FEEDING INNOVATIONS AND FOREBRAIN SIZE IN AUSTRALASIAN BIRDS

by

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Summary

Many authors have proposed that behavioural flexibility in the field is associated with learning ability in captivity, relative forebrain size and rate of structural evolution. In birds, the frequency of feeding innovations reported in the short notes sections of ornithology journals may be a good way to operationalize flexibility. In this paper, we examine in the birds of Australia and New Zealand the relationship between forebrain size and innovation frequency found in a previous study covering North America and the British Isles. From a methodological point of view, the two variables are highly reliable: innovation frequency per taxonomic group is similar when different readers judge innovation reports and when different editorial styles govern journals; relative forebrain size yields very similar estimates whether mean residuals from a log-log regression are used or ratios of forebrain to brainstem mass. Innovation frequency per taxon is correlated between the two Australasian zones and between these zones and the more northerly ones studied previously. Innovation frequency is also associated with relative forebrain size in Australia and, to a lesser extent, in New-Zealand; in Australia, parrots show the high frequency of innovations predicted by their large forebrain, but yield no innovations in the New Zealand sample. The forebrain/innovation trend is independent of juvenile development mode, but phylogeny appears to be an important intervening variable in Australasia, as evidenced by non-significant independent contrasts.

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Introduction

When ornithologists witness new or unusual feeding behaviours in birds, they often report these in the short notes section of avian journals. Systematically collated and quantified, these notes may be a good way to operationalize opportunism, adaptability and behavioural innovation rate in animals. Several authors have proposed that these variables are related to learning ability (Johnston, 1982; Gould & Marler, 1984), brain size (Klopfer, 1962; Jolicoeur *et al.*, 1984; Stephan *et al.*, 1988; Harvey & Krebs, 1990; Dunbar, 1992; Byrne, 1993) and rate of evolution (Wyles *et al.*, 1981; Wilson, 1985).

In a systematic survey of avian journals covering North America and the British Isles, Lefebvre *et al.* (1997) have shown that the number of feeding innovations reported per order is remarkably similar in the two geographic zones and is correlated with relative forebrain size. For instance, hawks and falcons were featured in respectively 36 and 18 of the 322 feeding innovations collated for North America and the British Isles, while ducks contributed only 3 and 6 cases respectively to the samples. The mean forebrain size (corrected for body weight) of birds of prey is approximately one and a half times that of ducks (Portmann, 1947); hawks and falcons also represent a smaller proportion of North American and British avian species, suggesting that the difference in innovation numbers is not a simple artefact of taxonomic abundance.

In this paper, we extend the results of Lefebvre *et al.* (1997) and examine some of the assumptions and decisions that could have influenced their results. First, the geographic zones previously covered were temperate and connected over evolutionary time, a similarity that could have contributed to the high correlation between them. Second, inclusion of a given report into the final innovation corpus depended on the judgement of a single reader; although inclusion criteria were standardized and independent judgements by different readers were used for the two zones, no attempt was made to assess the inter-judge reliability of the data collection precedure. Third, the style and readership of the journals reviewed varied considerably, from academic (*e.g. The Auk*) to journals that target more the amateur ornithologist (*e.g. British Birds*); these differences in publication criteria could be a potential source of bias if one style were over-represented in a portion of the data. Fourth, a large-brained taxon, owls was eliminated a priori, since the nocturnal lifestyle of these birds precludes ornithologists witnessing most of their feeding behaviour, be it novel or normal; the few reports that do appear on owl feeding are based on fecal data. Elimination of owls truncates the brain size axis at one of its extremes, leading to a possible linear artefact if these large-brained birds really do have a low innovation rate.

Fifth, to calculate mean forebrain size per order, Lefebvre *et al.* (1997) took Portmann's (1947)'s ratio of forebrain mass for a given species divided by the brainstem mass of the Galliforme (the most 'primitive' order with a wide range of body sizes) of equivalent weight. Several authors (*e.g.* Clutton-Brock & Harvey, 1980) disagree with the phyletic assumptions of the primitive baseline technique, which has also been used in contemporary work on mammals (Stephan *et al.*, 1988) and birds (Rehkämper *et al.*, 1991); critics of the primitive baseline technique use residual deviation from the log-log regression of brain size against body weight (Jerrison, 1973; 1984). Sixth, Lefebvre *et al.* (1997) used orders as their phyletic unit; they assumed that this remote level of common descent yielded quasi-independent data points for their regressions. The DNA hybridization work of Sibley & Alhquist (1990) suggests, however, that genetic relatedness could still affect taxonomic distribution of traits even at this level. When genetic similarity between taxa is high, traits may co-vary because of phyletic inertia rather than independent ecological adaptations, leading to spurious associations that are both statistically and theoretically misleading (Harvey & Pagel, 1991). Finally, an important allometric correlate of brain size, rate of juvenile development, was not assessed in Lefebvre *et al.* (1997)'s paper; Portmann (1946) has shown that nidifugous birds have a relatively smaller forebrain as adults than do nidicolous ones, a relationship that may have an intervening effect on ecologically-relevant variables like diet (Bennett & Harvey, 1985).

In the present paper, we address these problems by examining feeding innovations in birds of Australia and New Zealand. These countries, due to their British bird-watching tradition, have active ornithologist unions publishing national journals that frequently report feeding and other (nesting, habitat, ranging, *etc*) avian innovations: *Emu* in Australia and *Notornis* in New Zealand. In terms of geography, the two countries offer striking contrasts to the zones covered by Lefebvre *et al.* (1997). New Zealand includes alpine and coastal habitats, while Australia features a humid tropical avifaunal region in the north (Torresian), a semi-arid one in the interior (Eyrean) and a mediterranean region in the south-east and south-west (Bassian); on a world scale, the Australasian avifaunal region features 15 endemic families as a result of its geographical isolation (Simpson & Day, 1996). A high correlation between innovation trends for Australia, New Zealand, North America and Europe would suggest that the relationship found by Lefebvre *et al.* (1997) is a general one.

