possible biases, however, Reader and Laland (1999) found a significant effect of research effort on innovation frequency, a bias they removed through partial correlations. Observer bias may have had a similar confounding effect in our previous work on birds. In this paper, we assess this possibility in three ways. Like Reader and Laland (1999), we first estimate the number of full-length papers published on each avian taxon. Contrary to short notes, whose starting point is a serendipitous observation with a low probability of occurrence and a very short time frame, full-length papers reflect a deliberate and sustained effort that involves grant requests, research permits and long hours in the field. If feeding anecdotes are only chance events that occur in the context of these directed studies, then full-length paper frequency should account for innovation rate. Our second

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estimate of observer bias uses birding magazines. One of the reasons birds are so intensively observed by both academics and amateurs is their aesthetic appeal. If some taxa are more interesting to ornithologists than others, this might skew anecdotal reports in their favor. Full-length research papers can assess academic biases, but not those of amateur ornithologists. Birding magazines offer this possibility and the number of photographs of different avian taxa in these publications may be a good estimate of differential appeal. We focus on the two areas of the world where sufficient photographic data were available to us: North America and Australia. Our third measure of observer bias is more direct. Using a questionnaire, we asked a group of professional ornithologists attending an annual meeting in North America whether they would be more likely to notice and report a feeding innovation if it occurred in a particular taxonomic group.

Previous work on birds reveals a further problem that we examine here: the effect of sample size and restricted journal sources. For Australia and New Zealand, Lefebvre et al. (1998) had collated their innovation reports from a single journal per country, yielding sample sizes (Australia: 105 cases; New-Zealand: 54 cases) that were much smaller than those available in North America and the British Isles (Lefebvre et al. 1997). Phylogeny had a significant effect on the association between innovation rate and forebrain size in the Australian data set (Lefebvre et al. 1998), but not in a much larger database collected for Europe (507 cases from 11 journals; Nicolakakis and Lefebvre 2000). This raises the possibility that the Australian result is an artifact due to a small sample from a single journal, rather than a true effect of phylogeny in that particular avifauna. Here, we increase the sample size for Australia by looking at three journals we were unaware of in the previous study. We also examine the biasing effects of single journal sources by using a peculiarity of our North American database, the fact that one journal. The Wilson Bulletin, accounts for half the innovation cases. We do a split-half analysis of the North American data to see whether innovations reported in The Wilson Bulletin show different trends from those reported in six other journals.

Finally, we incorporate two confounding factors known to affect comparative work on avian brains: juvenile development mode and phylogeny. Taxa often share several traits because they inherited them from a common ancestor (Felsenstein 1985; Barraclough et al. 1998). Previous work on innovations minimized this possibility by using taxonomic levels where ancestry was very remote, i.e. the order (Lefebvre et al. 1997) and the parvorder (Lefebvre et al. 1998), but DNA hybridization measures of phyletic distance (Sibley and Ahlquist 1990) can be used even at these levels to factor out phylogeny. Nidicolous birds also have relatively larger brains as adults than do nidifugous ones (Portmann 1946). This difference could apply to innovation rates and lead to a spurious effect of the type found for ecological variables by Bennett and Harvey (1985).

#### **Methods**

#### Innovations

The short note sections of 11 generalist journals were examined for feeding innovation reports. For Australia, we searched Emu over the period 1940-1998 (volumes 40-98), as well as Sunbird, Corella and Australian Birdwatcher for the periods covered in the McGill library collection (Sunbird: 1970-1982, volumes 1-12; Corella: 1977–1981, volumes 1-5; Australian Birdwatcher: 1975–1982, volumes 6(4)-9). We found 140 innovation reports, of which 105 are identical to those used in Lefebvre et al. (1998); 108 of the 140 innovations were found in Emu. For North America, we targeted the 1970-1998 period and searched The Wilson Bulletin, The Auk, The Condor, The Journal of Field Ornithology, Ontario Birds, Bird Banding and The Oriole. For the first three journals, the McGill library had a complete collection for 1970-1998 (respectively volumes 82-110, 87-115, and 73-100). For the other four journals, the library had all volumes for 1980-1998 (volumes 51-69) of The Journal of Field Ornithology, 1983-1998 (volumes 1-16) of Ontario Birds, 1970-1979 (volumes 41-50) of Bird Banding and 1971–1981 (volumes 36–46) of The Oriole. Journals that deal exclusively with certain categories of birds (e.g. Journal of Raptor Research, Colonial Waterbirds) were not examined, since they carry an obvious taxonomic bias. We found 287 feeding innovations for North America, 106 of which were identical to those used in Lefebvre et al. (1997); 146 of the 287 innovations were from The Wilson Bulletin. A complete list of the 427 Australian and North American innovations is available upon request.

