Innovation Rate, Brain Size and Species Richness in Birds

by
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Abstract

The number of species varies greatly among taxa. In birds, for example, the parvorder Passerida contains 3556 species while the Odontophorida (New World Quails) contains only six species. This uneven distribution of species among avian taxa is not random and therefore warrants an explanation. The behavioral drive hypothesis stipulates that the capacity for innovation, coupled with the rapid transmission of the behavioral novelty to conspecifics, may expose individuals to new selective pressures and help fix mutations that would otherwise not be expressed. This should lead to accelerated rates of evolution. I test this hypothesis by examining the link between behavioral flexibility and the number of species per taxon. I adopt a comparative approach and seek a general explanation of richness, thereby removing the traditional focus placed on the success of the songbirds and on their complex singing apparatus. I use two measures of flexibility, feeding innovation rate and relative brain size. In the first two chapters, I develop the innovation index using the birds of northwestern Europe (chapter 1), and those of North America and Australia (chapter 2). I consider seven confounding variables that may bias the number of innovations reported in the literature - research effort, ornithologist interest, reporting bias, journal style, juvenile development mode, population size and common ancestry - and correct this number by the variable that comes out most significant in a step-wise multiple regression. Research effort was the most important variable that can inflate innovation numbers in certain taxa and was therefore used to correct innovation frequencies. I also validate the innovation index as a measure of flexibility by showing that, aside from research effort, innovation frequency is only predicted by relative forebrain size, but is independent of other confounding variables. In chapter 3, I use innovation rate, along with relative brain size, to test the link between flexibility and richness. I also examine the link between flexibility and extinction risk to determine whether flexibility affects richness via the rate of speciation or extinction. Both flexibility correlates were significantly associated with species number per taxon in the simple regression. However, only innovation rate remained in the final model. Relative brain size dropped out of the multiple regression due to its association with innovation rate. The number of species per taxon was the only variable associated significantly with the number of threatened species, thereby highlighting the stochastic nature of species extinctions. The same results were obtained on independent contrasts, indicating that behavioral flexibility predicts richness but not extinction risk in birds.

Résumé

Le nombre d'espèces varie d'un groupe taxonomique à l'autre. Chez les oiseaux, par exemple, le parvordre Passerida compte 3556 espèces tandis qu' Odontophorida n'en compte que six. Cette différence de richesse entre les taxa pourrait être expliquée par l'hypothèse de la "pousée comportementale" qui stipule que l'innovation comportementale accompagnée de la transmission culturelle du nouveau comportement aux congénères a un effet accélérateur sur la spéciation en amenant les individus à faire face à de nouvelles pressions sélectives et en fixant des mutations qui ne seraient pas exprimées autrement. J'évalue cette hypothèse en essayant de déterminer s'il existe un lien entre la flexibilité comportementale et le nombre d'espèces par groupe taxonomique. Je quantifie la flexibilité par le taux d'innovation alimentaire et la taille relative du cerveau. Dans les deux premiers chapitres, je développe le taux d'innovation en me servant de l'avifaune européene (chapitre1) et celles de l'Amérique du Nord et de l'Australie (chapitre 2). Je considère sept variables de confusion qui pourraient biaiser le nombre d'innovations rapportées dans la literature - l'effort de recherche, l'intérêt des ornithologues pour certains taxa, le biais dans la publication d'anecdotes alimentaires, le style de la revue, le mode de développement, la taille de la population et la phylogénie - et corrige ensuite ce nombre par la variable la plus significative dans une régression multiple. Cette variable, l'effort de recherche, a donc été utilisée pour corriger les fréquences d'innovation. J'ai également confirmé la validité du taux d'innovation comme mesure de la flexibilité en démontrant que le nombre d'innovations est associé avec la taille relative des hémisphères cérébraux, mais avec aucune autre variable de confusion (à part l'effort). Au chapitre 3, j'utilise le taux d'innovation ainsi que la taille relative du cerveau pour évaluer le lien entre la flexibilité et la richesse taxonomique. Je regarde également s'il y a un lien entre la flexibilité et le risque d'extinction pour ainsi déterminer si la flexibilité influence la richesse via le taux de spéciation ou d'extinction. Les deux mesures de la flexibilité étaient reliées de facon significative au nombre d'espèces dans la régression simple, mais seule l'innovation est restée significative dans la régression multiple. La taille du cerveau n'est pas restée significative dans le modèle final à cause de son lien avec le taux d'innovation. Seul le nombre d'espèces était significativement corrélé avec le nombre d'espèces à risque, démontrant ainsi la stochasticité du phénomène d'extinction. Les mêmes résultats ont été obtenus sur des contrastes indépendants, indiquant que la flexibilité prédit la richesse, mais pas le risque d'extinction chez les oiseaux.

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Preface

Authorship and Style

The Faculty of Graduate Studies and Research requires that the following text be reproduced in full in order to inform the reader of the Faculty regulations.

Candidates have the option of including, as part of the thesis, the text of a paper submitted or to be submitted for publication, or a clearly duplicated text of a published paper. These texts must be bound as an integral part of the thesis.

If this option is chosen, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.

The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: a table of contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a comprehensive review of the literature and a final conclusion and summary, and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgment to be made of the importance and originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Supervisors must attest the accuracy of such statements at the doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers.

This thesis consists of three chapters that are prepared as individual manuscripts for publication in peer-reviewed journals. Chapter 1 is co-authored with Dr. Louis Lefebvre (Dept. of Biology, McGill University) and has been published in Behaviour, volume 137, pages 1415 to 1429. Chapter 2 is co-authored with Dr. Lefebvre, Nikoleta Juretic and Sarah Timmermans and has been submitted to Animal Cognition. In this case, Dr. Lefebvre is first author because the paper brings together work from several students. Nikoleta Juretic gathered data on ornithologist interest. Sarah Timmermans and I conducted the phylogenetic analysis using independent contrasts. The remaining analyses using multiple regressions as well as the writing of the manuscript were done by myself and Dr. Lefebvre. Chapter 3 is being prepared for submission to Animal Behaviour. I am first author, while Drs. Lefebvre and Daniel Sol (Dept. of Biology, McGill University) are second and third authors, respectively. Both contributed to the development of the ideas presented in the third chapter in addition to providing editorial and technical advice. In the case of my supervisor, Dr. Lefebvre, editorial and technical advice has been given in all chapters of the thesis.

Contributions to original knowledge

Chapters 1 and 2. These are the first studies to examine the effect of confounding variables on anecdotal data. The studies are original in terms of the number of variables considered and the way potential biases were quantified. The confounding variables are interesting and useful in and of themselves because they can be used in other studies, where estimates on research effort, for example, are required. These studies also represent the first attempt to validate feeding innovation rate as a measure of flexibility, thereby providing a measure that is field-based, ecologically relevant, and available for a wide range of species, making it useful in large-scale comparative studies of behavior, ecology and evolution.

Chapter 3. This study is the first test of the behavioral drive hypothesis since its original formulation almost 20 years ago. It is also the first large-scale comparative study on richness in birds, encompassing six geographical areas and covering the global avifauna. The study also includes, to our knowledge, the largest avian brain database, with brain weights on 737 species in 36 molecular parvorders and 103 avian families.

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General Introduction

The number of species varies greatly among taxa. In birds, for example, the parvorder Passerida contains almost 600 times as many species as the parvorder Odontophorida (New World quails). The order Ciconiiformes counts one hundred times as many species as the Upupiformes (hoopoes). Many evolutionary biologists have attempted to explain the unequal distribution of species among avian taxa, and in particular the apparent success, in terms of number of species (5712), of the order Passeriformes. Traditionally, the extensive radiation of the passerines has been attributed to their complex singing apparatus and potential for dialect formation (Raikow 1986; Vermeij 1988). Although these variables may partially account for accelerated speciation in passerines, they cannot explain the success of the Ciconiiformes (1027), which have no complex song dialects, but are the second most speciose assemblage after the Passeriformes (Sibley and Monroe 1990). Song, therefore, cannot be considered the unitary explanation for differential rates of cladogenesis in avian taxa.

Alternatively, the success of the passerines has been explained by their small body size and its association with short generation time, which, theoretically, should lead to greater rates of speciation (Kochmer and Wagner 1988). However, songbirds are not the only small - bodied members of the class Aves; the Coliiformes and hummingbirds are also among the smallest birds, yet contrary to their speciose counterparts, they contain only six and 319 species, respectively. Therefore, small size seems an unlikely explanation for the great passerine diversification. In a recent study, Owens et al. (1999) also discounted small body size as an explanatory factor of high species richness, arguing that previous studies on richness had omitted phylogenetic analysis, thereby falsely treating species as independent data points.

Historically, there has been no shortage of explanations to account for the high speciation rate of the passerines. However, the intense focus of speciation research on a single taxon seems unwarranted. Rather than focus on a single data point, it seems more logical to adopt a comparative approach and seek explanations for species numbers in as many groups as possible, assuming that a single explanation applies to all groups. The comparative method is thus the approach that will be adopted in this thesis. Many studies on avian richness have compared taxa with respect to the number of species they contain, but most of these studies have usually adopted an ecological perspective. Their explanations of differential richness among avian groups include range size, extent of range fragmentation, habitat generalism and dispersal ability, among others (Owens et al. 1999). Very few studies, however, have addressed the issue from a behavioral point of view.