The two countries also feature two terrestrial, diurnal orders that are situated at the extremes of Portmann's relative forebrain size continuum: the large-brained Psittaciformes (parrots, parakeets and cockatoos; 10 species in New Zealand and 55 in Australia) and the large-bodied but small-brained Struthioniformes (two species endemic to Australia, the Emu and Cassowary; three species endemic to New Zealand, the Kiwis). Inclusion of Psittaciformes, the order with the highest relative forebrain ratio in Portmann (1947), strengthens the large-brained extreme of our neural variable, which is weakened by the a priori exclusion of the taxon with the second highest forebrain size, the nocturnal owls.

Third, the change in editorial style that occurred in 1969 in the journal *Emu* allows an assessment of potential reporting biases. Starting from volume 69 (1969), anecdotal reports in *Emu* are included in two sections called 'Short Notes' and 'Short Communications' and are mostly written by authors with institutional affiliations. Prior to volume 69, the report section is more casually termed 'Stray Feathers' and authors of the notes are often amateur ornithologists (albeit experienced and sophisticated) rather than academics. As literature surveys such as ours go back in time, zoological observations are more likely to be done by such amateur naturalists and to reflect discovery of the standard repertoire of a species rather than true departures from the norm; to assess these potential effects, we therefore separately reviewed the recent 'academic' period of *Emu* (1969-1997) and an equivalent 28-year period (1940-1968) reflecting the older, more 'amateur' publication style. We also tested a second component of report reliability, the similarity in judgement made by different readers on the innovation anecdotes surveyed. Two readers, differing in level of experience, independently looked at each issue of *Emu* and *Notornis* and the similarity in their judgement was assessed at the level of innovation frequencies per taxonomic group.

We also looked at the sensitivity of different forebrain measures by comparing the forebrain/brainstem indices used by Portmann (1947) and other recent workers (Jolicoeur *et al.*, 1984; Stephan *et al.*, 1988; Rehkämper *et al.*, 1991; Lefebvre *et al.*, 1997) to the residual deviation approach advocated by other evolutionary biologists (Jerison, 1973; Clutton-Brock & Harvey, 1980). Since nidifugous birds have relatively smaller brains as adults than do nidicolous ones (Portmann, 1946), we also examined the potential confounding effects of juvenile development (Bennett & Harvey, 1985) on the relationship between forebrain size and innovation frequency. Finally, we factored in phylogeny by using the molecularly-defined equivalents of the anatomical taxa used by Lefebvre *et al.* (1997); independent contrasts (Felsenstein, 1985) were then run on the forebrain-innovation relationship via the CAIC program (Purvis & Rambaut, 1995).

Methods

Feeding inovations

The short notes sections of *Emu* and *Notornis* were exhaustively reviewed for any mention in the title or text itself of a feeding innovation. The journals are respectively published by the Royal Australasian Ornithological Union and the Ornithological Society of New Zealand. Approximately 4000 and 1350 short notes were scanned respectively in the two journals. For *Notornis*, we examined all volumes available to us, *i.e.* volume 19 (1972) to volume 44 (1997). This is very similar to the time period reviewed by Lefebvre *et al.* (1997) for North American journals. For *Emu*, we separately reviewed volumes 41 to 68 (1940-1968) and volumes 69 to 97 (1969-97).

Two independent readers examined each of the three data sets (AG and LL for *Emu* 1940-1968 and *Emu* 1969-1997; SD and LL for *Notornis*), allowing us to calculate inter-judge agreement on the distribution of innovations per bird taxon. For each data set, the two readers differed in experience and knowledge of the hypothesis: one was blind to the hypothesis and new to the research area (AG and SD), while the other was both familiar with the hypothesis and has been working on avian foraging behaviour for several years. In deciding whether to include a given report, we used the same criteria as Lefebvre *et al.* (1997): innovations were 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 (or in a few cases, clearly implied) 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. Given the difference in experience of the two readers for each data set, agreement is likely to be highest when authors of the notes actually state that behaviours are ‘unusual’, ‘unknown’, ‘rare’, ‘opportunistic’, ‘strange’, ‘not noted before’, ‘not recorded’; inter-judge agreement is likely to be lowest when authors only imply that a given behaviour is new, with the more experienced reader potentially including more cases than the less experienced one.When a report featured several species, we credited each one with a feeding innovation. Four of the reports included between 5 and 11 species each performing the same innovation; since these reports could have undue quantitative influence on our conclusions, we ran two versions of the innovation/forebrain regressions, one including the four multiple species reports and one excluding them. Table 1 presents examples of the feeding innovations found, including (in italics) key words taken verbatim from the notes indicating the novelty of the behaviour. As seen in Table 1, our definition of a feeding innovation includes suspected cases of complex cognitive processing (*e.g.* tool use, Hobbs, 1971; Green, 1972) as well as opportunistic shifts in normal foraging behaviour (*e.g.* Johnston, 1973; Moffatt, 1982).

