ANIMAL BEHAVIOUR, 2003, **65**, 445–452
doi:10.1006/anbe.2003.2085

Behavioural flexibility predicts species richness in birds, but not extinction risk

NEKTARIA NICOLAKAKIS, DANIEL SOL & LOUIS LEFEBVRE
Department of Biology, McGill University

(Received 21 June 2001; initial acceptance 27 September 2001; final acceptance 30 May 2002; MS. number: A9095)

The number of species varies greatly among taxa. In birds, for example, the parvorder Passerida contains 3556 species while the Odontophorida contains only six species. This uneven distribution of species among bird groups is not a consequence of random branching patterns and therefore warrants an explanation. According to the behavioural drive hypothesis, behavioural innovation coupled with social transmission of the new skill to other members of the population may lead to accelerated rates of evolution, and could therefore account for differences in species richness. In this paper, we test the behavioural drive hypothesis by examining the link between behavioural flexibility and the number of species per taxon. We estimate flexibility with relative brain size and feeding innovation rate and predict that both will be positively associated with the number of species per taxon. Since the number of species at any given time results from a balance between speciation and extinction rates, we also examine the link between flexibility and the number of species threatened with extinction. We predict that the two flexibility correlates will be negatively associated with the number of species at risk. In simple regressions, both flexibility correlates were significantly associated with species number per taxon. However, only innovation rate remained in the final model. Relative brain weight dropped out of the multiple regression due to its association with innovation rate. Relative brain weight, innovation rate and species number per taxon were all significantly correlated with the number of threatened species in the simple regression, but only the latter remained significant in the final model. The same results were obtained on independent contrasts, indicating that behavioural flexibility predicts richness but not extinction risk in birds.

© 2003 Published by Elsevier Science Ltd on behalf of The Association for the Study of Animal Behaviour.

The number of species varies greatly among taxa. In birds, for example, the parvorder Passerida (Sibley & Monroe 1990) contains 3556 species while Odontophorida (New World quails) contains only six species. This unequal distribution of species among avian groups, and in particular the apparent success, in terms of number of species, of passerine birds, has intrigued many evolutionary biologists. Evidence suggests that unequal richness among taxa is not a consequence of random branching patterns (Dial & Marzluff 1989; Nee et al. 1992; Owens et al. 1999) and therefore warrants an explanation. Raikow's (1986) attempt to explain the extensive radiation of the passerines stimulated a series of papers in *Systematic Zoology*, in which it was proposed that relatively large brain size, high learning ability and overall behavioural plasticity may be responsible for the success of the group (Fitzpatrick 1988).

The view that behavioural plasticity can be a major driving force for evolution has been expressed elsewhere (Miller 1956; West-Eberhard 1989), but was most explicitly stated by A. C. Wilson and his co-workers (Wyles et al. 1983; Wilson 1985) in their behavioural drive hypothesis. They argued that behavioural innovation coupled with cultural transmission of the new skills to other members of the population could lead to greater rates of evolution. The idea is that individuals who adopt a new behaviour expose themselves to new selection pressures that may favour mutations conferring higher fitness in the new context. This should lead to the subsequent divergence of the mutants from the rest of the population and to the formation of a new species. A famous illustration of a new behaviour being propagated throughout a large population involves British tits (Fisher & Hinde 1949). When a few birds started opening milk bottles in the 1920s, the behaviour spread so rapidly that, within a few decades, thousands of tits had acquired the new feeding technique. This habit presumably exposed tits to a new set of selection pressures, including selection for the ability to digest the biochemical components in milk (see however Martinez del Rio 1993) or for physical traits that enhance the ability to open milk bottles.

Correspondence: L. Lefebvre, Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montréal, PQ H3A 1B1, Canada (email: louis.lefebvre@mcgill.ca).

0003–3472/02/$30.00/0 *© 2003 Published by Elsevier Science Ltd on behalf of The Association for the Study of Animal Behaviour.*

Another way in which behavioural flexibility can enhance speciation rates is by conferring species with a greater ability to invade new habitats (Mayr 1965; Greenberg 1990; Sol & Lefebvre 2000; Sol et al. 2002). Examples of successful invaders are the house sparrow, *Passer domesticus*, and the blackbird, *Turdus merula*, which have successfully colonized nine out of the 16 and 38 out of the 46 countries in which they have been introduced, respectively (Sol et al. 2002). Although not stated in the behavioural drive hypothesis, the possibility to enter new adaptive zones may lead to evolutionary divergence and favour the emergence of reproductive isolation between populations.