The idea that behavior may be at the root of differential rates of species production has been maintained by several authors (Miller 1956, West-Eberhard 1989), but was most explicitly formulated by A. C. Wilson and his co-workers (Wyles et al. 1983; Wilson 1985) in the development of the behavioral drive hypothesis. According to these authors, the capacity for innovation, i.e. the production of behaviors that are not part of an individual's normal repertoire, exposes large-brained animals to a new range of selection pressures, which may help fix mutations that would otherwise not be expressed. The ability to innovate, coupled with the transmission of the new behavior to other individuals through various mechanisms of social learning should lead to greater rates of evolution, and to the subsequent divergence of those individuals from the rest of the population. By means of allopatry, this should lead to the formation of a new species.

Hypotheses on speciation

The introduction, so far, has focused on the class Aves and the potential variables influencing speciation in this group. However, it is important to realize that the factors affecting speciation rates in one group of organisms may not be relevant to the success of another group, especially if groups differ with respect to morphology, life history, behavioral complexity, mobility, and so forth (Marzluff and Dial 1991). For example, microbial organisms may be expected to evolve more rapidly than macro - organisms because of relatively short generation times (about 20 minutes in bacteria, Purvis et al. 1997) resulting in the quick transmission of genetic novelties from one generation to the next. Furthermore, microorganisms, such as algae, are likely not subject to the same selection pressures as large-brained animals since the former lack, among other things, the neural substrate necessary for the behavioral complexity expressed in the latter. In this section, I therefore present various factors that may accelerate species formation in different taxa and attempt to place behavioral flexibility in the general framework of speciation research.

Differences in species richness among lineages may be attributed to two main regulators of the rate of speciation, intrinsic ecological factors or external environmental factors. A more plausible explanation is that the interaction of internal and external factors accounts for variation in species numbers across taxa (Cracraft 1982), though the nature of this interaction has yet to be determined (Owens et al. 1999). Intrinsic mechanisms of speciation include the degree of genetic variation expressed within a species, while external controls include the number of geological or climatic barriers that can isolate populations and eventually lead to their differentiation into separate species. The latter refers to the well-known and widely accepted mechanism of speciation by allopatry, which is considered the most important mechanism of species formation (Cracraft 1982, 1985; Purvis et al. 1997; Coyne and Price 2000). There is debate about whether sympatric speciation - the formation of a species through population differentiation without spatial isolation (Winker 1999) - is common or rare, and though the process is possible under particular conditions, most evolutionary biologists agree that the majority of speciations occur via geographic disjunction (Coyne and Price 2000). Allopatric speciation can occur in two ways: a barrier may arise within the distribution of a species and isolate populations or a population can disperse across a barrier, and establish itself in a new area, thereby isolating itself from conspecifics. Recent work indicates that colonizing species indeed experience very high rates of evolution (Reznick et al. 1997). This also points to the importance of good dispersal capabilities, an intrinsic attribute of species that can predispose them to high speciation rates (Marzluff and Dial 1991; Owens et al. 1999).

Although species originate mostly through allopatric separation, the importance of internal genetic complexity should not be overlooked. In fact, the rate at which species accumulate changes in their genome is just as important as the physical barriers that may potentially separate them since genomic changes provide the basis for future divergence and differentiation should barriers arise (Cracraft 1982). In addition to high internal complexity, another factor that has been associated with rapid rates of evolution is the occurrence of sexual selection. Ever since Darwin, it has been suggested that sexual selection by female choice may increase speciation rates and generate richness (Lande 1981; Schluter and Price 1993). This is expected to occur if female preference for a male trait varies between populations of a given species and if preference for the trait is correlated with its expression in males, as has been shown in guppies for example (Houde and Endler 1990). This would lead to assortative mating within populations and to the development of reproductive isolation (Barraclough et al. 1995). Several studies have demonstrated a link between sexual selection and richness (Barraclough et al 1995; Mitra et al. 1996; Owens et al. 1999), thereby supporting the idea that sexual selection could be a driving force for speciation.

Although many of the variables mentioned previously could account for richness in different taxa, the focus of this thesis is on one specific quality of species that may predispose them to being species-rich and that is their degree of behavioral flexibility. This is not to say that the other intrinsic and extrinsic factors have a lesser role to play, but that the role of behavioral flexibility in speciation research has been undermined and needs to be reconsidered in a more broad and detailed work. This thesis therefore attempts to place the emphasis on behavior by examining the link between flexibility and richness suggested in Wyles, Kunkel and Wilson's (1983; Wilson 1985) behavioral drive hypothesis.

Species concepts

It is important to mention one important underlying assumption of the recognition of species numbers in taxa. It depends largely, if not entirely, on the way species are defined. The issue is not a trivial one since any evolutionary biologist studying the process by which new species arise should be concerned with how species are defined (Harrison 1998). There are currently 22 species concepts in use by biologists of all disciplines, from ecologists to systematists to paleontologists (de Quieroz 1998). Some concepts view species as evolving lineages, i.e. groups of organisms descended from a single ancestor, distinguished from other such groups by a uniquely derived character (phylogenetic species concept, Rosen 1978; Nixon and Wheeler 1990). Others recognize species based on overall similarity among groups of organisms (phenetic species concept, Sneath 1976). The conceptualization of species has important implications on the way speciation is viewed. For example, if a species is thought of as any biological entity possessing a uniquely derived character, speciation will be viewed as the fixation of traits, and species can therefore be recognized in an unbranched lineage, i.e. anagenesis is the model for speciation (de Quieroz 1998). This is radically different from the belief that cladogenesis, the splitting of lineages, constitutes true speciation (Ridley 1989).

Most studies in vertebrate zoology, especially ornithology and mammalogy, use Mayr's biological species concept (BSC), which he introduced in 1963 to make species recognition more practical and objective. He has since reviewed and revised it in several publications. According to the most recent version of the BSC, a species is a 'group of interbreeding natural populations that is reproductively isolated from other such groups' (Mayr and Ashlock 1991). This view of species therefore emphasizes gene flow (or the absence of it) and isolating mechanisms between sexually reproducing populations. As such, however, it also excludes asexual organisms and hybrids, cases where reproductive isolation between populations breaks down. Despite the problems associated with the

BSC, (its lack of generality, for example, due to the exclusion of a significant portion of biodiversity; reviewed in Mayden 1997), it continues to exert great influence in the field of biology: it is the concept of species most biologists and most textbooks employ. It is also the concept used by Sibley and Ahlquist (1990) to construct their avian phylogeny, currently the most comprehensive phylogeny of the class Aves, and is the concept that will be used in this thesis. Consequently, the results of this thesis will depend to a great extent on the ability of the BSC to accurately delineate species, as well as on the reliability of Sibley and Ahlquist's (1990) avian phylogeny.

Specific research goals

As stated earlier, the specific goal of this thesis is to test the predictions of the behavioral drive hypothesis, namely that opportunistic behavior should lead to greater rates of evolution and higher species richness in flexible taxa. Research on primates has provided evidence for one assumption of the behavioral drive hypothesis, i.e. the association between innovation rate, brain size and social transmission (Reader and Laland 1999). In this thesis, I provide a test of the other component of the behavioral drive hypothesis, the link between behavioral innovation and accelerated rates of evolution, by attempting to demonstrate a positive correlation between behavioral flexibility and the number of species in avian taxa. Due to the large-scale nature of the study, the measure of behavioral flexibility must encompass as many species as possible and be representative of the entire avifauna. I employ two measures that satisfy these criteria: feeding innovation rate and relative brain size.

The first measure of flexibility, feeding innovation rate, expresses the capacity for rapid adjustments in behavior when an individual is faced with unexpected foraging situations. The measure is a literature count of new and unusual feeding behaviors (new food types or techniques) displayed by avian groups around the world. It is corrected for the research effort per taxon to account for the fact that certain bird groups are more intensely studied than others and could, for that reason alone, end up with higher innovation frequencies. This is the correction that Reader and Laland (1999) also applied to their innovation measure in their work on primates. In addition to the behavioral measure of flexibility, I also use a neuroanatomical one, relative brain size. The most obvious advantage of this measure is that it is available for over 700 bird species. It is also closely correlated with the weight of the finer telencephalic predictors of flexibility, the forebrain and the neostriatum/hyperstriatum ventrale complex (Timmermans 1999), which are only available for 140 and 32 species, respectively.

I attempt to correlate relative brain size and feeding innovation rate with the number of species in avian taxa in order to test the hypothesis that innovative behaviors should lead to greater species richness. It should be noted, however, that the number of species at any given time is the result of a balance between speciation and extinction rates (Cracraft 1985; Marzluff and Dial 1991; Owens et al. 1999). A taxon may contain many species through a high rate of speciation combined with a low rate of extinction or through equally high rates of species production and species loss. Both mechanisms must therefore be examined before one can conclude that flexible behavior leads to high species richness via a high rate of species birth alone.