We found 160 feeding innovations in the two journals, 108 for Australia and 52 for New Zealand (Table 2); the complete list is available upon request. Innovations that occurred in other parts of the world (*e.g.* Fidji and other Pacific islands) were excluded from the corpus even if they were published in *Emu* or *Notornis*. Innovations occurring in Australia and New Zealand, but reported in journals other than *Emu* and *Notornis*, were also excluded; this is the case, for example, with the suspected social learning of automatic door manipulation in house sparrows in New Zealand (Breitwisch & Breitwisch, 1991), which was published in *The Wilson Bulletin* and included in Lefebvre *et al.* (1997). For each area, we tabulated the number of innovations per taxonomic group, using molecularly-defined taxa that were as close as possible to those of Lefebvre *et al.* (1997). In approximately half the cases, this corresponds to Sibley and Alhquist’s orders. In the other half, the taxon corresponds to what Sibley & Ahlquist call ‘parvorders’, a division that is particularly useful for the new molecular orders that include very large numbers of species, Passeriformes and Ciconiiformes. In three cases (Ralli, Tyranni and Caprimulgi), we used Sibley & Ahlquist ‘suborder’, a decision that includes, for instance, Australian frogmouths and Holarctic nightjars in the same group for the purpose of inter-zone correlations; for suborder Tyranni, the decision brings together Nearctic Tyrant flycatchers, Australian Pittas and New Zealand Accanthisittid wrens. In the rest of this paper, we will use the terms ‘taxon’ and ‘taxonomic group’ to refer to the categories in Table 1, be they orders, parvorders or suborders. As in Lefebvre *et al.* (1997), we excluded the nocturnal owls (suborder Strigi) from our study. We also excluded penguins, since Simpson & Day (1996) state that most Australian penguin records are either of rare vagrants, winter migrants or individuals caught out and obliged to come ashore; it should be noted that this decision works against our hypothesis, since inclusion of the large-brained penguins in the highly innovative Ciconniida (Lefebvre *et al.*, 1997) would increase mean residual forebrain size for this parvorder.

Simpson & Day (1996) and Falla *et al.* (1979) provided the total number of species per taxonomic group for the two areas, a value that allowed us to correct observed innovation frequencies for the number expected on the basis of species diversity. In Australia for instance, the parvorder Corvida, which includes 35% of all species, is likely to yield more innovations than the parvorder Gruida, which has only two species; in New Zealand, the parvorder Ciconiida (25% of species) is potentially subject to the same confound. Inter-zone correlations of species number per taxon values allows us to compare Australasian

TABLE 1. *Examples of feeding innovations in birds of Australia and New Zealand*

Species	Innovation	Reference
Australia		
Southern skua	Takes milk from lactating elephant seals alongside the pups; *opportunistic feeder*	Johnston, 1973
Orange-winged sittella	Using and carrying twigs to open wood-borer grubs; *tool use*	Green, 1972
White-winged chough	Uses empty mussel shell as hammering tool to open closed mussel; *usually feeds on insects, tool use*	Hobbs, 1971
Southern giant petrel	Attacked by drowning and ate a Black-browed albatross; *no previous record*	Cox, 1978
Crimson rosella	Catching insects on the wing; *unusual method*	Stokes, 1967
Australian (Mallee) ringneck	Shredding and eating a caterpillar during a caterpillar plague; *unexpected*	McCulloch, 1966b
Pacific gull	Dropping mussels on asphalt road to break them, dodging speeding cars to eat them	Wheeler, 1946
Bald coot	Holds unripe fig with foot against hard substrate to chop it up with bill; *does not appear to be described before, elaborate method*	Rowley, 1968
Brolgas crane + Sarus crane	Predation on mice; *first report of taking mammalian prey in wild or captivity*	Brown & Archibald, 1977
Black kite	Uses bread as bait to catch fish; *unusual, no published account*	Roberts, 1982
Blue bonnet + Australian magpie + Pied butcherbird + Noisy miner	Use babblers to feed at termite gallery; *opportunistic, no records*	Moffatt, 1982
Fan-tailed cuckoo	Eats ants when foraging with Thornbills; *usually eats caterpillars, little evidence of feeding in mixed species flocks*	Bell, 1986
Shrike tit	Breaking caterpillar skin to extract digestive tube filled with partially digested leaf tissue; *learned by experience, seem to indicate a high degree of avian intelligence*	Hindwood, 1947

TABLE 1. (*Continued*)

Species	Innovation	Reference
Lyrebird	Dipping the tip of its beak into an orange and tossing each piece into its mouth; *does not appear to have been recorded, example of adaptation*	Chisholm, 1951
Silver gull	Preys in swift-like fashion on cricket plague near city from dusk to well after dark; *temporarily alter habits in a strange manner*	Hanks, 1957
Fork-tailed swift + Spine-tailed swift	Use bushfires to feed on insects caught up in pall of smoke	McCulloch, 1966a
New Zealand		
Rock wren	Softening up large grasshopper by battering it 'to a pulp' on a piece of corrugated iron; *tool use, prey very large for size of bird*	Sibson, 1974
Spotted shag + Black-backed gull	Scrounging on prey brought close to surface by associating with Hector's dolphins; *not well known, similar interactions reported elsewhere, but not in NZ*	Hawke, 1994
Asiatic whimbrel	Catching and eating crabs in avocet-like manner; *different dietary habits, first whimbrel we have seen (doing this*)	Harrison, 1980
New Zealand falcon	Predation on arboreal rat; *first record*	Read, 1985
Greenfinch + House sparrow	Taking insects from car radiator grille; *learned, initiative; developped independently (from similar innovations in UK and US*)	Flux & Thompson, 1988
Tui	Fed by probing on marine crustacea on surface; *surprising, unusual, adaptability*	Daniel, 1982
Buller's shearwater	Congregates near boats, feeds on offal; *first published report*	Langlands, 1991
Yellowhead	Ate fruits of bush lily; *so far known to be entirely insectivorous*	Child, 1978
Australasian harrier	Attacks Black-billed gull sitting on water; *unable to find a previous record*	Cooper, 1991
Spotless crake	Washed caterpillar; *feeding technique... not seen this species use*	Johnson, 1976

Terms used by authors to characterize novelty are in italics.