Since the association between flexibility and accelerated rates of evolution was originally proposed by Wilson and his colleagues nearly 20 years ago, it has yet to be tested. In this paper, we test the behavioural drive hypothesis by attempting to show that there is a positive correlation between behavioural flexibility and the number of species in avian taxa. We estimate flexibility with relative brain size and a behavioural measure, feeding innovation rate. We predict that large-brained, innovative bird groups should contain more species than their smaller-brained, less innovative counterparts. It should be noted, however, that the number of species at any given time is not solely attributable to the rate of speciation, but is the result of a balance between speciation and extinction rates (Cracraft 1985; Owens et al. 1999). Both mechanisms must therefore be considered before concluding that flexibility leads to high species richness through a high speciation rate alone. It is reasonable to assume that if flexibility has a positive effect on richness, it should conversely have the opposite effect on extinction risk. Greater flexibility should in fact provide species with a greater chance of survival should the environment change, either by allowing them to modify their behaviour and adapt to the novel environmental conditions or by giving them the possibility to leave and colonize new areas (Sol & Lefebvre 2000; Sol et al. 2002). Therefore, the second hypothesis we test is that flexibility is negatively associated with the number of species at risk.

The first measure of flexibility, innovation rate, is a frequency count of the number of opportunistic feeding behaviours displayed by avian orders and parvorders, corrected for the research effort per taxon. This correction is required because the innovation measure is a frequency count taken from the literature, which will by definition be inflated in taxa that are intensively studied by researchers (Nicolakakis 2001; Reader & Laland 2002). Corrected innovation frequency is correlated with the size of neural structures presumed to underlie cognition, the forebrain and two telencephalic equivalents of the mammalian neocortex, the hyperstriatum ventrale (HV) and neostriatum (Neo; Lefebvre et al. 1997, 1998; Timmermans et al. 2000). A similar association between corrected innovation frequency and relative size of the neocortex and striatum has also been demonstrated in primates (Reader & Laland 2002), indicating that the link between innovation and neural substrate size might be a general one.

In addition to its generality, innovation rate is a much finer estimation of flexibility than the categorization of this variable into broad dietary groups such as generalist and specialist. The assignment of a species to these dietary categories does not express the degree to which it is flexible, only whether it is or not. In addition, generalism is not necessarily equivalent to flexibility, and specialization does not necessarily imply a lack of flexibility. Raptors, for example, are considered to be specialist carnivores. However, these opportunistic birds are known to often change their feeding technique and produce novel behaviours, a capacity reflected by their high innovation rate. In a previous study on avian richness, Owens et al. (1999) found an association between a categorical dietary variable, feeding generalism/specialization, and a continuous one, species richness. In this study, we attempt to link the number of species with a continuous variable, feeding innovation rate.

The second measure of flexibility, relative brain size, is readily available for about 767 species in 36 molecular parvorders (Mlíkovský 1989a, b, c, d). Although innovative feeding is best predicted by localized structures like the hyperstriatum ventrale and neostriatum (Timmermans et al. 2000), detailed data on telencephalic areas are only available for 32 avian species (Boire 1989; Rehkämper et al. 1991). Because the Neo/HV complex occupies 50% of the telencephalon, however (Dubbledam 1998) and is the area that increases the most in size in birds with relatively large brains (Rehkämper & Zilles 1991), relative size of the whole brain can be a good estimate of Neo/HV size. Relative brain size accounts for 96.5% of the variance in relative HV size at the species level (N=32) and 96.2% of the variance at the level of the parvorder (N=17; data from Boire 1989; Rehkämper et al. 1991).

We predict that relative brain size (regressed against body weight) and corrected innovation rate will be positively associated with species number per parvorder and negatively associated with the number of species per parvorder that risk extinction.

METHODS

Innovations

Innovation reports were gathered through an exhaustive survey of a median of 30 years (1970–2000) in the short note sections of 65 generalist ornithology journals (see Nicolakakis 2001 for a list of the journals) covering six areas of the world. The six areas, chosen for their good journal coverage of innovations, include islands (Australia and New Zealand) and continental habitats (Europe, North America, Southern Africa and the Indian subcontinent), the northern and southern hemispheres, temperate and hot climates, as well as dry (Australia, Southern Africa) and wetter zones. A total of 1787 feeding innovations were found in the six zones, 176 from India, 237 from Southern Africa, 57 from New Zealand, 224 from Australia, 413 from North America and 680 from north-western Europe; the entire innovation corpus is available upon request. The innovations from the first 11

European journals (see Nicolakakis 2001) are the same as those in Nicolakakis & Lefebvre (2000). Those from the first four Australian and first seven North American journals are similar to those in Lefebvre et al. (2001). The Indian innovations are the same as those in Timmermans et al. (2000). L.L. gathered the remaining innovations, as well as the majority of those from Southern Africa.

A behaviour qualifies as innovative if the report features key words like 'unusual', 'first reported instance' or 'novel'. As in Lefebvre et al. (1997, 1998), a feeding innovation was defined as either the ingestion of a new food type or the use of an unusual foraging technique. Reports on owls (suborder Strigi) were excluded since innovations by these nocturnal birds are rarely observed but rather inferred from faecal evidence. Notes on penguins (parvorder Ciconiida) were also excluded because the geographical location of these Antarctic birds makes them less accessible to scientists and may lead to an underestimation of their innovation frequency. Innovation reports were gathered by independent readers, most of them blind to the hypothesis, yielding high inter-reader agreement levels (r=0.835–0.926, all P<0.001; Lefebvre et al. 1998; Nicolakakis & Lefebvre 2000).