It is reasonable to assume that species that can alter their behavior in response to environmental changes should have greater chances of survival should disturbances occur. The ability to switch to a different food source or to leave and colonize new areas in a time of resource depletion or habitat loss should allow opportunists to persist when their less flexible counterparts would perish. Behavior can therefore be a critical factor in extinction risks (Reed 1999). However, relevant behavioral characteristics, in particular the degree of behavioral plasticity, are rarely incorporated into extinction models, and this can be a significant oversight (Reed 1999, Cracraft 1985). The second hypothesis I therefore test is that greater flexibility should be associated with a lower number of threatened and extinct species. I estimate these numbers from the 1996 IUCN Red List of Threatened Animals (Baillie and Groombridge 1996), which includes three categories of threat: vulnerability, endangerment and critical endangerment. I combine the three in order to increase sample size and to minimize the effect, if any, of a change in the status of a species from one level of threat to another.

In the main chapter of this thesis (chapter 3), I test the idea that species richness in birds is positively associated with feeding innovation rate and relative brain size. I also test the idea that the two flexibility correlates are negatively associated with extinction risk. In the other chapters (chapters 1 and 2), I examine two problems with the measure of innovation rate. First, I validate the use of research effort as a control for inflated innovation frequencies in certain groups of birds. Research effort is the control used by Reader and Laland (1999) in their study on primates. In birds, species number per taxon has been the traditional control used in previous studies of innovation (Lefebvre et al. 1997, 1998; Timmermans et al. 2000). However, it cannot be used here because it is the variable I am trying to predict. The number of innovations must therefore be corrected by the second strongest confound of innovation frequency after species number per taxon, research effort.

Secondly, I test the possible effect of six confounding variables on innovation frequencies. Innovation reports taken from short notes are anecdotal and often treated as subjective and unreliable (reviewed in Mitchell et al. 1997 and the open peer commentary following Whiten and Byrne 1988). These problems can be circumvented by using independent data gatherers blind to the hypothesis, and calculating inter-reader agreement levels. Another solution is to control for factors that may bias the number of feeding anecdotes found in the literature. For example, bird groups that are photographed more often or studied more intensively by researchers may yield more innovation reports than groups that receive less scientific attention. Several biases must therefore be quantified in order to test the validity of the innovation measure. The first four originate from ornithologists, while the remaining three stem from the birds themselves: research effort (estimated from the number of articles per taxon), ornithologist interest (number of photographs in birding magazines), reporting bias (assessed by a survey to professional ornithologists), journal style, juvenile development mode (nidicolous birds have larger brains as adults than do nidifugous ones, Portmann 1946), population size, and common ancestry. If feeding innovation rate can be shown in chapters 1 and 2 to be a valid operational estimate of flexibility, then it can be used with confidence in chapter 3 to test the behavioral drive hypothesis on birds.

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Introduction to Chapters 1 and 2

In the first two chapters of this thesis, I develop the innovation index. I look at seven potential confounding variables that may bias the number of innovations reported in the literature. I then correct this number by the confounding variable that comes out most significant in a multiple regression that does not include the number of species. The first four biases originate from ornithologists, while the remaining three stem from the birds themselves: research effort (estimated from the number of articles per taxon), ornithologist interest (number of photographs in birding magazines), reporting bias (assessed by a survey to professional ornithologists), journal style, juvenile development mode, population size, and common ancestry.

I also attempt to demonstrate that feeding innovation rate is a valid way of quantifying behavioral flexibility in the field. To do this, I show that the link between innovation frequency and relative forebrain size is not due to confounding variables. If differences in the number of innovations per taxon are not caused by confounding variables but by differences in cognitive capacities, then feeding innovation rate can be considered a valid operational estimate of flexibility, and can be used with confidence in chapter three to test the behavioral drive hypothesis.

Chapter 1

Forebrain size and innovation rate in European birds: feeding, nesting and confounding variables

Abstract

Previous work has shown a positive correlation between relative forebrain size and feeding innovation frequency, corrected for species number, over different taxonomic groups of birds. Several confounding variables could account for this relationship: ornithologists could notice and report innovations more often in certain taxa because of biased expectations, greater research effort, editorial bias in journals or large population sizes of the taxa. The innovation-forebrain correlation could also be spuriously caused by phylogeny or juvenile development mode. We examined these possibilities by entering species number per taxon, population size, number of full-length papers, expectations (assessed by a questionnaire), journal source and development mode in multiple regressions that also included relative forebrain size. We did this with and without phylogenetic corrections and tested two behavioral categories, feeding and nesting, where flexibility and learning are clearly thought to differ, but confounds should have similar effects. Through an exhaustive survey covering 30 years in 11 journals, a total of 683 innovations was gathered for the northwestern part of Europe, 507 for feeding and 176 for nesting. Species number per taxon was the only significant confounding variable for both feeding and nesting reports. When species number was not included in the analysis, research effort took its place as the main confounding variable of feeding anecdote frequency. As predicted, forebrain size was a second significant predictor for feeding innovations (corrected for either species number or research effort), but not for nesting. The frequency of feeding innovations in the short notes of ornithology journals thus appears to be a valid and reliable way to operationalize behavioral flexibility in birds.

Introduction

When birds show behaviors that are unusual with respect to their species norm. ornithologists routinely report these in the short notes section of avian journals. Most often, the notes concern new feeding behaviors, sightings of vagrant individuals away from the species' range or unusual materials and places used for nesting. Lefebvre et al. (1997, 1998) have proposed that these notes, when exhaustively collated, may be a good way to quantify taxonomic differences in behavioral flexibility: all other things being equal, a taxonomic group (e.g. the order Passeriformes; Wyles et al. 1983) that shows more opportunism, more generalism, more learning and innovation. should appear more often in these short notes. For novel feeding behaviors, a consistent pattern of taxonomic differences has been found in birds of Europe, North America (Lefebvre et al. 1997), Australia and New Zealand (Lefebvre et al. 1998): once species diversity is taken into account (Passeriformes will appear in more notes because there are so many species in this order), groups like the Corvida. Ciconiida and Accipitrida show high rates of innovation. while Phasianida. Columbiformes and Apodiformes do not.

Part of this variation is associated with the relative size of the forebrain. Avian taxa characterized by a relatively large forebrain (e.g. Holarctic Corvida and Piciformes. Australian Psittaciformes) tend to show higher feeding innovation rates (Lefebvre et al. 1997, 1998); a similar relationship between innovation rate and relative size of the neocortex has recently been shown in primates (Reader and Laland 1999). Avian species that have successfully established themselves in new areas have a relatively larger forebrain and a higher innovation rate than species that have failed to do so (Sol and Lefebvre 2000). Similar links between the complexity of a behavior and the size of its neural substrate in birds and mammals have been established for spatial memory (reviewed by Sherry et al. 1992; Balda et al. 1996), song repertoires (de Voogd et al. 1993; Brenowitz and Kroodsma 1996), social networks (reviewed by Dunbar 1998), tactical deception (Byrne 1993), social learning and tool use (Reader and Laland 1999).

Innovation reports taken from short notes are anecdotal, a data-gathering technique that is often criticized for its subjectivity and dependence on ad libitum observations (reviewed in Mitchell et al. 1997 and the open peer commentary following Whiten and Byrne 1988). Previous papers on feeding innovations have attempted to minimize this problem by avoiding cognitive interpretations and using independent readers blind to the hypothesis, yielding high levels of inter-judge agreement (Lefebvre et al. 1997, 1998). However, short notes may nevertheless carry a hidden bias, leading to a spurious relationship between innovation rate and relative forebrain size.

One way to deal with this problem is to compare short note categories that are thought to involve different degrees of behavioral flexibility. Nest building is a good candidate for comparison with feeding: it is the third most frequent category in short notes (after ranging and feeding) and is thought to be more constrained than feeding. A review by Hansell (1984) concludes on the 'substantial degree of genetic control' (p. 218) over nest building and the paucity of evidence for modification of this behavior through experience, with at most a sharpening of pre-programmed tendencies through practice (Collias and Collias 1964). Sargent (1965) suggests that 'innate predispositions tend to bias birds in favor of species-specific nesting materials and situations, with experience playing only a limited role' (p.59). Nesting is also more specialized than feeding: there is, for example, no nesting equivalent of the omnivore strategy in feeding. Given these differences, the information processing capacity associated with a larger forebrain should affect feeding more than it should nesting; in contrast, there is no reason to expect that observer bias and chance will act differentially on the two behavioral categories.

A second problem posed by the innovation/forebrain link is its potential dependence on confounding variables. The most obvious confounding variable, species number per taxon, was removed in previous work, but variables like population size, reporting bias or research effort could also affect the relationship between innovation frequency and forebrain size: do Passerida, for example, show a high innovation frequency because the parvorder contains so many species or because it is intensively studied by ornithologists, who both expect and report more innovative behaviors in this highly populous group? Phylogeny could also be an important confounding variable: a high innovation rate and large forebrain could co-occur in Passerida and Corvida, on the one hand, and Accipitrida and Falconida, on the other, because of common ancestry (Harvey and Pagel 1991). Taxonomic levels chosen for previous analyses were very general, i.e. classical orders (Lefebvre et al. 1997), which are often equivalent to molecular parvorders (Lefebvre et al. 1998); even at this remote level, however, genetic distances between taxa vary considerably (Sibley and Ahlquist 1990).