TABLE 2. *Frequency of feeding innovations and mean residual forebrain size per taxon in Australia and New Zealand; order of taxa corresponds to genetic proximity in Sibley & Ahlquist (1990)*

Taxonomic group	Frequency		Mean residual forebrain size
	Aus	NZ	
Struthioniformes	0	0	−0.264
Craciformes	0	na	na
Phasianida	2	0	−0.303
Anseriformes	0	1	−0.065
Turniciformes	0	na	na
Coraciformes	4	2	−0.192
Cuculiformes	1	1	−0.126
Psittaciformes	13	0	0.354
Apodiformes	2	0	−0.231
Strigi	na	na	0.319
Caprimulgi	1	na	−0.421
Columbiformes	3	0	−0.293
Otidides	0	na	na
Gruida	2	na	0.070
Ralli	3	1	−0.100
Scolopacida	0	2	−0.178
Charadriida	9	11	−0.085
Accipitrida	8	3	0.038
Falconida	4	3	0.111
Podicipedida	2	0	−0.234
Phaetontida	0	0	na
Sulida	1	3	0.007
Ciconiida	10	2	0.001
Tyranni	0	2	na
Corvida	35	12	0.257
Passerida	8	9	0.014
Total	108	52	

na = non-applicable or non-available.

and Holarctic avifaunal distributions (see Table 3), a potential confound for inter-zone similarity in innovation trends.

We used two measures of innovation frequency: the natural logarithm of innovation numbers per taxonomic group, a transformation required by the non-normal distribution of our data; as in Lefebvre *et al.* (1997), many groups yield very small frequencies (0, 1 or 2), while a few groups yield large ones (*e.g.* Corvida: 35 for Australia and 13 for New Zealand). Contrary to Lefebvre *et al.* (1997), we factored out species per taxonomic group (also ln transformed due to the presence of very small and very large values) using partial correlations instead of the χ values calculated in the previous paper; χ is not normally distributed (positive values are likely to be much larger than negative ones) and partial correlations are a much more standard way of removing the effects of a confounding variable. All analyses, except for independent contrasts, were conducted with the Systat program (Wilkinson, 1987).

Forebrain size

We used Portmann (1947) as the source of the forebrain data. Portmann's work covers 139 avian species in 119 genera. His data are presented as ratios of forebrain weight for a given species divided by the brainstem weight of the Galliforme of equivalent body weight; Portmann calls the latter measure 'indice basal' (basal index), while the forebrain ratio is called 'indice hémisphérique' (hemispheric index). Multiplying Portmann's basal index by his hemispheric index yields the actual mass of the cerebral hemispheres; the same can be done with Portmann's 'indice du tronc' (brainstem index), yielding the actual mass of the brainstem.

For each taxonomic group, we calculated, as in Lefebvre *et al.* (1997), the mean ratio of forebrain size to Galliforme baseline (FB/GB, identical to Portmann's 'indice hémisphérique') and the mean ratio of forebrain to brainstem size (FB/BS); the latter is obtained by cancelling out the Galliforme baseline (Portmann's 'chiffre basal') in both the denominator (hemispheric index) and the numerator (brainstem index) of the FB/GB ratio, yielding a measure that is independant of the evolutionary assumptions of Portmann (1947) and other, more recent, workers (Jolicoeur *et al.*, 1984; Stephan *et al.*, 1988; Rehkämper *et al.*, 1991). To calculate means per group, we first averaged Portmann's brain size data at the level of genera. Contrary to Lefebvre *et al.* (1997), we included all 119 genera found in Portmann, not simply those that occur in the geographical zones covered by the journals suveyed, under the assumption that these genera yield an unbiased sample of inter-taxon differences in relative forebrain size. To assess the relationship between these ratio measures and the residuals often used by other workers in comparative biology, we regressed ln forebrain mass against ln body weight for the 119 genera and averaged for each taxonomic group the residual deviation of each genus from this regression. Note that Strigi are included in this analysis (see mean residual forebrain size in Table 2).

To examine the potential masking effect of juvenile development on the relationship between innovations and forebrain size, we classified each taxonomic group as nidifugous or nidicolous (based on Lack, 1975, and Bennett & Harvey, 1985) and included this as a dichotomous variable in multiple regressions linking forebrain size and innovation frequency. In dealing with phylogeny, we constructed a tree based on average linkage clustering of DNA-DNA hybridization distances (Sibley & Ahlquist, 1990). This tree was then used in a phylogenetically-controlled test performed by the CAIC program (Comparative Analysis of Independent Contrasts, Purvis & Rambaut, 1995). This technique identifies sets of independent comparisons within the branching pattern of the phylogenetic tree. Independent contrasts are created by comparing the values of sister taxa; values for ancestral nodes in the phylogeny are estimated by averaging the values of extant taxa. Contrasts were standardised to homogenize variances (Garland *et al.*, 1992). The predicted association in standardized contrasts of innovation frequency and forebrain size was tested with linear regressions forced through the origin (Grafen, 1989).

Results

Feeding innovations

Table 2 presents the frequency of innovations per taxonomic group found in the Australian and New Zealand samples. As suggested by Wyles *et al.* (1981) and similar to the trend found for North America and the British Isles, Passeriformes (parvorders Passerida and Corvida) yield the highest number of reports in both zones. The large-brained Psittaciformes show a high frequency of innovations in Australia (13), as predicted, but not in New Zealand.

Innovation frequencies per group are significantly correlated between the Australian and New Zealand samples (Table 3), as the two samples are with the zones studied by Lefebvre *et al.* (1997). Frequencies obtained

TABLE 3. *Correlations between data sets for Australia, New Zealand and the two zones studied by Lefebvre et al. (1997)*