As in previous work (Lefebvre et al. 1997, 1998; see tables in these papers for examples of innovations and a more detailed description of our method), an innovation was defined as either the ingestion of a new food type or the use of a new foraging technique. For a given report, the food item or foraging technique had to be stated by the author to be highly unusual for the species and/or the author had to state that this was the first known published report of the behaviour. To avoid subjective bias in data collection, we based our decisions on statements made by the authors rather than our own opinion of the reports, looking for key words like "unusual", "unknown", "rare", "noteworthy", "opportunistic", "adaptable", "strange", "interesting", "not noted before", "not recorded", "not mentioned". In most cases (6 out of 7 readers), the journal searches were done by readers who were blind to the hypothesis. When a report featured several species, we credited each one with a feeding innovation. When the same innovation was mentioned more than once in the literature for a given species, we kept only the oldest report and counted the innovation as a single case. Our collection procedure is reliable: readers independently covering the same journals or different halves of the same regional data set show similar distributions of cases per taxon (Australia: r=0.853; New Zealand: r=0.843, Lefebvre et al. 1998; Europe: nesting: r=0.827; feeding: r=0.910, all P<0.001, Nicolakakis and Lefebvre 2000).

#### Biases stemming from ornithologists

The full-length paper section of the journals were sampled over the same periods as above. Of the 11 journals, 4 (Corella and Sunbird in Australia; Ontario Birds and Bird Banding for North America), which yielded 5% of the innovations, predominantly publish short articles and do not have a distinct full-length research paper section; we did not include them in this part of the analysis. In the other 7 journals, one or two issues per volume, depending on publication frequency, were selected for each journal and the species studied in all field-based full-length papers were noted. We excluded all studies done in captivity or based on data from other papers since this kind of research cannot yield innovation reports; we also excluded zoological surveys that simply name species present in a particular area, since they focus on identification, not behaviour, and can potentially skew taxonomic frequencies due to the large number of species in each paper. A total of 1677 species entries were sampled for North America and 608 for Australia.

For the photographic estimate of ornithologist interest, we looked at seven publications that were available to us: Wingspan (1993–1998), Birds International (1989–1991), International Wildlife (1971–1998), Audubon (1971–1998), National Wildlife (1972-1998), Birding (1988-1998) and Bird Watcher's Digest (1987–1998). The first one deals exclusively with Australia, while the next two offer good coverage of that country as well as other zones; the last four publications predominantly cover North America. We noted the identity of all species pictured in articles, advertisements, tables of contents and covers. When there were several photographs of the same species in the same article, we counted this as a single entry; when the same advertisement re-appeared in different issues of the same magazine, we also counted the species only once. For North America, a total of 3224 species entries were obtained from the photographs, of which 766 were from Audubon, 759 from National Wildlife, 563 from Birding and 967 from Bird Watcher's Digest. International Wildlife contributed 153 photos of North American birds. For Australia, 496 total species entries were obtained, 364 of which were from Wingspan, 43 from International Wildlife and 80 from Birds International.