The number of innovations per taxonomic group was tabulated using Sibley & Monroe's (1990) molecular parvorders, which roughly correspond to the classical orders used by Lefebvre et al. (1997). Innovation frequencies per taxon were log transformed, ln (freq+1), because they tend to have a non-normal distribution (i.e. some groups have very small innovation frequencies and others have very large ones). Nested analyses of variance (ANOVAs) (Statistica 1999) on the nontransformed number of innovations per species, family and parvorder allowed us to decide whether to calculate innovation rate at the level of parvorders, as in previous work by Lefebvre and his colleagues (1998, 2001) or to follow Owens et al.'s (1999) decision and work at the family level. In all six geographical regions, species with an innovation frequency of zero were excluded from the nested analysis of variance since it is impossible to know whether a zero indicates the species' lack of innovations or the absence of observers to report it.

Generating Innovation Rate

As in Nicolakakis & Lefebvre (2000) and Lefebvre et al. (2001), research effort was estimated from the number of full-length papers per taxonomic group. One to two issues per volume, depending on publication frequency, were randomly sampled in the same journals that were surveyed for short notes, and all species studied in field-based full-length articles were noted. Studies done in captivity or based on literature surveys were not included in the estimate of research effort, since the former may not report natural behaviour, and the latter are, by definition, secondary reports. Zoological surveys that simply catalogue the species present in a particular area were excluded as well since they focus on identification, not behaviour, and can inflate innovation frequencies due to the large number of species listed in the survey. A total of 4602 species entries were obtained for our research effort estimate.

Innovation rate was generated by regressing innovation frequency against research effort per taxon and taking the standardized residuals. The innovation rate of each taxon was then averaged over the six geographical zones and weighed by the total number of innovations contributed by each zone. For example, parrots are present in the wild in Australia, New Zealand, India and Southern Africa. Regressed against research effort, the 23 Australian, 0 New Zealand, 6 Indian and 0 Southern African innovations reported for Psittaciformes yield respective residuals of 1.259, −1.903, 1.392 and −0.552. We then multiplied the residuals by the proportion of innovations contributed by each zone, and summed them to obtain a weighted innovation rate of 0.415 (i.e. $1.259 \times 224/694 + 1.903 \times 57/694 + 1.392 \times 176/694 + 0.552 \times 237/694$).

Relative Brain Size

Out of a total of 767 species, all of those with brain weights beyond two standard deviations from the family mean were eliminated. Thirty outliers were therefore removed from the brain database because they did not conform to this statistical criterion. As before, nested ANOVAs on brain weight and residual brain weight per species, family and parvorder enabled us to choose the level at which to average our neuroanatomical measure of flexibility. Relative brain size was calculated by running a brain–body weight regression on 413 genera (r=0.942, P<0.001) and averaging the standardized residuals at the taxonomic level indicated by the nested ANOVA.

A large part of the brain data is in the form of brain case measurements by Mlíkovský (1989a, b, c, d) and fresh brain weights the author obtained from the literature (Armstrong & Bergeron 1985; Boire 1989; Rehkämper et al. 1991). The fresh weights were used to check the Mlíkovský data. Body weights were taken from the *CRC Handbook* (Dunning 1993), the standard international reference for body masses.

Number of Species

The number of species per taxon was taken from Sibley & Monroe (1990). Data on extinction risk was provided by the *IUCN Red List of Threatened Animals* (Baillie & Groombridge 1996) which lists all the vulnerable, endangered and critically endangered species, as well as those that have gone extinct in the last 400 years. The total number of species at risk was obtained by summing up the number of species in the three categories of threat. All numbers were ln transformed due to the presence of very large and very small values.

Testing the Hypotheses

The hypotheses on richness and risk of extinction were tested with stepwise multiple regressions (SYSTAT 5.2) in which feeding innovation rate and relative brain size were the independent variables and number of species,

Table 1. Percentage of variance in brain size, relative brain size and innovation frequency per taxonomic level, based on nested ANOVA

	Taxonomic level		
Percentage of variance in	Parvorder	Family	Species
Brain weight	62.9	17.4	19.8
Relative brain weight	63.9	16.4	19.7
Innovation frequency per region			
North western Europe	8.5	0	91.5
North America	14.5	0	85.5
Southern Africa	0	0	100.0
Australia	4.0	0	96.0
India	0.8	0	99.2
New Zealand	0	21.8	78.2

number of threatened species and number of extinct species were, in turn, the dependent ones. In addition to the flexibility correlates, the regression on risk also included the number of species as an independent variable, while that on extinction included both number of species and number of threatened species as predictors. Following Owens et al. (1999), we repeated the analyses after having removed 12 taxa belonging to the two unusually large avian assemblages, the Ciconiiformes (9 parvorders, 1027 species) and Passeriformes (3 parvorders, 5712 species).