Data sets	r	p
Reliability		
Emu: readers 1 & 2	0.853	0.001
Notornis: readers 1 & 2	0.843	0.001
Emu: 1940-68 & 1969-97	0.647	0.001
Innovation frequency		
Australia & New Zealand	0.516	0.020
Australia & North America	0.625	0.003
Australia & Europe	0.557	0.013
New Zealand & North America	0.739	0.001
New Zealand & Europe	0.830	0.001
Innovation rate (residuals)		
Australia & New Zealand	0.322	0.166, NS
Australia & North America	0.667	0.001
Australia & Europe	0.343	0.150, NS
New Zealand & North America	0.524	0.026
New Zealand & Europe	0.805	0.001
Species per taxonomic group		
Australia & New Zealand	0.692	0.001
Australia & North America	0.690	0.001
Australia & Europe	0.717	0.001
New Zealand & North America	0.681	0.002
New Zealand & Europe	0.598	0.014

by different readers are strongly correlated in the two Australasian data sets, as are the innovation frequencies generated by the 1940-1968 and 1969-97 sub-samples of *Emu*. Innovation frequency is strongly affected by the number of species per taxon in Australia ($r = 0.741$, $p < 0.001$); in New Zealand, however, this effect is only marginally significant ($r = 0.446$, $p = 0.049$). In general, inter-zone correlations on innovation rates (residuals of innovations frequencies regressed against species number per taxon) are lower than those conducted on absolute frequencies (Table 3); two of these correlations fail to reach significance, those that compare the relative innovation frequency of Australia to that of New-Zealand and Europe respectively. Differences in innovation trends are more likely the cause of this than differences in species per taxonomic group, since the zone comparisons that yield the lowest correlations for relative innovation frequency (Australia *vs* New-Zealand and Europe) show the most similar avifaunal distributions (Table 3).

Forebrain size

Mean residual forebrain size is more strongly correlated with Portmann (1947)'s ratio (Fig. 1A: $r = 0.964$, $p < 0.001$) than it is with the second measure used by Lefebvre *et al.* (1997), forebrain divided by brainstem ($r = 0.913$, $p < 0.001$). The curvilinearity evident in Fig. 1A can be corrected with a logarithmic transformation of Portmann's ratio, yielding an almost perfect correlation between mean residual and ln FB/GB (Fig. 1B: $r = 0.989$, $p < 0.001$); in contrast, the relationship between FB/BS and mean residual is poorer when FB/BS is logged ($r = 0.905$). Given these trends, all tests below are conducted with mean residual per taxon as the measure of relative forebrain size.

Residual forebrain size is significantly related to ln innovation frequency in birds of Australia ($r = 0.638$, $F_{1,18} = 12.368$, $p = 0.002$; Fig. 2A) and New Zealand ($r = 0.474$, $F_{1,16} = 4.646$; $p = 0.047$; Fig. 2B: lower slope). As is evident in Fig. 2B, the data point for New Zealand Psittaciformes (letter P in Fig. 2B) has a strong effect on the regression: removing it yields an r of 0.800 ($F_{1,15} = 26.598$; $p < 0.001$; higher slope in Fig. 2B). Exclusion of the four Australian reports that include a large number of species yields very similar conclusions ($r = 0.692$, $p < 0.001$), indicating that these reports do not bias the analysis. The effect of forebrain size is not

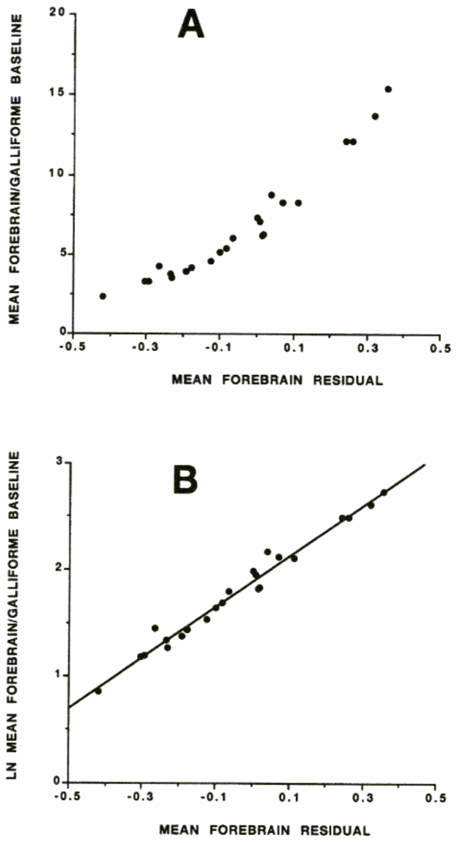

Fig. 1. Relationship between mean residual and (A) mean forebrain/Galliforme baseline ratio (Portmann, 1947), (B) mean ln forebrain/Galliforme baseline ratio.

due to the intervening effects of juvenile development mode, which is non-significant in multiple regressions for both countries (p for development effect respectively 0.109 for Australia and 0.975 for New Zealand).

Forebrain size remains the best predictor of innovation frequency even when species number per taxon is included in the multiple regressions. In Australia, both species and forebrain size remain significant (forebrain: $p = 0.032$; species number: $p = 0.042$), yielding a partial correlation of 0.492 between forebrain size and innovation rate. In New Zealand, the forebrain size effect is just below the 0.05 threshold ($p = 0.047$), while species number is non-significant ($p = 0.129$); if we conservatively allow this variable to remain in the regression, however, setting the entry thresh-

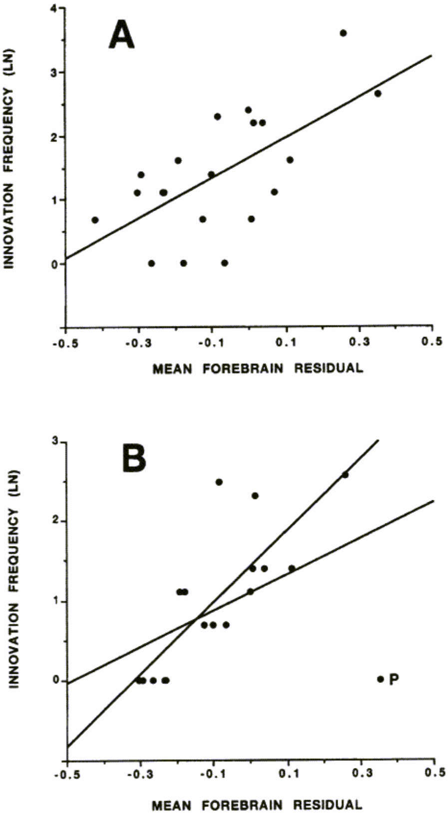

Fig. 2. Relationship between mean residual forebrain size and ln inovation frequency per taxon for (A) Australia and (B) New Zealand. The letter P in section B refers to Psittaciformes; the two regression lines in this section are based respectively on inclusion (lower slope) or exclusion (higher slope) of the Psittaciforme data point.