In this paper, we use the largest regional data set available for short notes, that of northwestern Europe, the region that is also best covered by the forebrain size sample of Portmann (1947). Through an exhaustive survey of 30 years (1970-1999) in 11 journals, we increase the database gathered for Great Britain by Lefebvre et al. (1997) on feeding and apply the same procedure to nesting reports. If nesting is more tightly constrained than feeding and if innovation reports are a valid estimate of the behavioral flexibility allowed by larger information processing structures, then only feeding should be associated with forebrain size. Secondly, if the association is not caused by common ancestry, independent contrasts on the European data should yield results similar to previously reported trends at the level of classical orders (Lefebvre et al. 1997). Thirdly, if population size, reporting bias and research effort are responsible for variation in the number of short notes published per avian taxon, they should account for the previously reported effects of species number and forebrain size when entered with them in multiple regressions. We estimate population size per taxon from the recent Atlas of European Birds (Hagemeijer and Blair 1997), reporting bias by a questionnaire given to professional ornithologists and research effort by the taxonomic distribution of full-length papers in the journals where our innovations were collated.

Finally, we look at the effect of journal source on our conclusions: in Europe, the best source for innovations is *British Birds*, which contributes approximately 70% of our database. Contrary to other journals, many of the short notes in *British Birds* are submitted by non-academics, albeit after careful review (and frequent printed comment) by an eight-member Behavior Notes panel. We thus separate our innovation data into two categories, *British Birds* vs. all other journals, to determine if the importance of the former journal and its particular editorial policy have a biasing effect on the innovation/forebrain correlation.

Methods

The short notes sections of *Ibis, Bird Study, British Birds, Scottish Birds, Ornis Scandinavica/Journal of Avian Biology, Ornis Fennica, Ardea, Die Vogelwarte* (Englishlanguage papers and summaries only), *Alauda*, *Nos Oiseaux* and *Aves* were exhaustively reviewed for any mention in the title or text itself of a feeding or nesting innovation. The first three journals cover England and Wales, while the others respectively cover Scotland, the Scandinavian countries, Finland, the Netherlands, Germany, France, and the French-speaking areas of Switzerland and Belgium. Approximately 11 400 short notes were scanned in the journals for the period 1970 to 1999 (except *Aves* where the last year available to us was 1981). A total of 683 innovations was found over the 30 years, 507 for feeding and 176 for nesting; a complete list of the innovations is available upon request. Of the feeding innovations, 124 were identical to the ones used in Lefebvre et al. (1997); 228 were gathered by a second, independent reader (DC) for 1973-1982 and 1993-1997 in *British Birds* and *Scottish Birds*, and for 1970-1997 in *Alauda* and *Nos Oiseaux*. The remaining 155 innovations were collated by a third reader (LL). The use of independent readers allowed us to calculate inter-judge agreement, an important control given the nature of our data collection technique. For nesting, 124 of the innovations were collated by NN for the 1977-1999 period in *British Birds* and *Scottish Birds*, as well as in *Aves* (1970-1981) and in *Die Vogelwarte* (1970-1999); a second, independent reader (DC), covering *British Birds* and *Scottish Birds* for 1970-1976, *Alauda*, *Nos Oiseaux*, and *Ornis Fennica*, *Ornis Scandinavica/Journal of Avian Biology*, *Ardea*, *Bird Study*, and *Ibis* for 1970-1999, again allowed us to calculate inter-judge agreement for this behavior.

As in previous work (Lefebvre et al. 1997, 1998), a feeding innovation was defined as either the ingestion of a new food type or the use of a new foraging technique. For a given report, the food item or foraging technique had to be stated (or in a few cases, clearly implied) by the author to be unusual for the species and/or the author had to state that this was the first known published report of the behavior. To avoid subjective bias in data collection, we based our decisions on statements made by the authors rather than our own opinion of the reports, looking for key words like 'unusual', 'unknown', 'rare', 'opportunistic', 'strange', 'not noted before', 'not recorded', 'first report'. When a report featured several species, we credited each one with a feeding innovation. When the same behavior was mentioned more than once in the literature for a given species, we kept only the oldest report and counted the behavior as a single innovation. When a report stated that a behavior, although unusual, had been noted by other authors, we did not include it. Nesting innovations were defined as either the use of an unusual material or site. Some of the short notes we scanned concerned unusual timing of nesting behavior; we excluded these cases, however, since they are likely to be more affected by hormonal variables (the major determinants of nest timing) than information-processing, thus biasing the data in favor of our hypothesis. For nesting, we searched for the same key words as we did for feeding innovations and used the same multiple entry rule when two or more species were featured in the same report. Once again, reports of identical behaviors for the same species were only considered once. Table 1 presents examples of the nesting innovations found, including the descriptors taken verbatim from the original reports that justify the novelty of the observation.

For each behavioral category, we tabulated the number of innovations per taxonomic group, using molecularly defined taxa (Sibley and Monroe 1990) that were as close as possible to the classical orders used by Lefebvre et al. (1997). In approximately half the cases, this corresponds to molecular orders; in the other half, the taxon corresponds to what Sibley and Monroe call 'parvorders', a division that is particularly useful for the new molecular orders that include very large numbers of species, i.e. Passeriformes and Ciconiiformes. In three cases (Grui, Ralli and Caprimulgi), we used Sibley and Monroe's 'suborder' and, in one case (Pteroclides), 'infraorder'. In the rest of this paper, we will use the terms 'taxon' and 'taxonomic group' to refer to the categories in Table 2. As in previous papers (Lefebvre et al. 1997, 1998), we excluded the nocturnal owls (suborder Strigi) from our study, since innovations in this group are almost never witnessed, but instead inferred from fecal evidence. To calculate species per taxon, we used a recent atlas of the breeding birds of Europe (Hagemeijer and Blair 1997), excluding vagrants and species found only outside the zone covered by our 11 journals, e.g. southern Spain or the Balkans.

Innovation frequencies per taxon were log transformed (ln [freq + 1]) because of their non-normal distribution: many groups yield very small frequencies, while a few groups yield very large ones (e.g. Passerida: 152 feeding innovations, 84 nesting innovations). In contrast to previous work on feeding innovations in Europe (Lefebvre et al. 1997), we factored out species per taxon (also ln transformed due to the presence of very small and very large values) using partial correlations instead of *chi* values; *chi* 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 (Lefebvre et al. 1998). We also factored out population size per taxon using the same method. For each of the European species, we took the median value of the population number (ln converted as well) given by Hagemeijer and Blair (1997) and summed all species in a taxon, again excluding vagrants and birds found outside the range covered by the journals.

Research effort was estimated from full-length papers published in the same journals we surveyed for short notes. Either one or two issues per volume, depending on publication frequency, were randomly sampled for each journal and all species studied in field-based full-length papers in the issue were noted. We excluded studies done in captivity or based on data from the literature, since this kind of research cannot yield innovation reports; we also excluded zoological surveys that simply name species present in a particular area, since they focus on identification, not behavior, and can potentially skew taxonomic frequencies due to the large number of species in each paper. A total of 1214 species entries were obtained. Reporting bias was estimated from a questionnaire (see Lefebvre et al. submitted, for details). Professional ornithologists attending a national meeting were asked to assign a score between 1 and 5 to their likeliness to notice and report a new food type or foraging technique in each of the taxonomic groups. Mean scores per taxon were calculated from the 25 questionnaires returned to us.

As in previous papers, we used Portmann (1947) as the source of the forebrain data. Portmann's work covers 140 avian species in 119 genera. His data are presented as ratios of forebrain weight for a given species divided by the brainstem weight of a Galliforme of equivalent body weight: Portmann calls the latter measure the basal index, while the forebrain ratio is called the hemispheric index. Multiplying Portmann's basal index by his hemispheric index yields forebrain weight. Using the body weights also provided by Portmann, we ran log-log regressions on the 119 genera (Strigi included), then calculated mean residual deviations for the taxa defined above.

Two statistical approaches were used: (1) multiple regressions (Systat, version 5.2) that assumed, as did Lefebvre et al. (1997), that orders, parvorders and suborders are taxonomically remote enough for common ancestry to be negligible; and (2) independent contrasts (CAIC, Purvis and Rambaut 1995). The latter technique is based on the construction of a phyletic tree using average linkage clustering of DNA-DNA hybridization distances given in Sibley and Ahlquist (1990). The tree is then used in a phylogenetically controlled test performed by an independent contrast program; the 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. The independent variables in the multiple regressions were (1) number of species per taxon, (2) population size, (3) number of full-length papers, (4) mean score for likeliness to report and (5) mean residual forebrain size. We also added a known confound of avian brain size, juvenile development mode (Portmann 1946; Bennett and Harvey 1985), which was entered as a dichotomous variable (nidicolous vs. nidifugous, based on Sibley and Monroe 1990). In the multiple regressions and the independent contrasts, we predict a significant partial correlation between feeding innovation frequency and mean residual forebrain size, but no such correlation for nesting report frequency. With the 21 taxonomic categories used, the probability of detecting a difference at the 0.05 level between a partial correlation for feeding (expected $r = 0.700$, based on Lefebvre et al. 1997) and no partial correlation for nesting (expected $r = 0.000$) is 0.80 (Cohen 1988).