To control for phylogenetic effects, the regressions were run a second time on independent contrasts generated by CAIC (comparative analysis by independent contrasts; Purvis & Rambaut 1995). The technique is based on the construction of a phyletic tree. Contrasts are created by comparing the trait values of sister taxa on the tree; values for ancestral nodes are estimated by averaging the values of extant taxa and weighing them by phyletic distance. We used Sibley & Monroe's (1990) phylogeny, currently the most comprehensive molecular phylogeny of the class Aves (Sibley & Ahlquist 1990; Barraclough et al. 1995) and obtained DNA–DNA hybridization distances from Sibley & Ahlquist (1990) to estimate branch lengths in the tree.

RESULTS

The largest proportion of variance in brain size and relative brain size (corrected for body weight) occurred at the level of the parvorder (62.9 and 63.9%, respectively, based on nested ANOVA, Table 1), thereby justifying the use of this taxonomic level to calculate our neuroanatomical correlate of flexibility. Most of the variance in innovation frequency was located at the level of the species. Since species number per taxon is the variable we are trying to predict, however, we cannot use this level to calculate innovation rate. We must therefore choose the level that explains the second highest proportion of variance in the number of innovations. In all regions, except New Zealand, which has a very small sample, it is the parvorder (Table 1), again justifying the test of our hypotheses at this level. It is noteworthy that the proportion of variance explained by the parvorder appeared

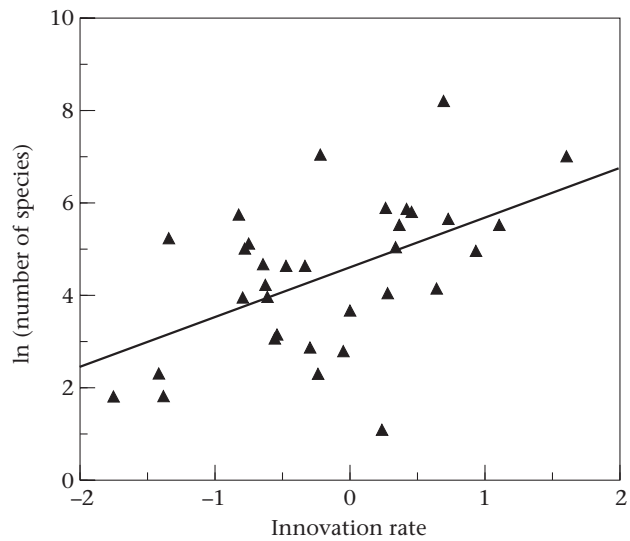

Figure 1. Log-transformed number of species versus feeding innovation rate in 33 avian taxa, as defined by Sibley & Monroe (1990). Y=4.6149+1.0777X, P=0.001.

to increase with the number of innovations gathered in each region.

The number of species per taxon was significantly correlated with relative brain size (Pearson correlation: r_{34}=0.418, P=0.015) and feeding innovation rate (r_{31}=0.558, P=0.001). However, only innovation rate remained in the final model, accounting for 31.1% of the variance in species number (overall r^2 of the multiple regression=0.311, $F_{1,31}$=14.014, P=0.001; Fig. 1). Relative brain size was excluded from the multiple regression due to its association with innovation rate (r_{31}=0.570, P=0.001). The relationship between innovation and richness held even after the removal of 12 taxa belonging to the two most speciose avian lineages, the Passeriformes and the Ciconiiformes (partial r_{31}=0.525, P=0.015; overall r^2 of the multiple regression=0.275, $F_{1,19}$=7.223, P=0.015; Fig. 2).

Extinction risk, defined as the number of vulnerable, endangered and critically endangered species, was strongly related to the number of species per taxon (Pearson correlation: r_{36}=0.885, P<0.001); richness

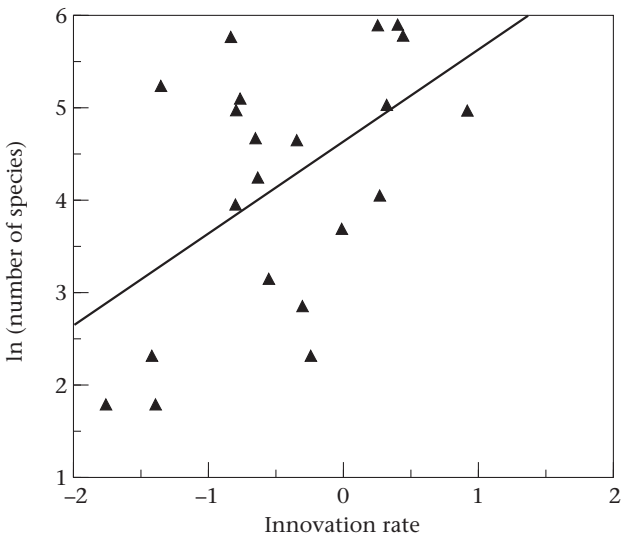

Figure 2. Log-transformed number of species versus feeding innovation rate in 21 avian taxa; 12 taxa belonging to the two most speciose orders, the Passeriformes and Ciconiiformes, were removed. Y=4.6076+0.99175X, P=0.015.