Reporting bias was estimated from a questionnaire given to ornithologists attending the annual meeting of the Society of Canadian Ornithologists (McGill University, Montréal, 6–7 August 1999). Out of a possible total of 56 attending, 25 people answered the following question: "In the field, you witness a bird eating a food type that is not part of its known diet or using a foraging be-

haviour that strikes you as unusual or new. Would you be more likely to notice and report what you saw in a short note to an or-nithology journal if the bird were a..." with the names of 29 taxonomic groups (based on the molecular taxonomy of Sibley and Monroe 1990) then listed sequentially. Next to the Latin name of each taxon, one to three examples of species in the group were given (e.g. Struthioniformes: ostrich, emu, kiwi; Piciformes: woodpecker, barbet; Podicipedida: grebe). To control for possible effects of the order in which the taxa were listed on the questionnaire, one of three different versions was given to each ornithologist: one in which taxa were ordered from Struthioniformes to Passerida following the sequence used by Sibley and Monroe (1990), one in which this order was reversed, and one in which position on the list was randomized. Next to each taxonomic entry, a five-point scale was printed, where 1 corresponded to "extremely unlikely" (to notice and report) and 5 to "extremely likely"; subjects circled the appropriate number for each taxon. Mean scores per taxonomic group were calculated for this variable from the 25 questionnaires returned to us. The birds of Canada are routinely classified with the rest of North American species in ornithological handbooks and avifaunal lists. We can thus assume that Canadian ornithologists are an adequate sample for our North American data set, but the assumption is less tenable for Australian birds; we therefore restrict our use of the questionnaire results to the North American zone.

 Table 1
 Number of full-length papers, photographs and innovations per taxon for North America and Australia, as well as reporting bias for North America. Taxonomy is according to Sibley and Ahlquist (1990)

Taxon	North An		Australia						
	Papers	Photos	Reporting bias	Innovations			Papers	Photos	Innovations
				WB <sup>a</sup>	Others <sup>b</sup>	Total			
Struthioniformes	_	_	_	_	_		7	9	0
Craciformes	1	0	2.7	0	0	0	5	5	0
Phasianida	37	113	2.9	1	0	1	1	3	2
Odontophorida	6	19	2.6	0	0	0	_	_	_
Anseriformes	89	385	3.1	6	1	7	22	16	0
Turniciformes	_	_	_	_	_	_	2	1	0
Piciformes	78	101	3.5	9	10	19	_	_	_
Coraciiformes	10	10	3.3	0	0	0	7	11	4
Cuculiformes	7	25	3.1	0	6	6	8	0	1
Psittaciformes	_	_	_	_	_	_	27	76	13
Apodiformes	5	3	3.2	1	1	2	4	0	2
Trochiliformes	21	75	3.5	0	10	10	_	_	_
Caprimulgi	4	10	3.2	0	0	0	4	5	1
Columbiformes	23	33	2.6	0	0	0	10	15	3
Ralli	9	34	2.9	3	2	5	10	10	4
Grui	5	52	2.9	3	1	4	3	4	2
Scolopacida	49	140	3.5	4	1	5	19	26	0
Charadriida	211	368	3.2	16	8	24	50	48	11
Falconida	22	49	3.5	4	8	12	13	7	9
Accipitrida	69	251	3.4	15	21	36	13	15	14
Podicipedida	11	26	3.3	0	1	1	4	0	2
Phaethontida	0	2	2.7	0	0	0	3	1	0
Sulida	21	43	3.2	0	1	1	9	12	1
Ciconiida	134	419	3.3	21	21	42	90	60	15
Tyranni	53	53	3.1	6	2	8	4	5	0
Corvida	92	117	3.1	11	16	27	221	126	47
Passerida	720	896	3.4	46	31	77	72	41	9