Results

Table 2 presents the frequency of nesting and feeding innovations found for the

21 taxa. As in previous papers, groups like Passerida, Corvida, Accipitrida and Charadriida show high frequencies, while Phasianida and Columbiformes show low frequencies. Our data collection procedure is highly reliable: frequencies per taxon obtained by the independent readers are very similar for both nesting ($r = 0.827$, $p < 0.001$) and feeding ($r = 0.910$, $p < 0.001$).

The best predictor of innovation frequency per taxon is species number, which respectively accounts for 84% ($p < 0.001$) and 68% ($p < 0.001$) of the feeding and nesting innovations. None of the other potential confounding variables come out significant in the multiple regressions. Neither mode of juvenile development (partial $r = 0.257$, $p = 0.304$), population size (partial $r = -0.194$, $p = 0.441$), research effort (partial $r = 0.338$, $p = 0.171$) nor reporting bias (partial $r = 0.382$, $p = 0.117$) predict feeding innovation frequency when species number is present in the model (overall r^2 of the multiple regression = 0.879, $F_{2,17} = 70.167$, $p < 0.001$). When it is not included in the model, but forebrain size and all the other confounding variables are, research effort becomes the best predictor of innovation frequency ($r = 0.889$, $p < 0.001$). Relative forebrain size is the only other variable that remains significant in both cases (with species number included in the model: partial $r = 0.564$, $p = 0.012$; without species number: partial $r = 0.565$, $p = 0.012$; overall r^2 of the multiple regression = 0.857, $F_{2,17} = 51.105$, $p < 0.001$). When regressions are run on the split data sets from the two journals sources, there is a significant difference ($p = 0.005$) in innovation frequency per taxon between *British Birds* ($n = 346$ innovations) and all other journals ($n = 161$). Taken separately, however, both journal sources yield significant effects of relative forebrain size with species number also included in the multiple regression (*British Birds*: partial r

of forebrain size = 0.543, $p = 0.020$; all other journals, partial $r = 0.500$, $p = 0.034$), indicating that divergence between sources does not invalidate the innovation-forebrain link.

For nesting innovations, the only significant predictor in the multiple regression is the number of species per taxon (partial $r = 0.821$, $p < 0.001$; overall r^2 of the multiple regression = 0.678, $F_{1,19} = 43.166$, $p < 0.001$). Neither forebrain size (partial $r = 0.244$, $p = 0.313$) nor juvenile development mode (partial $r = 0.386$, $p = 0.103$) reach significance thresholds for the nesting data; the same is true for population size (partial $r = 0.141$, $p = 0.565$), research effort (partial $r = 0.124$, $p = 0.613$) and reporting bias (partial $r = -0.206$, $p = 0.397$). The non-significant association between forebrain size and nesting is consistent with our prediction, but the partial correlations of forebrain size on nesting (0.244) and feeding (0.564) do not differ enough to reach statistical significance (t test on the coefficients of the partial correlations = 0.60, $df = 34$, ns). Furthermore, taxonomic trends in nesting and feeding reports are significantly correlated: residuals of the two sets of frequencies, each regressed against species number per taxon, yield an r of 0.482 ($p = 0.027$). These residuals are illustrated in Fig. 1, along with mean residual forebrain size.

Independent contrasts show the link between forebrain size and feeding innovation rate cannot be attributed to common ancestry: results from CAIC reveal a significant association of the two variables once phyletic effects have been removed (partial $r = 0.538$, $p = 0.018$). The independent contrasts for nesting also confirm the results obtained on phyletically-uncorrected taxa; as in the multiple regressions presented above, the effect of forebrain size on nesting reports is non- significant (partial $r = 0.216$, $p = 0.373$). As in the preceding analyses, no other variables come out significant in the multiple regressions conducted on independent contrasts.

Fig. 2 illustrates the taxonomic trends in the different confounding variables. If we reverse the logic of our earlier multiple regressions and now enter research effort or population size as the dependent variable and all other factors as independent ones, we find that species number is the only significant predictor for both variables, explaining respectively 52 and 90 % of their variance. Taxa that contain more individuals than would be expected on the basis of species number (positive residuals in Fig. 2a) are the Passerida, Corvida and Columbiformes, while taxa that contain relatively fewer individuals (negative residuals in Fig. 2a) are groups like the Accipitrida and Falconida. Taxa like Cuculiformes and Sulida are studied more often than would be expected on the basis of species number (positive residuals in Fig. 2b), while groups like Coraciiformes and Ralli are studied less often (negative residuals in Fig. 2b). The third confounding variable, reporting bias, is illustrated in Fig. 2c as relative mean score, standardized around the grand mean for all taxa to make it visually compatible with other variables. The taxa where ornithologists say they would be most likely to notice and report an innovation are the Scolopacida, Falconida and Piciformes, while the taxon where this is least likely is Columbiformes. In multiple regressions, the best predictor of reporting bias is innovation frequency.

Discussion

Of the six potential confounding variables examined in this study - population size, reporting bias, research effort, journal source, juvenile development mode and common ancestry - none account for the correlation between innovation frequency and relative forebrain size. A very similar result was obtained in a recent study of North America and Australia (Lefebvre et al. submitted); as in Europe, forebrain size and species number per taxon were the only significant predictors of innovation frequency in multiple regressions that included research effort, journal source, reporting bias, juvenile development mode, common ancestry and an additional measure of differential interest on the part of ornithologists, the taxonomic distribution of photographs in birding magazines. In multiple regressions that did not include species number, research effort was the only significant confound of feeding innovation frequency, as it is in the present study. The results are thus consistent in the three zones studied up to now. Once frequency is corrected by the main confounding variable, innovative bird groups can otherwise be predicted by the relative size of their forebrain: birds with a relatively large neural substrate, such as the corvids, are more opportunistic than the smaller-brained pigeons, pheasants, and nightjars, and produce a greater number of innovations.

As predicted, short notes of unusual nesting behaviors do not follow the trend found for feeding. Number of species per taxon is the only significant predictor here, while forebrain size is non-significant. The failure of the nesting/forebrain relationship to reach significance is unlikely to be due to sample size (n = 176): the feeding sub-sample taken from all journals other than *British Birds* (n = 161), despite being smaller than the sample for nesting, yields a significant correlation with forebrain size. The non-significant effect of forebrain size on nesting is consistent with the literature, which emphasizes the pre-programmed aspect of this behavior, rather than its dependence on information-processing and behavioral flexibility. Three results nevertheless suggest some caution here. First, the t test on differences between partial correlations for nesting and forebrain size, on the one hand, and feeding and forebrain size, on the other, is far from significant. Secondly, the correlation between nesting innovation rate and forebrain size is still positive, even if non-significant. Third, the residuals of feeding and nesting, once regressed against species number per taxon, are significantly correlated, with groups such as Charadriida, Falconida and Corvida showing positive values in Fig. 1 for both feeding and nesting, while Cuculiformes and Anseriformes produce fewer feeding and nesting innovations than predicted by species number. Until further work is done, the data thus offer only ambiguous support for the prediction tested in our study.

Several interesting trends emerge when the potential confounding variables are treated as dependent variables. The first surprising result is the very high proportion of variance (90%) in full-length paper frequency that is explained by species number per taxon. It is as if an 'ideal free distribution' determines a large part of this variable, with research effort being more or less proportional to the diversity of taxa. Deviations from this ideal free distribution (Fig. 2a) could reflect factors such as conservation needs, with Falconida, for instance, showing higher residuals than Columbiformes. The effect of species number on population size is much smaller (52% of the variance), although it is again the only significant predictor in our models. The second surprising result is that of reporting bias, which is best predicted by innovation frequency; this is all the more surprising because the converse is not true, i.e. innovation frequency cannot be predicted by reporting bias when forebrain size and species number are also included with it in multiple regressions. This suggests that ornithologists expect to see in birds the trends they read in the literature, but do not in turn bias their reports on the basis of these expectations. Added to the results on photo frequency in North America and Australia, our data thus suggest that feeding innovation rate is a property of birds, not of the ornithologists that study them.

Coupled with a recent study on North America and Australia (Lefebvre et al. submitted), this paper demonstrates that the relationship between forebrain size and feeding innovation rate, corrected for species number per taxon (or research effort), cannot be accounted for by the confounding variables studied up to now. Innovation rate has been linked to neural substrate size in both birds and primates (Reader and Laland 1999), suggesting that the trend could be general. As a measure of flexibility, innovation rate is quantitative, ecologically valid because it is gathered from field observations and as easily available for a broad range of taxa as are body weight and life history data. It avoids the limited taxonomic coverage of comparative learning studies, as well as the often arbitrary nature of the tasks and the potential dependence of results on contextual variables that can favor one species over another. The disadvantages of the measure (largely due to its anecdotal basis) can be minimized if cognitive interpretations of innovation reports are avoided, inter-judge reliability is assessed and confounding variables removed. For the moment, feeding innovation rate appears to be a valid and reliable way of operationalizing behavioral flexibility in the field.