explained 78.3% of the variance in risk, with some of the most speciose groups, such as the Passerida and the Corvida, containing the highest number of threatened species. However, the slope of the relationship was significantly less than one (t test: t_{36}= − 3.919, P<0.001). Innovation rate was positively correlated with extinction risk (partial r_{31}=0.447, P=0.009) but this relationship was an artefact of the richness–innovation link; innovation rate dropped out of the multiple regression when species number was included (overall r^2 of the multiple regression=0.725, $F_{1,36}$=94.885, P<0.001). Similar conclusions were reached when we used the proportion of species threatened rather than the absolute number: neither relative brain size (P=0.359) nor feeding innovation rate (P=0.405) was a significant predictor of extinction risk.

The number of species per taxonomic group that went extinct in the past 400 years was correlated with the richness of the group (Pearson correlation: r_{36}=0.563, P=0.001), but more so with the number of species at risk (r_{34}=0.721, P<0.001), which in itself, explained 52% of the variance in extinction (overall r^2 of the multiple regression=0.546, $F_{1,36}$=43.365, P<0.001). When the number of recently extinct species was added to the number of species at risk, richness (Pearson correlation: r_{36}=0.861, P<0.001) was the only significant predictor in the final model, explaining 74.1% of the variance in risk and actual extinction (overall r^2 of the multiple regression=0.695, $F_{1,36}$=81.956, P<0.001). As before, innovation rate was significant in the simple regression (partial r_{31}=0.431, P=0.012) but dropped out of the final model due to its association with richness.

Multiple regressions on independent contrasts yielded similar results to those prior to phylogenetic correction. Relative brain size (r=0.403, P=0.022) and innovation rate (r=0.495, P=0.004) were the main correlates of richness, with innovation rate explaining 24.5% of the variance in the final model (before CAIC, relative brain size: r=0.418, P=0.015; innovation rate: r=0.558, P=0.001; overall r^2 of the multiple regression =0.245, $F_{1,31}$=10.047, P=0.003). Relative brain size (r=0.411, P=0.019), innovation rate (r=0.465, P=0.007) and number of species per taxon (r=0.914, P<0.001) were all significantly correlated with the number of threatened species per taxonomic group in the simple regression; however, as before, the only predictor of risk in the final model was the number of species, which accounted for 83.6% of the variance (before CAIC, relative brain size: r=0.325, NS; innovation rate: r=0.447, P=0.009; species number: r=0.885, P<0.001; overall r^2 of the multiple regression=0.836, $F_{1,31}$=157.905, P<0.001).

DISCUSSION

This paper reports two main findings. First, differences in richness among avian taxa are linked to differences in their behavioural flexibility, and second, extinction risk is not related to flexibility but to the number of species per taxonomic group. The first result indicates that species-rich taxa like the Passerida, Corvida, Psittaciformes, Accipitrida and Ciconiida, for example, are those with the capacity for quick adjustments in their feeding behaviour. Opportunistic birds that can switch from one food source to another or that can employ new foraging techniques, have produced, over evolutionary time, a greater number of species than their less-adaptable counterparts. This is in agreement with Owen et al.'s (1999) finding that feeding generalism is correlated with species richness in avian families, but is an even stronger test of the flexibility-richness hypothesis since it uses more detailed behavioural information (the continuous variable, feeding innovation rate, rather than the categorical dietary variable, generalism/specialization) and a broader coverage of the class Aves (33 parvorders versus 13 pairs of families). Furthermore, the regression on independent contrasts indicates that the relationship between innovation rate and number of species is not due to common ancestry, and that it is therefore robust since it holds regardless of methodology, taxonomic level and phylogeny.

The significant association between richness and innovation lends support to the behavioural drive hypothesis, which predicts accelerated rates of evolution in animals with the capacity for both behavioural innovation and the transmission of the novel behaviour to other members of the species (Wyles et al. 1983; Wilson 1985). As a result of acquiring the new skill, individuals face new selection pressures that may favour the expression of mutations that can increase individual fitness in the new context and lead to divergence and speciation. In their work on primates, Reader & Laland (2002) demonstrated an association between neural substrate size, innovation rate and social learning, thereby satisfying the key assumption of the behavioural drive hypothesis. Additional work showing a link between social learning and high species richness would be required to further validate the behavioural drive hypothesis. Nevertheless, taken together, the two studies indicate that behavioural flexibility may be a trait that can accelerate evolution.