old at $p = 0.150$ (the default value in Systat; Wilkinson, 1987), the partial correlation between forebrain and residual innovation rate falls slightly above the significance threshold (partial $r = 0.439$, $p = 0.078$). As with innovation frequency, this borderline effect appears to be due to Psittaciformes: removing this order yields a partial r of 0.785 for forebrain size ($F_{1,14} = 24.164$; $p < 0.001$), with species number again falling above the 0.05 significance threshold ($p = 0.065$). Trends are once again independent of the four Australian cases with multiple species (same result as above, $r = 0.692$, since species effect is NS for this regression) and of mode of juvenile development (p respectively 0.180 and 0.575 for Australia and

New Zealand). Finally, independent contrasts show that the relationship between forebrain size and innovation rate in the two Australasian countries can be partially attributed to common descent: in both Australia and New Zealand, the p values of the multiple regressions on phyletically-corrected nodal values fall above significance thresholds (Australia: $p = 0.172$; New Zealand: $p = 0.098$).

Discussion

This study confirms and extends several conclusions from previous work: (1) innovation frequencies show a similar taxonomic distribution in four highly different areas of the world, two in the Northern hemisphere (Lefebvre *et al.*, 1997) and two in the Southern one; (2) innovation frequencies are positively correlated with relative forebrain size per taxon in the four areas; (3) different measures of relative forebrain size per taxon are highly correlated, suggesting that divergence of opinion on this variable has a negligible effect on the types of relationships tested here. From a methodological point of view, our study further shows that the collation of innovation reports is reliable and that the forebrain/innovation relationship is not due to intervening developmental variables.

Two of our results contrast with previous work. First, the New Zealand data show only a borderline relationship between innovation frequency and forebrain size: including the effect of species per group makes the p value of the relationship go from 0.047 to 0.078 in the multiple regressions, despite the fact that species number has a non-significant effect on innovation frequency ($p = 0.129$). Two possibilities could explain this borderline trend: the small size of the New Zealand data set or the absence of innovations in taxa that show high frequencies in other parts of the world. For example, our survey yields no reports of innovations in New Zealand Ciconiida, yet this taxon is featured in 31 reports for Australia, North America and Europe. Similarly, Psittaciformes yield 13 innovations in Australia, but none in New Zealand; this is somewhat surprising, since many parrots in both countries are opportunistic enough to adapt to habitats modified by human settlement: 5 of the 10 New Zealand Psittaciformes are found in orchards, agricultural areas and suburban gardens (Falla *et al.*, 1979), a very similar proportion to the 23 out of 55 Psittaciformes who show similar flexibility in Australia (Simpson & Day, 1996). In New Zealand, the genus *Nestor* in particular shows a degree of opportunism that is often associated with feeding innovations in other groups; the Kea (*N. notabilis*) is very exploratory, feeds on dead sheep and carrion and can forage on garbage (Soper, 1984), while the Kaka (*N. meridionalis*) is found in settled districts and city gardens (Falla *et al.*, 1979). It is therefore possible that the absence of innovations reported for New Zealand parrots is an artefact of the small size of our data set, despite the fact that 27 years were covered and that parrots are intensively studied by ornithologists. The small size of the New Zealand data set is a further argument for caution in other taxa: with a total of only 52 feeding innovations, the expected number of cases per taxonomic group is only 2.5, under the null hypothesis of random distribution over 20 taxa. The fact that larger data sets (North America, Europe and Australia all have an $N > 100$, which yields an expected > 5 per taxon for 20 groups, the traditional threshold for expected frequencies) show similar significant trends may underline an important statistical limitation of the type of data used here, the constraints on sample size that may make tests on small geographic units or taxonomic levels finer than the parvorder (*e.g.* the family, as in Bennett & Harvey, 1985) difficult to conduct.

The second most notable feature of our results is the intervening role of phylogeny in the forebrain-innovation relationship: when phyletic distance is factored into our analysis through independent contrasts, the link between forebrain size and innovation frequency falls above the significance threshold. This contrasts sharply with the pattern seen for Europe and North America: Lefebvre *et al.* (in prep.) have augmented the data set previously collected for North America and Europe and conducted a re-analysis of the trends previously reported, using, as we do here, independent contrasts on molecularly-defined orders, suborders and parvorders. Contrary to the trend for Australasia, independent contrasts yield a highly significant relationship between the two variables ($p = 0.008$ for Europe and 0.004 for North America). It is impossible at this stage to say whether the discrepancy between the Holarctic and Australasian data argues against a general, phyletically independent trend in the forebrain-innovation link. One important factor might be the representativeness of Portmann's data set, which is biased towards Holarctic species; it is therefore not surprising that the brain-behaviour relationship works better in the part of the world where the brain sample is best represented. One can possibly add to this a sampling error effect: zones with larger data sets (Lefebvre *et al.* (in prep.) have collated a total of 562 innovations for North America and Europe) yield more positive results than zones with smaller data sets (160 cases in the present paper).