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Table 1. Examples of nesting innovations in birds of northwestern Europe

Species	Innovation	Reference
Golden eagle	nesting in grouse moors; *unlikely because of human persecution*	Watson 1982
Common teal	nesting on ledges; *unusual*	Meek and Little 1980
Black guillemot	nesting in a building sited in an area of heavy industrialization; *unusual site, no record*	Carnduff 1981
Carrion crow	nest made from leftover ends of fencing wire; *unusual*	Mitchell 1985
Eurasian hobby	nesting on a pylon; *no records*	Trodd 1993
Eurasian siskin	nesting in a hanging flower pot; *unusual nest site*	Billett 1989
Common moorhen	nest cup composed of polythene	Dean 1992
Willow ptarmigan	nest made of straw; *exceptional in the material used and its thickness*	Watson 1977
Eurasian blackbird	nesting in a commuter station	Montier 1980
Winter wren	seen excavating nest; *no mention of wrens excavating cavities*	Harper 1991
Common starling	seen excavating nest holes in sand dunes: *first recorded instance*	Summers 1989
Blue tit	seen using house martin nest; *no other records*	McNeil 1992
Common kestrel	nesting on an urban chimney; *interesting*	Smith 1992
Common kingfisher	nesting in peat-cuttings; *no records*	Limbert 1991
Common woodpigeon	nesting on sea cliffs and inside buildings; *exceptional, atypical*	Rebecca 1988

Terms in italics are taken verbatim from original papers and indicate novelty.

Table 2. Nesting and feeding innovation frequencies for 21 bird taxa

Taxonomic group	Nesting innovation frequency	Feeding innovation frequency		
		BB[a]	others[b]	total
Phasianida	2	2	2	4
Anseriformes	8	15	4	19
Piciformes	1	10	3	13
Upupiformes	0	0	0	0
Coraciiformes	1	2	0	2
Cuculiformes	0	0	1	1
Apodiformes	0	1	1	2
Caprimulgi	0	0	0	0
Columbiformes	6	3	0	3
Grui	1	1	0	1
Ralli	3	10	2	12
Pteroclides	0	0	0	0
Scolopacida	1	24	4	28
Charadriida	18	49	28	77
Accipitrida	7	18	25	43
Falconida	16	22	17	39
Podicipedida	2	4	2	6

Sulida	2	4	3	7
Ciconiida	7	22	13	35
Corvida	17	44	19	63
Passerida	84	115	37	152
Total	176	346	161	507

[a] Innovations found in *British Birds*.

[b] Innovations found in all other European journals.

Figure 1. (A) Phyletic tree for the taxonomic groups used in this study based on DNA/DNA hybridization distances in Sibley and Ahlquist (1990). (B) Standardized residual of forebrain size regressed against body weight. Standardized residual of innovation frequency regressed against species number per taxon for feeding (C) and nesting (D)

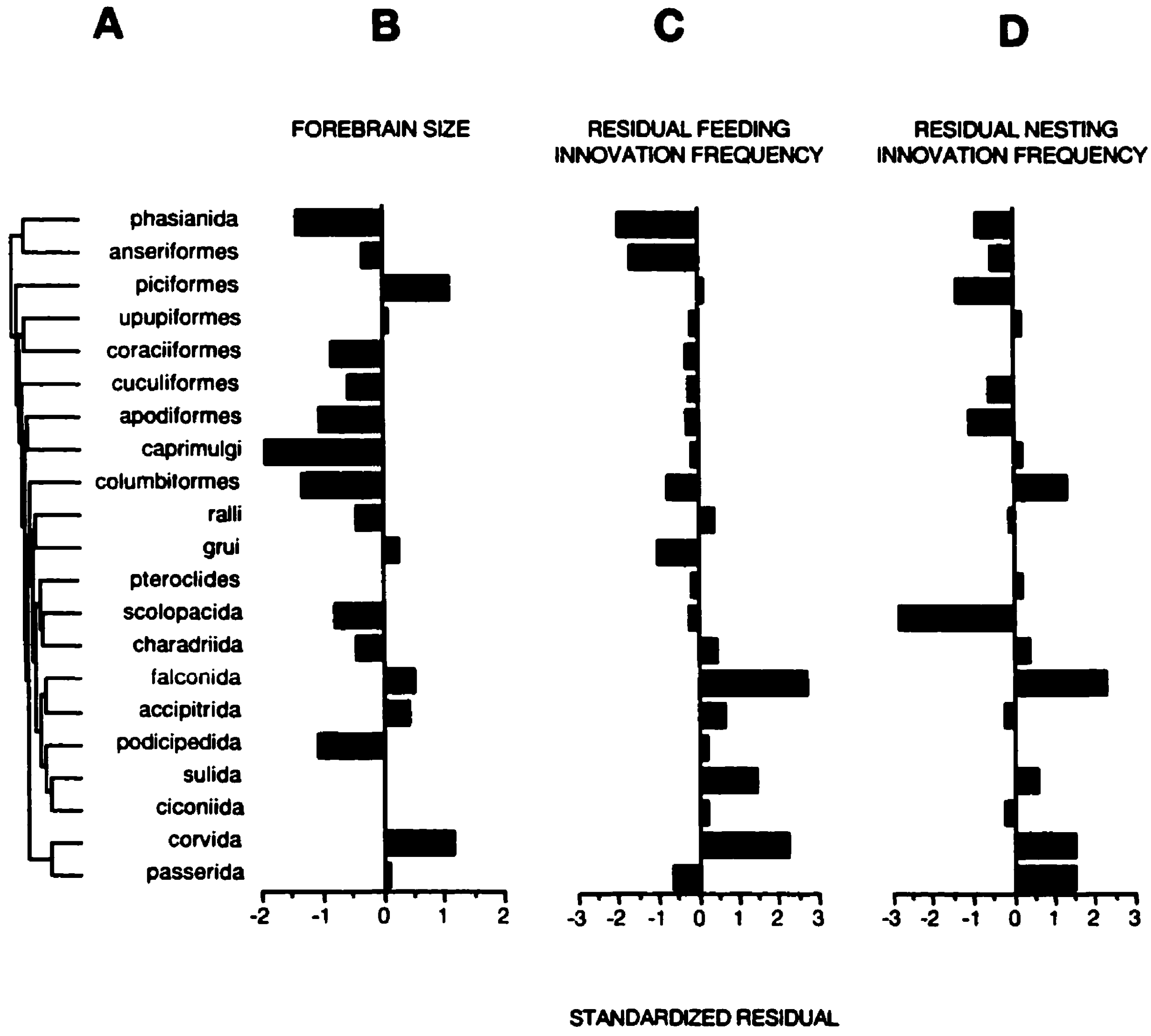
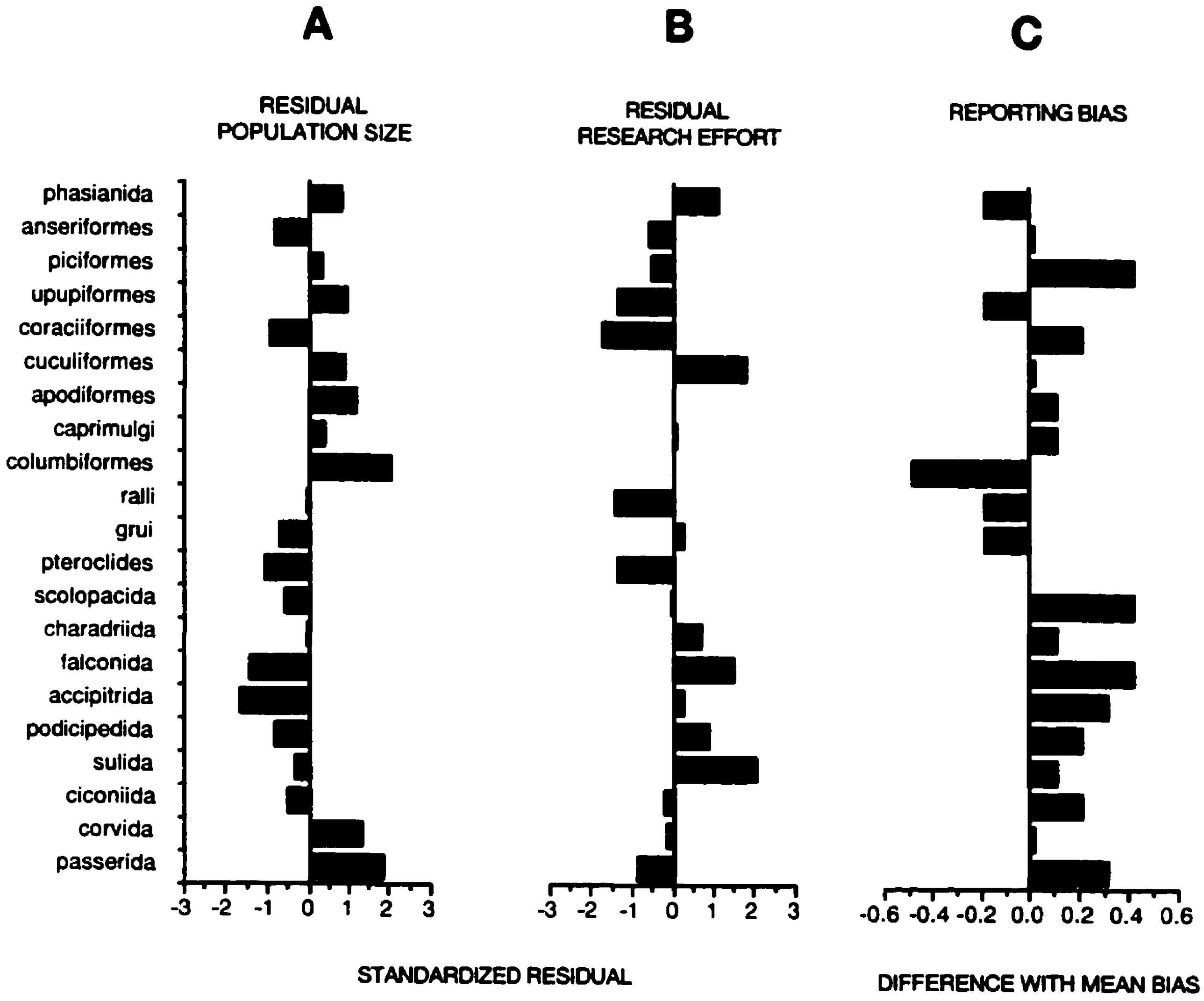