Table 2. Association between the flexibility correlates and (1) the number of species per taxon and (2) the number of species at risk per taxon

	Before CAIC			After CAIC		
	Initial *r*	Initial *P*	Final *P*	Initial *r*	Initial *P*	Final *P*
Number of species per taxon						
Innovation rate	0.558	0.001	0.001	0.495	0.004	0.004
Brain size	0.418	0.015	NS	0.403	0.022	NS
	r^2=0.311, $F_{1,31}$=14.014, P=0.001			r^2=0.245, $F_{1,31}$=10.047, P=0.003		
Number of species at risk per taxon						
Innovation rate	0.447	0.009	NS	0.465	0.007	NS
Brain size	0.325	NS	NS	0.411	0.019	NS
Number of species	0.885	<0.001	<0.001	0.914	<0.001	<0.001
	r^2=0.725, $F_{1,36}$=94.885, P<0.001			r^2=0.836, $F_{1,31}$=157.905, P<0.001		

Furthermore, the comparative approach adopted in this study has shifted the focus away from the Passeriformes and put their success in perspective with that of other speciose groups, such as the parrots, eagles and gulls. As a result, the traditional focus on the evolutionary success of songbirds and the importance given to their vocal sophistication and potential for dialect formation (Raikow 1986; Fitzpatrick 1988; Vermeij 1988) has been replaced by a study directed at the entire avifauna with, at its centre, a more general explanation of evolutionary success based on behavioural differences and the capacity for innovation.

In addition, by validating the behavioural drive hypothesis, the present study emphasizes the role of behaviour in explaining unequal richness among taxa. Traditionally, aside from work on sexual selection and mating behaviour (Barraclough et al. 1995; Mitra et al. 1996; Møller & Cuervo 1998), most attempts to account for richness have focused on ecological and/or abiotic factors, often overlooking the importance of behavioural attributes. This study clearly adopts a behavioural perspective and argues that the ability to produce new behaviours may be important in driving the production of species by exposing individuals to new situations and allowing the expression of mutations favourable to the new circumstances. Although there has been some scepticism about how learnt behaviours might lead to evolutionary change, the idea is slowly being accepted (ten Cate 2000). Recent work on the rapid speciation of brood-parasitic indigobirds (Viduidae) has demonstrated that young male parasites can quickly learn to behave like the new host and lose interest in conspecifics raised by the traditional host: young males learn the songs of the new host; females prefer this song and will preferentially lay their eggs in the nests of the new host (Payne et al. 2000), thereby producing offspring that are reproductively isolated from the rest of the parasitic species. Taken together, the study on indigobirds, as well as the present study, exemplify how the cultural transmission of learnt information can lead to evolutionary change.

Although behavioural characteristics may play a role in accelerating speciation in birds, other factors are undoubtedly at work, as is suggested by the relatively modest proportion of variance that is explained by our flexibility correlate, feeding innovation rate (24.5%) and the many studies that have shown other traits to be relevant. For example, Owens et al. (1999) found species richness to be associated with plumage dichromatism (a measure of the occurrence of sexual selection), habitat generalism, annual dispersal capability, geographical range size and the extent of range fragmentation. In our study, these data were not available at the taxonomic level that explained the highest proportion of variance in flexibility, the parvorder. There were therefore two choices. The first was to work at a level where several potential confounding variables could easily be coded (i.e. the species, genus or family), but where variance in flexibility was low. The second was to choose a level that maximized the variance explained in the variables that were important for the hypothesis, the parvorder, but where many confounds would be difficult to code. We chose the latter approach, if only to counterbalance the opposite choice made by Owens et al. (1999). The fact that both their study and ours confirm the role of feeding flexibility provides robust support for the behavioural drive hypothesis.

The prediction that increased flexibility should be associated with a reduced risk of extinction was not supported by our analyses. The number of species currently considered at risk was strongly associated with the number of species contained within the taxon: the more species-rich the taxon, the higher the number of species reported vulnerable, endangered and critically threatened. This means that, ironically, speciose groups like the Passerida, Tyranni and Corvida, with 3556, 1151 and 1101 species, respectively, are more threatened by extinction than the species-poor colies (6 species), turacos (23) and hoopoes (10). This finding supports the statement made in the IUCN (Baillie & Groombridge 1996) that the greatest number of extinct avian species are reported in the largest order, the Passeriformes, which also ranks among the top five orders with the largest number of species at risk. The observation seems to hold in other vertebrate classes as well: the greatest number of mammal extinctions has been among the rodents and bats, which are the largest orders and also have the largest number of threatened species (Baillie & Groombridge 1996). Note however, that the slope of the relationship between

extinction risk and species number was significantly smaller than one, indicating that speciose groups have proportionately fewer threatened species. There might therefore be an indirect effect of flexibility on risk through richness. The intuitively obvious result that extinction is predicted by risk should be treated with caution, however, as it only represents recent extinction in the last four centuries and does not necessarily reflect the situation that predominated in the past and throughout the entire evolutionary history of a lineage. Rather, it reflects a phenomenon accelerated by anthropogenic factors (extinction of one bird species every 4 years, Temple 1986), which differs markedly from the natural situation millions of years ago.