<sup>a</sup>Innovations found in *The Wilson Bulletin* 

<sup>b</sup>Innovations found in all other North American journals

#### Phylogeny

Taxonomic distributions for the frequency of feeding innovations, the frequency of full-length papers and the frequency of photographs were tabulated for the groups listed in Table 1. Since we need genetic distance to factor in phyletic confounds, we used Sibley and Monroe's molecular taxonomy. This system is based on DNA-DNA hybridization and is currently the most comprehensive molecular phylogeny of the class Aves (Sibley and Ahlquist 1990; Barraclough et al. 1995). The taxonomic level chosen is that of the parvorder, as defined by Sibley and Monroe (1990); in taxa where this level does not exist (e.g. Psittaciformes, a single order made up of a single family), we used the next highest level, the suborder, the infraorder or the order. At such levels, there are enough taxa for multiple regressions to be feasible and for expected innovation frequencies per taxon to exceed the statistical minimum of five per cell. Nested ANOVAs also show that a greater proportion of the variance in brain size and innovation rate is found at that level than at lower ones like the family (Nicolakakis 2001). Most of the traditional orders and nearly 90% of the families based on morphological similarities are confirmed by DNA hybridization techniques (Sibley et al. 1988). Some of the more controversial findings of Sibley and Ahlquist (1990), e.g. their decision to create a very large order Ciconiiformes, are minimized by using the parvorder level; many taxa that were placed in different orders in classical taxonomies are still placed in different parvorders of the new order Ciconiiformes by Sibley and Monroe (1990), e.g. Falconiformes, classical Ciconiiformes, Charadriiformes, Pelecaniformes and Podicipediformes.

Genetic distances obtained from Sibley and Ahlquist (1990) were used to estimate branch lengths in the avian phylogenetic tree. The tree was then used to calculate independent contrasts, which are differences in trait values between adjacent pairs of nodes or terminal taxa in the tree, weighed by their genetic distance (Ricklefs and Starck 1996). Independent contrasts were generated using comparative analysis by independent contrasts (CAIC; Purvis and Rambaut 1995), then entered as data points in multiple regressions.

#### Multiple regressions

All potential confounding variables were included as independent variables in multiple regressions (SYSTAT, version 5.2) where innovation frequency was the dependent variable. All frequencies (innovations, photos, full-length papers) were ln-transformed before analysis, since they often feature very small (e.g. Apodiformes) and very large values (e.g. Passerida). As in previous work, the number of species per taxonomic group (also In-transformed) was included in all the multiple regressions. For Australia, it was determined from Simpson and Day (1996), who use the molecular taxonomy of Sibley and Monroe (1990). For North America, the number of species per taxon was determined from Scott (1987), as in Lefebvre et al. (1997), and reclassified using Sibley and Monroe (1990). Juvenile development mode was entered as a dichotomous variable (nidicolous or nidifugous, taken from Sibley and Ahlquist 1990). The final independent variable in the regressions was residual forebrain size. As in previous papers, we used data from Portmann (1947) and regressed ln(mass of the cerebral hemispheres) (his *indice hemisphérique* multiplied by his *chiffre basal*) against ln(body weight) for the 119 genera provided, then averaged the standardized residuals of these regressions at the level of the taxonomic group.

If confounding variables account for the previously reported correlation between innovations and neural substrate size, mean residual forebrain size should fail to reach significance in the multiple regressions and be replaced by one or more of the confounding variables. If common ancestry is one of these variables, then the multiple regressions conducted on independent contrasts will show a non-significant association between innovation frequency and forebrain size. If ornithologists are preferentially interested in large-brained, innovative species, then reversing the logic of the multiple regressions and placing forebrain size and innovation frequency among the independent variables and each confounding variable in turn as a dependent variable should yield significant partial correlations between the confounding variable and the two measures of behavioural flexibility.

#### Results

For each taxonomic group, Table 1 presents the frequency of innovations, photos and full-length papers found for North America and Australia. The innovation data are broken down into those taken from *The Wilson Bulletin* versus the other six North American journals. Table 1 also includes, for each taxon, mean likeliness to notice and report an innovation in North America.