Overall, the four geographic zones covered in this study and in Lefebvre *et al.* (1997) nevertheless show broadly similar trends. The similarities are more striking for absolute innovation frequency than they are for innovation rate corrected for species diversity: including the North America-by-British Isles correlations in Lefebvre *et al.* (1997), the r for innovation frequency ranges from 0.516 to 0.985, compared to a range of 0.322 to 0.805 for corrected innovation rate. To what extent these trends reflect observer bias vs bird behaviour is difficult to determine: avian taxa may be showing similar innovation trends in different parts of the world, but ornithologists may also be making similar decisions concerning the types of innovations they notice and report. One argument against observer bias is the diversity of the groups that consistently yield high innovation frequencies in the various geographic zones: Accipitrida, Falconida, Passerida, Corvida, Ciconiida and Charadriida. The taxa show sharp differences in foraging mode: Accipitrida and Falconida are aerial predators, Ciconiida are freshwater, sit-and-wait predators, Charadriida are coastal and open sea foragers on invertebrates and fish, Corvida are omnivores, while Passerida are insectivores, terrestrial frugivores and granivores. The abundance and proximity to humans of these taxa, which likely affects their observability, is also very different: Passeriformes are abundant and often feed in cities and suburban gardens; Accipitrida and Falconida have a relatively low abundance, while Ciconiida and Charadriida (except for the ubiquitous genus *Larus* and the invasive cattle egret, *Bubulcus ibis*) feed in aquatic habitats that can be difficult to reach. Finally, attention payed by professional and amateur ornithologists to the taxa is also variable: gulls are probably less sought out than songbirds and falcons. Until observer bias can be operationalized and quantitatively removed from the analysis, these arguments tentatively suggest that the innovation distributions reported here and in Lefebvre *et al.* (1997) are basic properties of the avian groups observed and not of the observers themselves.

Two features of our analysis suggest that the trends reported here and in Lefebvre *et al.* (1997) are reliable: the non-significant effect of juvenile development and the high correlations between the different estimates of our independant and dependant variables. Mode of juvenile development is not responsible for the significant trends in our data, nor was it responsible for the trends found by Lefebvre *et al.* (1997): a re-analysis of their data reveals a non-significant effect of development mode in multiple regressions (same procedure as present study; $p = 0.323$ and 0.252 respectively for North America and Europe; Lefebvre *et al.*, in prep). The cautionary note of Bennett & Harvey (1985) on brain size and ecological variables in birds therefore does not seem to apply to feeding innovations: mode of juvenile development does not seem to be linked to the forebrain/innovation relationship at the level of orders and parvorders the way it is for diet and forebrain size at the level of families. It should be pointed out, however, that the ecological theory of learning predicts a three-way association between behavioural flexibility, forebrain size and juvenile development. Johnston (1982), in the clearest exposition of the ecological view, suggests that learning should provide the greatest benefits to animal taxa that encounter more environmental variability and that delayed development (*e.g.* fledging, reproductive maturity) and larger neural structures are costs that should be traded-off against this benefit. If, as ecological theories assume, opportunism in the field is associated with learning, both costs should be related to forebrain size and development, with opportunistic animals having larger relative forebrains and a slower development due to information acquisition and growth of neural structures. As a cautionary note, it is important to point out that learning is not the only behavioural variable likely to co-vary with opportunism; opportunistic animals may also have a broader motor repertoire and a wider diet, both of which could be associated with a larger forebrain and more frequent feeding innovations.

The second technical contribution of our paper is to show that different measures of feeding innovations and forebrain size yield very similar results. As illustrated by Fig. 1A and B, Portmann (1947)'s ratio (forebrain to Galliforme brainstem) is very highly correlated with mean residuals per taxon; the ratio slightly over-estimates the forebrain size of large-brained groups, but a logarithmic transformation can easily eliminate this (Fig. 1B). The forebrain to brainstem ratio developed by Lefebvre *et al.* (1997) to do away with the Portmann's Galliforme baseline is the least reliable of the forebrain indices and should probably be dropped from further work. Disagreement between authors who use baseline indices (Portmann, 1947; Jolicoeur *et al.*, 1984; Stephan *et al.*, 1988; Rehkämper *et al.*, 1991) and those who prefer residuals from a log-log regression (Clutton-Brock & Harvey, 1980; Bennett & Harvey, 1985) therefore does not appear to have an important effect on the results of innovation/forebrain relationships.

Our study further shows that the inevitable degree of subjectivity that enters into decisions to include or not a given anecdote has little impact on the biological trends reported. Whether readers are experienced or not, they end up with similar patterns of innovation frequency per taxon, with groups like Passeriformes, Accipitrida and Ciconiida consistently providing many cases and Anseriformes, Galliformes and Columbiformes providing very few. Added to the fact that independent readers found similar trends in the two northerly data sets of Lefebvre *et al.* (1997), these results suggest that disagreement over the inclusion of a given anecdote has a negligible effect on innovation distributions. Our results also suggest that pooling of anecdotes over long historical periods from journals with different editorial styles and contributor backgrounds is reliable. The 1941-68 and 1969-97 periods of *Emu* differ on all three counts, yet yield a high correlation for innovations per taxon. The major difference between the periods lies in the number of cases found, with the 1941-1968 sample yielding twice the number of anecdotes ($N = 74$) than the more recent one ($N = 34$); the striking fact remains that these totals are distributed in similar ways among the different taxa, with Corvida, for instance, yielding respectively 26 and 9 cases in the two periods, Psittaciformes 10 and 3, and Charadriida 6 and 3. Taken together, our high inter-reader and inter-period correlations suggest that innovation frequency is a reliable way to quantify comparative differences in behavioural flexibility in the field, a variable that has long been difficult to operationalize despite its central role in ecological theories of learning.

References

Bell, H.L. (1986). The participation by cuckoos in mixed-species flocks of insectivorous birds in South-eastern Australia. — Emu 86, p. 249-253.

Bennett, P.M. & Harvey, P.H. (1985). Relative brain size and ecology in birds. — J. Zool. Lond. 207, p. 151-169.

Breitwisch, R. & Breitwisch, M. (1991). House sparrows open an automatic door. — Wilson Bull. 103, p. 725.

Brown, C.B. & Archibald, G.W. (1977). Captive brolgas and sarus cranes prey on wild mice. — Emu 77, p. 39-40.

Byrne, R.W. (1993). Do larger brains mean greater intelligence? — Behav. Brain Sci. 16, p. 696-697.

Child, P. (1978). Yellowhead not entirely insectivorous. — Notornis 25, p. 252-253.