Although we have found that the richness of a taxon will dictate whether its species will be categorized as threatened or not, other authors have shown an association between extinction risk and morphological and life-history traits, such as body size and fecundity rates (Bennett & Owens 1997). At a more local ecological scale, Cracraft (1985) has argued that predation and competition may also be important. According to Reed (1999), the main causes of decline and extinction in birds are habitat loss and fragmentation, introduced predators and diseases as well as exploitation by humans. These factors may account for the residual variance in risk (i.e. after the removal of the effect of species number). Nevertheless, it is safe to conclude that extinction is largely a stochastic event, where bigger taxa contain more threatened species than smaller taxa. If so, this means that behavioural flexibility is associated with the number of species via the rate of speciation, and that high species richness is achieved through high rates of species birth rather than low rates of species loss. Not only is this finding consistent with the predictions of the behavioural drive hypothesis (accelerated rates of evolution in flexible species), but it also has a major theoretical implication. It suggests that different factors control speciation and extinction rates, and challenges the traditional view that speciation and extinction are simply opposite sides of the same biological phenomenon. As Owens et al. (1999) pointed out, lineages could experience high rates of species loss, but compensate by equally high rates of species production, as appears to be the case with the Passerida and Corvida.

Acknowledgments

We are grateful to Mathieu Filion and Simran Kurir for their assistance in gathering innovation reports and to Danielle Choquette for her help in gathering data on research effort. We also thank Patrick-Jean Guay for his help in checking the Mlíkovský brain data against fresh weights from other sources. This work was funded by an NSERC grant to Louis Lefebvre, an FCAR postgraduate fellowship to Nektaria Nicolakakis and a postdoctoral fellowship from the Ministère de l'Education du Québec to Daniel Sol.

References

Armstrong, E. & Bergeron, R. 1985. Relative brain size and metabolism in birds. *Brain, Behavior and Evolution*, **26,** 141–153.

Baillie, J. & Groombridge, B. 1996. *The 1996 IUCN Red List of Threatened Animals*. Gland, Switzerland: IUCN.

Barraclough, T. G., Harvey, P. H. & Nee, S. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society of London, Series B*, **259,** 211–215.

Bennett, P. M. & Owens, I. P. F. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London, Series B*, **264,** 401–408.

Boire, D. 1989. Comparaison quantitative de l'encéphale, de ses grandes subdivisions et de relais visuels, trijumaux et acoustiques chez 28 espèces d'oiseaux. Ph.D. thesis, Université de Montréal.

Cracraft, J. 1985. Biological diversification and its causes. *Annals of the Missouri Botanical Garden*, **72,** 794–822.

Dial, K. P. & Marzluff, J. M. 1989. Nonrandom diversification within taxonomic assemblages. *Systematic Zoology*, **38,** 26–37.

Dubbledam, J. L. 1998. Birds. In: *The Central Nervous System of Vertebrates* (Ed. by R. Nieuwenhuys, H. J. TenDonkelaar & C. Nicholson), pp. 1525–1620. Berlin: Springer-Verlag.

Dunning, J. B. 1993. *CRC Handbook of Avian Body Masses*. Boca Raton, Florida: CRC Press.

Fisher, J. & Hinde, R. A. 1949. The opening of milk bottles by birds. *British Birds*, **42,** 347–357.

Fitzpatrick, J. W. 1988. Why so many passerine birds? A response to Raikow. *Systematic Zoology*, **37,** 71–76.

Greenberg, R. 1990. Ecological plasticity, neophobia and resource use in birds. In: *Avian Foraging: Theory, Methodology and Applications* (Ed. by M. L. Morrison, C. J. Ralph, J. Verner & J. R. Jehl Jr), pp. 431–437. Lawrence, Kansas: Allen Press.

Lefebvre, L., Whittle, P. W., Lascaris, E. & Finkelstein, A. 1997. Feeding innovations and forebrain size in birds. *Animal Behaviour*, **53,** 549–560.

Lefebvre, L., Gaxiola, A., Dawson, S., Timmermans, S., Rozsa, L. & Kabai, P. 1998. Feeding innovations and forebrain size in Australasian birds. *Behaviour*, **135,** 1077–1097.

Lefebvre, L., Juretic, N., Nicolakakis, N. & Timmermans, S. 2001. Is the link between forebrain size and feeding innovations caused by confounding variables? A study of Australian and North American birds. *Animal Cognition*, **4,** 91–97.

Martinez del Rio, C. 1993. Do British tits drink milk or just skim the cream? *British Birds*, **86,** 321–322.