Simple regressions conducted on phyletically uncorrected taxa for Australia and North America show that all the variables, except for development mode in North America, are strongly correlated with innovation frequency. In multiple regressions, however, only species number per taxon and forebrain size remain significant predictors (Table 2). None of the other confounding variables appears in the final models. In the case of research effort and photo frequency, this is due to the common effect of species number on the variables, causing them to be excluded from the multiple regressions (Table 2). The taxo-

**Table 2** Correlations between innovation frequency and the independent variables in simple regressions and *P*-values in simple (*P* simple) and multiple (*P* mult) regressions

Variable	North Amer	rica		Australia				
	r	<i>P</i> simple	P mult	r	<i>P</i> simple	P mult		
Forebrain size	0.740	< 0.001	< 0.001	0.674	0.001	0.016		
Species number	0.787	< 0.001	< 0.001	0.637	0.002	0.038		
Full-length papers	0.791	< 0.001	0.876	0.660	0.001	0.832		
Photo frequency	0.777	< 0.001	0.901	0.565	0.008	0.797		
Development mode	0.196	0.409	0.775	0.500	0.021	0.145		
Reporting bias	0.517	0.020	0.491	_	_	_		
Total $r^2$ of the regression		0.837		0.525	0.525			
F <sub>2,18</sub>		52.446		12.057	12.057			
P		< 0.001		< 0.001				



**Fig.1** Phyletic tree based on Sibley and Ahlquist (1990) for the taxonomic groups used in this study; branch lengths are proportional to genetic distance. Standardized residual of innovation frequency regressed against species number per taxon for North American and Australian birds, as well as mean standardized residual per taxon of forebrain size regressed against body weight

STANDARDIZED RESIDUAL

tree in the figure represents genetic distances estimated by Sibley and Ahlquist (1990).

As can be seen in Fig. 1, common ancestry plays a negligible role in the association between innovation rate and forebrain size. The results of the independent contrasts are very similar to those of the regressions run on the uncorrected taxa (Figs. 2, 3). Again, only species number and forebrain size remain significant predictors in both Australia and North America (Australia: forebrain P of partial correlation=0.032; species number P=0.043; all

nomic distribution of residual forebrain size and residual innovation rate (frequency regressed against species number) in both geographical zones is illustrated in Fig. 1. The





**RESIDUAL FOREBRAIN SIZE** 

**Fig.3** Correlation between independent contrasts for residual innovation rate (after regression against species number) against residual forebrain size in Australia



**RESIDUAL FOREBRAIN SIZE** 

others ns; total  $r^2=0.474$ ,  $F_{2,18}=9.073$ , P=0.002; North America: forebrain P=0.003; species number P<0.001; all others ns; total  $r^2=0.754$ ,  $F_{2,18}=29.568$ , P<0.001). Journal source has no effect on the innovation-forebrain link in North America. The multiple regression conducted on the 146 cases taken from *The Wilson Bulletin* yields identical conclusions to the one conducted on the whole data set (forebrain P=0.001; species number P<0.001; all others ns; total  $r^2=0.811$ ,  $F_{2,18}=43.879$ , P<0.001), as well as that conducted on the 141 cases taken from the six other North American journals (forebrain P<0.001; species number P=0.003; all others ns; total  $r^2=0.719$ ,  $F_{2,18}=26.555$ , P<0.001). The taxonomic distribution of innovations in the two journal sources shows a highly significant correlation (r=0.763, P<0.001, n=24).

Interesting trends emerge when we reverse the logic of the multiple regressions, placing innovation frequency among the independent variables and each confounding variable in turn as the dependent variable. Full-length paper frequency is the only significant predictor of photo frequency in both North America and Australia (P<0.001 in both zones; North America: total  $r^2=0.841$ ,  $F_{1.22}=122.354$ ; Australia: total  $r^2=0.688$ ,  $F_{1.22}=51.769$ ), while species number per taxon is the only significant predictor of fulllength paper frequency (P=0.002 for North America, total  $r^2$  of the multiple regression=0.899,  $F_{3,18}$ =63.41; P<0.001 for Australia, total  $r^2$  of the multiple regression=0.776,  $F_{1,22}$ =80.853). Ornithologists do not appear to be preferentially interested by innovative, large-brained taxa: in both geographic zones, neither residual forebrain size nor innovation frequency come out significant in the final regression models predicting research effort and photo frequency. Surprisingly, innovation frequency is the only significant predictor of reporting bias in North America (P=0.002; total  $r^2$  of the multiple regression=0.334,  $F_{1,22}$ =12.533).