A
B
C
D
FOREBRAIN SIZE
RESIDUAL FEEDING INNOVATION FREQUENCY
RESIDUAL NESTING INNOVATION FREQUENCY
phasianida
anseriformes
piciformes
upupiformes
coraciiformes
cuculiformes
apodiformes
caprimulgi
columbiformes
ralli
grui
pteroclides
scolopacida
charadriida
falconida
accipitrida
podicipedida
sulida
ciconiida
corvida
passerida
-2 -1 0 1 2
-3 -2 -1 0 1 2 3
-3 -2 -1 0 1 2 3
STANDARDIZED RESIDUAL

Figure 2. Standardized residual of population size (A) and research effort (B) per taxon, regressed against species number. (C) Reporting bias per taxon. expressed as the difference between the overall mean and the mean score for each taxon


A
B
C
RESIDUAL POPULATION SIZE
RESIDUAL RESEARCH EFFORT
REPORTING BIAS
phasianida
anseriformes
piciformes
upupiformes
coraciiformes
cuculiformes
apodiformes
caprimulgi
columbiformes
ralli
grui
pteroclides
scolopacida
charadriida
falconida
accipitrida
podicipedida
sulida
ciconiida
corvida
passerida
-3 -2 -1 0 1 2 3
-3 -2 -1 0 1 2 3
-0.6 -0.4 -0.2 0.0 0.2 0.4 0.6
STANDARDIZED RESIDUAL
DIFFERENCE WITH MEAN BIAS

Chapter 2

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

Abstract

The short notes of ornithology journals feature new and unusual feeding behaviors, which, when systematically collated, could provide a quantitative estimate of behavioral flexibility in different bird groups. Taxonomic variation in the frequency of new behaviors (innovations) is correlated with variation in relative forebrain size. In this paper, we examine six potential confounding variables that could be responsible for this correlation in North American and Australian birds. Aside from species number per taxon, which was taken into account in previous work, we looked at research effort (frequency of full-length papers), ornithologist interest (frequency of photos in birding magazines), reporting bias (a questionnaire given to ornithologists at a meeting), journal source (*The Wilson Bulletin* vs. six other North American journals), mode of juvenile development (nidicolous vs. nidifugous) and common ancestry (independent contrasts weighed by genetic distance). In simple regressions, each of these variables (except for development mode in North America) was significantly correlated to innovation frequency. In multiple regressions, however, only forebrain size and the number of species per taxon remained significant. When species number was not entered in the multiple regressions, research effort was the only significant confounding variable. Research effort was also the best predictor of photo frequency and was best predicted by species number. Ornithologists are thus not preferentially interested in innovative, large-brained taxa, suggesting that the correlation between innovations and neural substrate size is not a spurious effect of the confounding variables examined here.

Introduction

When birds display behaviors that deviate from their species' norm, ornithologists routinely report this in the short notes section of avian journals. Most often, the notes record sightings of a species outside its known range, but the second most frequent category concerns feeding innovations, i.e. unusual, rare or unreported food types and foraging techniques. The frequency with which a taxon appears in these notes could yield a quantitative estimate of its feeding flexibility. All other things being equal, birds that have a broader diet (generalists), respond more quickly to new feeding possibilities (opportunists) and show innovative solutions to feeding problems should be featured in more notes. A larger neural substrate for processing and integrating information could favor innovative feeding (Wyles et al. 1983). Short note frequency, corrected for species number, is correlated with relative size of the forebrain across avian taxa (Lefebvre et al. 1997, 1998; Nicolakakis and Lefebvre 2000), in particular that of the hyperstriatum ventrale, the telencephalic equivalent of the mammalian neocortex (Timmermans et al. 2000). A similar frequency count of feeding innovations in primates is correlated with relative size of the neocortex (Reader and Laland 1999).

Groups with large numbers of species (e.g. songbirds) can obviously yield more innovation reports than groups with fewer species (e.g. Upupiformes); species diversity was therefore taken into account in previous work (Lefebvre et al. 1997, 1998). Beyond this obvious confounding variable, however, it is still an open question whether variation in anecdote frequency is generated by birds themselves, by ornithologists or by other factors. If corvids, for example, yield a high innovation frequency, is it because they are truly flexible or because ornithologists watch and study them more intensively and expect them to show more complex behaviors? The difficulty is to quantify such biases in order to assess their possible effect on the correlation between innovation rate and neural substrate size. For the two areas of the world where the best data were available to us, North America and Australia, we considered six potential confounding variables and used multiple regressions to assess their relative importance.

Four of the confounding variables dealt with potential biases originating in the ornithologists: research effort, photographic interest for particular avian taxa, reporting bias and journal source. Research effort can be easily estimated by counting the number of field-based full-length papers dedicated to each taxonomic group; Reader and Laland (1999) have used a similar measure in their study on primates. Contrary to short notes, whose starting point is normally a serendipitous observation with a low probability of occurrence and a very short time frame, full-length papers reflect a deliberate and sustained effort that involves grant requests, animal ethics clearance and long hours in the field; if feeding anecdotes are only chance events that occur in the context of these directed studies, then full-length paper frequency should account for innovation rate.

Our second estimate of observer bias used birding magazines (e.g. *Birdwatcher's Digest*, *Wingspan*), which target both the professional and amateur ornithologist. Many of the journals where we gathered innovations publish contributions by these two types of observers. Potential biases in non-professionals cannot be assessed by full-length research papers, but they may show up in the relative importance given to particular avian groups in birding publications. We used the frequency with which avian taxa appeared in photographs in these magazines as an estimate of interest on the part of birdwatchers; if some birds are considered more interesting or appealing than others, this might skew anecdotal reports in their favor. Thirdly, using a questionnaire, we asked a group of professional ornithologists attending an annual meeting whether they would be more likely to notice and report a feeding innovation if it occurred in a particular taxonomic group. Fourth, we used journal differences in short note frequency to estimate potential biases due to publication policy. Some academic journals, e.g. *The Wilson Bulletin*, publish a relatively large number of feeding innovations notes. Other journals, in contrast, publish few feeding anecdotes, e.g. *The Auk* in recent years. These differences could skew taxonomic trends, by restricting innovation reports in the latter case to spectacular behavioral categories and species; a skew of this type is an obvious possibility in the publication by *Nature* of a tool manufacture report in crows (Hunt 1996).

The two other biases we assessed dealt with birds, not ornithologists. Following Bennett and Harvey (1985), we included juvenile development mode in our multiple regressions; nidicolous birds have relatively larger brains as adults than do nidifugous ones (Portmann 1946) and this confounding variable alone could cause a spurious relationship with innovation rate, as it did for the apparent link between ecological variables and brain size in Bennett and Harvey's study. Finally, we look at the possible effect of common ancestry by using independent contrasts (Felsenstein 1985; Purvis and Rambaut 1995). Taxa often share several traits because they inherited them from a common ancestor (Barraclough et al. 1998); as a result, high innovation frequencies could co-occur with a large forebrain in closely related taxa because of this phyletic confound. Previous work minimized this possibility by using taxonomic levels where ancestry was very remote, i.e. the order (Lefebvre et al. 1997) and the parvorder

(Lefebvre et al. 1998), but DNA hybridization measures of phyletic distance (Sibley and Ahlquist 1990) can be used even at these levels to factor out phylogeny.