Mayr, E. 1965. The nature of colonizations in birds. In: *The Genetics of Colonizing Species* (Ed. by H. G. Baker & G. L. Stebbins), pp. 29–43. New York: Academic Press.

Miller, A. H. 1956. Ecologic factors that accelerate formation of races and species of terrestrial vertebrates. *Evolution*, **10,** 262–277.

Mitra, S., Landel, H. & Pruett-Jones, S. 1996. Species richness covaries with mating system in birds. *Auk*, **113,** 544–551.

Mlíkovský, J. 1989a. Brain size in birds: 1. Tinamiformes through Ciconiiformes. *Vestnik Ceskoslovenska Spolecnosti zoologicka*, **53,** 33–47.

Mlíkovský, J. 1989b. Brain size in birds: 2. Falconiformes through Gaviiformes. *Vestnik Ceskoslovenska Spolecnosti zoologicka*, **53,** 200–213.

Mlíkovský, J. 1989c. Brain size in birds: 3. Columbiformes through Piciformes. *Vestnik Ceskoslovenska Spolecnosti zoologicka*, **53,** 252–264.

Mlíkovský, J. 1989d. Brain size in birds: 4. Passeriformes. *Acta Societatis Zoologicka Bohemoslovacae*, **54,** 27–37.

Møller, A. P. & Cuervo, J. J. 1998. Speciation and feather ornamentation in birds. *Evolution*, **52,** 859–869.

Nee, S., Mooers, A. O. & Harvey, P. H. 1992. Tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences, U.S.A.*, **89,** 8322–83268.

Nicolakakis, N. 2001. Innovation rate, brain size and species richness in birds. M.Sc. thesis, McGill University.

Nicolakakis, N. & Lefebvre, L. 2000. Forebrain size and innovation rate in European birds: feeding, nesting and confounding variables. *Behaviour*, **137**, 1415–1429.

Owens, I. P. F., Bennett, P. M. & Harvey, P. H. 1999. Species richness among birds: body size, life history, sexual selection or ecology. *Proceedings of the Royal Society of London, Series B*, **266**, 933–939.

Payne, R. B., Payne, L. L., Woods, J. L. & Sorenson, M. D. 2000. Imprinting and the origin of parasite–host associations in brood-parasitic indigobirds (*Vidua chalybeata*). *Animal Behaviour*, **59**, 69–81.

Purvis, A. & Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences*, **11**, 247–251.

Raikow, R. J. 1986. Why are there so many kinds of passerine birds? *Systematic Zoology*, **35**, 255–259.

Reader, S. M. & Laland, K. 2002. Social intelligence, innovation and enhanced brain size in primates. *Proceedings of the National Academy of Sciences, U.S.A.*, **99**, 4436–4441.

Reed, M. J. 1999. The role of behaviour in recent avian extinctions and endangerments. *Conservation Biology*, **13**, 232–241.

Rehkämper, G. K. & Zilles, K. 1991. Parallel evolution in mammalian and avian brains: comparative cytoarchitectonic and cytochemical analysis. *Cell and Tissue Research*, **263**, 3–28.

Rehkämper, G. K., Frahm, H. D. & Zilles, K. 1991. Quantitative development of brain structures in birds (Galliformes and Passerifomes) compared to that in mammals (Insectivores and Primates). *Brain, Behavior and Evolution*, **37**, 125–143.

Sibley, C. G. & Ahlquist, J. E. 1990. *Phylogeny and Classification of Birds: a Study in Molecular Evolution*. New Haven, Connecticut: Yale University Press.

Sibley, C. G. & Monroe, B. L. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven, Connecticut: Yale University Press.

Sol, D. & Lefebvre, L. 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, **90**, 599–605.

Sol, D., Timmermans, S. & Lefebvre, L. 2002. Behavioural flexibility and invasion success in birds. *Animal Behaviour*, **63**, 495–502; **64**, 516.

Temple, S. A. 1986. The problem of avian extinctions. In: *Current Ornithology* (Ed. by R. F. Johnston), pp. 453–485. New York: Plenum.

ten Cate, C. 2000. How learning mechanisms might affect evolutionary processes. *Trends in Ecology and Evolution*, **15**, 179–180.

Timmermans, S., Lefebvre, L., Boire, D. & Basu, P. 2000. Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. *Brain, Behavior and Evolution*, **56**, 196–203.

Vermeij, G. J. 1988. The evolutionary success of passerines: a question of semantics? *Systematic Zoology*, **37**, 69–71.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, **20**, 249–278.

Wilson, A. C. 1985. The molecular basis of evolution. *Scientific American*, **253**, 148–157.

Wyles, J. S., Kunkel, J. G. & Wilson, A. C. 1983. Birds, behaviour and anatomical evolution. *Proceedings of the National Academy of Sciences, U.S.A.*, **80**, 4394–4397.