## Discussion

The results of this study show that observer bias does not account for the correlation between innovation rate and relative forebrain size in North American and Australian birds. All our estimates of bias are significantly associated with innovation frequency when taken alone (Table 2), but are eliminated in multiple regressions when forebrain size and species number are entered. Contrary to earlier work on Australia, our study further shows that common ancestry plays a negligible role in the association between innovations and forebrain size. Since common ancestry also fails to account for the innovation-forebrain correlation in Western Europe (Nicolakakis and Lefebvre 2000), we can only conclude that the previous phyletic effect on the Australian data was due to sampling error, a possibility raised in that paper (Lefebvre et al. 1998). Our splithalf analysis of the North American data suggests that a single journal source has no effect on the association between innovation rate and forebrain size when samples are large enough (over 140 cases in each of the halves). A similar conclusion was reached for Europe, where the journal British Birds provides a large proportion of the total database (Nicolakakis and Lefebvre 2000).

The results on research effort, reporting bias and ornithologist interest reveal consistent patterns. All three variables fail to predict innovation frequency when species richness per taxon and forebrain size are included with them in multiple regressions. Conversely, neither photo nor full-length paper frequency are predicted by innovation rate, forebrain size or development mode. Researchers thus do not appear to preferentially study largebrained, nidicolous, innovative taxa, nor do they publish more feeding anecdotes on the taxa they study and photograph more intensively. As far as reporting bias is concerned, an intriguing trend emerges in North America, where bias does not predict actual published innovation frequency, but is instead predicted by it. The ornithologists sampled appear to expect what the literature actually publishes, but provide no evidence that, all other factors being equal, they publish anecdotes based on their expectations. We are not sure why this is the case but the same trend is found in Western Europe (Nicolakakis and Lefebvre 2000), suggesting it is consistent at least for the Holarctic avifauna.

Taxonomic variation in feeding innovation frequency thus appears to be determined by two major variables: the diversity of the taxon, as well as its mean relative forebrain size. It was obviously not the goal of this paper to test all the variables that significantly predict interest and effort by ornithologists; our purpose was to test the restricted role of avian innovation rate and brain size both as independent and dependent covariates of ornithologist behaviour. Factors like conservation needs could explain a large part of the residual variance in effort and interest: during the writing of this paper, for example, four of the cover photos on current publications in the McGill library (*Natural History, International Wildlife, Canadian Field Naturalist, Vår Fågelwärld*) featured cranes, which are endangered in many parts of the world.

Up to now, taxonomic variation in innovation rate has proven to be a reliable and easily quantified index of feeding flexibility in the field. Anecdotal data should be treated with caution (reviewed in Mitchell et al. 1997 and the open peer commentary following Whiten and Byrne 1988), but they may solve some of the problems inherent in other comparative approaches, which rely on indirect, ecological correlates of flexibility (e.g. frugivory assumed to require more memory than folivory, Clutton-Brock and Harvey 1980) or ad hoc expectations about learning performance in captivity (e.g. Gossette and Riddell 1966). Innovation rate, which the present study suggests is an intrinsic property of avian groups, not of ornithologists, common ancestry or development mode, is a promising tool that could be applied to other correlates of flexibility and to other animal taxa (e.g. primates, Reader and Laland 1999). For example, Sol and Lefebvre (2000) have shown that colonization success of birds introduced into New Zealand can be predicted by both forebrain size and innovation rate. Other links between flexibility and evolutionary ecology need to be tested, in particular the prediction made by Wyles et al. (1983) that innovative, largebrained taxa can fix mutations at a higher rate, since their flexibility raises the probability of encountering environmental conditions favorable to the phenotypic change.

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