Chisholm, A.H. (1951). Food-eating tactics. — Emu 50, p. 208.

Clutton-Brock, T.H. & Harvey, P.H. (1980). Primates, brain and ecology. — J. Zool. Lond. 190, p. 309-323.

Cooper, W. (1991). Harrier attacking black-billed gull. — Notornis 38, p. 72.

Cox, J.B. (1978). Albatros killed by giant petrel. — Emu 78, p. 94-95.

Daniel, M.J. (1982). Tui feeding on sandhoppers. — Notornis 29, p. 180.

Dunbar, R.I.M. (1992). Neocortex size as a constraint on group size in primates. — J. Human Evol. 20, p. 469-493.

Falla, R.A., Sibson, R.B. & Turbott, E.G. (1979). The new guide to the birds of New Zealand. — Collins, Auckland.

Felsentein, J. (1985). Phylogenies and the comparative method. — Am. Nat. 125, p. 1-15.

Flux, J.E.C. & Thompson, C.F. (1988). Birds taking insects from car radiators. — Notornis 35, p. 202.

Garland, T., Harvey, P.H. & Ives, A.R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. — Syst. Biol. 41, p. 18-32.

Gould, J.L. & Marler, P. (1984). Ethology and the natural history of learning. — In: The biology of learning (P. Marler & H.H. Terrace, eds). Springer Verlag, Berlin, p. 47-74.

Grafen, A. (1989). The phylogenetic regression. — Phil. Trans. Roy. Soc. Lond. B 326, p. 119-156.

Green, C. (1972). Use of tool by orange-winged sitella. — Emu 72, p. 185-186.

Hanks, E.S. (1957). Gulls and crickets. — Emu 57, p. 130.

Harrison, K.C. (1980). Unusual behaviour of Asiatic whimbrel. — Notornis 27, p. 394-395.

Harvey, P.H. & Krebs, J.R. (1990). Comparing brains. — Science 249, p. 140-146.

— — & Pagel, M.D. (1991). The comparative method in evolutionary biology. — Oxford University Press, Oxford.

Hawke, D.J.(1994). Seabird association with hector's dolphins and trawlers at Lytelton Harbour mouth. — Notornis 41, p. 206-209.

Hindwood, K.A. (1947). A feeding habit of the shrike-tit. — Emu 46, p. 284-285.

Hobbs, J.N. (1971). Use of tools by the white-winged chough. — Emu 71, p. 84-85.

Jerison, H.J. (1973). Evolution of the brain and intelligence. — Academic Press, New-York.

Johnson, I.W. (1976). Washing of food by spotless crake. — Notornis 23, p. 357.

Johnston, G.C. (1973). Predation by southern skua on rabbits on Macquarie island. — Emu 73, p. 25-26.

Johnston, T.D. (1982). The selective costs and benefits of learning: an evolutionary analysis. — Adv. Stud. Behav. 12, p. 65-106.

Jolicoeur, P., Pirlot, P., Baron, G. & Stephan, H. (1984). Brain structure and correlation patterns in Insectivora, Chiroptera, and primates. — Syst. Zool. 33, p. 14-29.

Klopfer, P.H. (1962). Behavioral aspects of ecology. — Prentice-Hall, Englewood Cliffs.

Langlands, P.A. (1991). Buller's shearwater foraging around fishing vessels. — Notornis 38, p. 266.

Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. — Anim. Behav. 53, p. 549-560.

McCulloch, E.M. (1966a). Swifts and bushfires. — Emu 65, p. 290.

— — (1966b). Birds eating soldier caterpillars. — Emu 66, p. 45-46.

Moffatt, J.D. (1982). Other species feeding at termite galeries opened by grey-crowned babblers. — Emu 82, p. 310-311.

Portmann, A. (1946). Etudes sur la cérébralisation des oiseaux. — I. Alauda 14, p. 2-20.

— — (1947). Etudes sur la cérébralisation des oiseaux. II. — Les indices intra-cérébraux. — Alauda 15, p. 1-15.

Purvis, A. & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. — Comp. Appl. Biosci. 11, p. 247-251.

Read, A. (1985). Predation on an arboreal rat by a New Zealand falcon. — Notornis 32, p. 155.

Rehkämper, G., Frahm, H.D. & Zilles, K. (1991). Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that of mammals (Insectivora and Primates). — Brain Behav. Evol. 37, p. 125-143.

Roberts, G.J. (1982). Apparent baiting behaviour by a black kite. — Emu 82, p. 53-54.

Rowley, I. (1968). Unusual feeding technique of bald coot. — Emu 67, p. 295-296.

Sibley, C.G. & Ahlquist, J.E. (1990). Phylogeny and classification of birds: a study in molecular evolution. — Yale University press, New Haven.

Sibson, R.B. (1974). Rock wren using an anvil. — Notornis 21, p. 305.

Simpson, K. & Day, N. (1996). The Princeton field guide to the birds of Australia. — Princeton University Press, Princeton.

Soper, M.F. (1984). Birds of New Zealand and outlying islands. — Whitcouls, Christchurch.

Stephan, H., Baron, G. & Frahm, H.D. (1988). Comparative size of brains and brain components. — In: Comparative primate biology; Vol 4: Neurosciences (H.D. Steklis & J. Erwin, eds). Allan R. Liss, New-York, p. 1-38.

Stokes, T. (1967). Crimson rosella catches insect on the wing. — Emu 66, p. 371.

Wheeler, R. (1946). Pacific gulls and mussels. — Emu 45, p. 307.

Wilkinson, L. (1987). Systat: the system for statistics. — Systat Inc, Evanston.

Wilson, A.C. (1985). The molecular basis of evolution. — Sci. Amer. 253 (4), p. 164-173.

Wyles, J.S., Kunkel, J.G. & Wilson, A.C. (1981). Birds, behaviour and anatomical evolution. — Proc. Nat. Acad. Sci. (USA) 80, p. 4394-4397.