Methods

Innovations

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

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

Biases stemming from ornithologists

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

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

Reporting bias was estimated from a questionnaire given to ornithologists attending the annual meeting of the Society of Canadian Ornithologists (McGill University, Montréal, August 6-7, 1999). Twenty-five people (out of a possible total of 56 attending) answered the following question: 'In the field, you witness a bird eating a food type that is not part of its known diet or using a foraging behavior that strikes you as unusual or new. Would you be more likely to notice and report what you saw in a short note to an ornithology journal if the bird were a... ', with the names of 29 taxonomic groups (based on the molecular taxonomy of Sibley and Monroe 1990) then listed sequentially. Next to the latin name of each taxon, one to three examples of species in the group were given (e.g. Struthioniformes: ostrich, emu, kiwi; Piciformes: woodpecker, barbet; Podicipedida: grebe). To control for possible effects of the order in which the taxa were listed on the questionnaire, one of three different versions was given to each ornithologist: one in which taxa were ordered from Struthioniformes to Passerida following the sequence used by Sibley and Monroe (1990), one in which this order was reversed, and one in which position on the list was randomized. Next to each taxonomic entry, a five-point scale was printed, where 1 corresponded to 'extremely unlikely' (to notice and report) and 5 to 'extremely likely'; subjects circled the appropriate number for each taxon. Mean scores per taxonomic group were calculated for this variable from the

25 questionnaires returned to us. The birds of Canada are routinely classified with the rest of North American species in ornithological handbooks and avifaunal lists. We can thus assume that Canadian ornithologists are an adequate sample for our North American data set, but the assumption is less tenable for Australian birds; we therefore restrict our use of the questionnaire results to the North American zone.

Phylogeny

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

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

Multiple regressions

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

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

Results

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

Simple regressions conducted on phyletically uncorrected taxa for Australia and North America show that all the variables, except for development mode in North America, are strongly correlated to innovation frequency. In multiple regressions, however, only species number per taxon and forebrain size remain significant predictors (Table 2). None of the other confounding variables appears in the final models. In the case of research effort and photo frequency, this is due to the common effect of species number on the variables, causing them to be excluded from the multiple regressions (Table 2). In multiple regressions where the number of species is not entered, relative forebrain size is still a significant predictor but research effort is the main confounding variable (North America: forebrain: partial $r = 0.679$, $p = 0.001$; research effort: $r = 0.791$, $p < 0.001$; overall r^2 of the multiple regression = 0.814, $F_{2,18} = 39.317$, $p < 0.001$; Australia: forebrain: $r = 0.674$, $p = 0.001$; research effort: partial $r = 0.421$, $p = 0.064$; overall r^2 of the multiple regression = 0.454, $F_{1,19} = 15.789$, $p < 0.001$). The relationship between forebrain size and innovation rate (frequency regressed against species number) is illustrated in Fig. 1.

Common ancestry (illustrated by the taxonomic tree in Fig. 1) plays a negligible role in the association between innovation rate and forebrain size. The results of the independent contrasts are very similar to those of the regressions run on the uncorrected taxa. Again, only species number and forebrain size remain significant predictors in both Australia and North America (Australia: forebrain p of partial correlation = 0.032; species number $p = 0.043$; all others ns; total $r^2 = 0.474$, $F_{2,18} = 9.073$, $p = 0.002$; North America: forebrain $p = 0.003$; species number $p < 0.001$; all others ns; total $r^2 = 0.754$, $F_{2,18} = 29.568$, $p < 0.001$). Journal source has no effect on the innovation-forebrain link.

The multiple regression conducted on the 146 cases taken from *The Wilson Bulletin* yields identical conclusions to the one conducted on the whole data set (forebrain $p = 0.001$; species number $p < 0.001$; all others ns; total $r^2 = 0.811$, $F_{2,18} = 43.879$, $p < 0.001$), as well as that conducted on the 141 cases taken from the six other North American journals (forebrain $p < 0.001$; species number $p = 0.003$; all others ns; total $r^2 = 0.719$, $F_{2,18} = 26.555$, $p < 0.001$). The taxonomic distribution of innovations in the two journal sources shows a highly significant correlation ($r = 0.763$, $p < 0.001$, $n = 24$).

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

Discussion

The results of this study show that five potential confounding variables, ornithologist interest, reporting bias, journal source, mode of juvenile development and common ancestry fail to account for the correlation between innovation rate and relative forebrain size in North American and Australian birds. Although some of these variables may be significantly associated with innovation frequency when taken alone, they are eliminated in multiple regressions when forebrain size and species number or research effort are entered. Our results confirm those obtained on the birds of northwestern Europe by Nicolakakis and Lefebvre (2000), who examined all the confounding variables studied here except photo frequency. Taken together, the results show that species number and research effort are the strongest confounds of short note frequency and either one needs to be removed when assessing the link between forebrain size and innovations.

The independent contrasts suggest that common ancestry plays a negligible role in the association between innovations and forebrain size. For Australia, these results differ from those reported in a previous study, which had used a smaller innovation sample (Lefebvre et al. 1998). Since common ancestry also fails to account for the innovation-forebrain correlation in North America (this paper) and northwestern Europe (Nicolakakis and Lefebvre 2000), we can only conclude that the previous effect of phylogeny on the Australian data was due to sampling error, a possibility raised in that paper (Lefebvre et al. 1998). It should be pointed out that our conclusions apply only to the taxonomic levels used up to now, those of orders (Lefebvre et al. 1997) and parvorders (Lefebvre et al. 1998; Nicolakakis and Lefebvre 2000; this paper), which yield a sufficiently small number of categories for our frequency data to be validly analyzed.

As the innovation data sets become larger, through the inclusion of new journals and earlier time periods or the weighted combination of information from different geographic zones, it will be possible to distribute the frequencies among many more categories and to test predictions at a finer taxonomic level (e.g. the family, Bennett and Harvey 1985; Owens et al. 1999).

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

The results on journal source also parallel those found in Europe. The journal *British Birds* provides almost 70% of the 413 innovations gathered in this zone (Nicolakakis and Lefebvre 2000). Nevertheless, splitting the data into two parts, *British*

Birds vs. ten other European journals, yields similar conclusions, as does the split here between *The Wilson Bulletin* and the six other North American journals. In a few taxa, the journal sources yield obvious differences. In Table 1, for example, none of the ten hummingbird or six Cuculiforme innovations are reported in *The Wilson Bulletin*. Sampling effects are probably behind these slight differences, which are in any case not large enough to modify the overall trends.

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

Up to now, taxonomic variation in innovation rate has proven to be a reliable and easily quantified index of feeding flexibility in the field. Anecdotal data should be treated with caution (reviewed in Mitchell et al. 1997 and the open peer commentary following Whiten and Byrne 1988), but they may solve some of the problems inherent in other comparative approaches, which rely on indirect, ecological correlates of flexibility (e.g. frugivory assumed to require more memory than folivory, Clutton-Brock and Harvey 1980) or ad hoc expectations on learning performance in captivity (e.g. Gossette and

Riddell 1966). Innovation rate, which the present study suggests is an intrinsic property of avian groups, not of ornithologists, common ancestry or development mode, is a promising tool that could be applied to other correlates of flexibility and to other animal taxa (e.g. primates, Reader and Laland 1999). For example, Sol and Lefebvre (2000) have shown that colonization success of birds introduced into New Zealand can be predicted by both forebrain size and innovation rate. Other links between flexibility and evolutionary ecology need to be tested, in particular the prediction made by Wyles et al. (1983) that innovative, large-brained taxa can fix mutations at a higher rate, since their flexibility raises the probability of encountering environmental conditions favorable to the phenotypic change.

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Table 1. Number of full-length papers, photographs and innovations per taxon for North America and Australia, as well as reporting bias for North America

	North America						Australia		
Taxon	Papers	Photos	Repbias	Inno			Papers	Photos	Inno
				WB[a]	others[b]	total			
Struthioniformes	-	-	-	-	-	-	7	9	0
Craciformes	1	0	2.7	0	0	0	5	5	0
Phasianida	37	113	2.9	1	0	1	1	3	2
Odontophorida	6	19	2.6	0	0	0	-	-	-
Anseriformes	89	385	3.1	6	1	7	22	16	0
Turniciformes	-	-	-	-	-	-	2	1	0
Piciformes	78	101	3.5	9	10	19	-	-	-
Coraciiformes	10	10	3.3	0	0	0	7	11	4
Cuculiformes	7	25	3.1	0	6	6	8	0	1
Psittaciformes	-	-	-	-	-	-	27	76	13
Apodiformes	5	3	3.2	1	1	2	4	0	2
Trochiliformes	21	75	3.5	0	10	10	-	-	-
Caprimulgi	4	10	3.2	0	0	0	4	5	1
Columbiformes	23	33	2.6	0	0	0	10	15	3
Ralli	9	34	2.9	3	2	5	10	10	4
Grui	5	52	2.9	3	1	4	3	4	2

Scolopacida	49	140	3.5	4	1	5	19	26	0
Charadriida	211	368	3.2	16	8	24	50	48	11
Falconida	22	49	3.5	4	8	12	13	7	9
Accipitrida	69	251	3.4	15	21	36	13	15	14
Podicipedida	11	26	3.3	0	1	1	4	0	2
Phaethontida	0	2	2.7	0	0	0	3	1	0
Sulida	21	43	3.2	0	1	1	9	12	1
Ciconiida	134	419	3.3	21	21	42	90	60	15
Tyranni	53	53	3.1	6	2	8	4	5	0
Corvida	92	117	3.1	11	16	27	221	126	47
Passerida	720	896	3.4	46	31	77	72	41	9

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[a] Innovations found in *The Wilson Bulletin*.

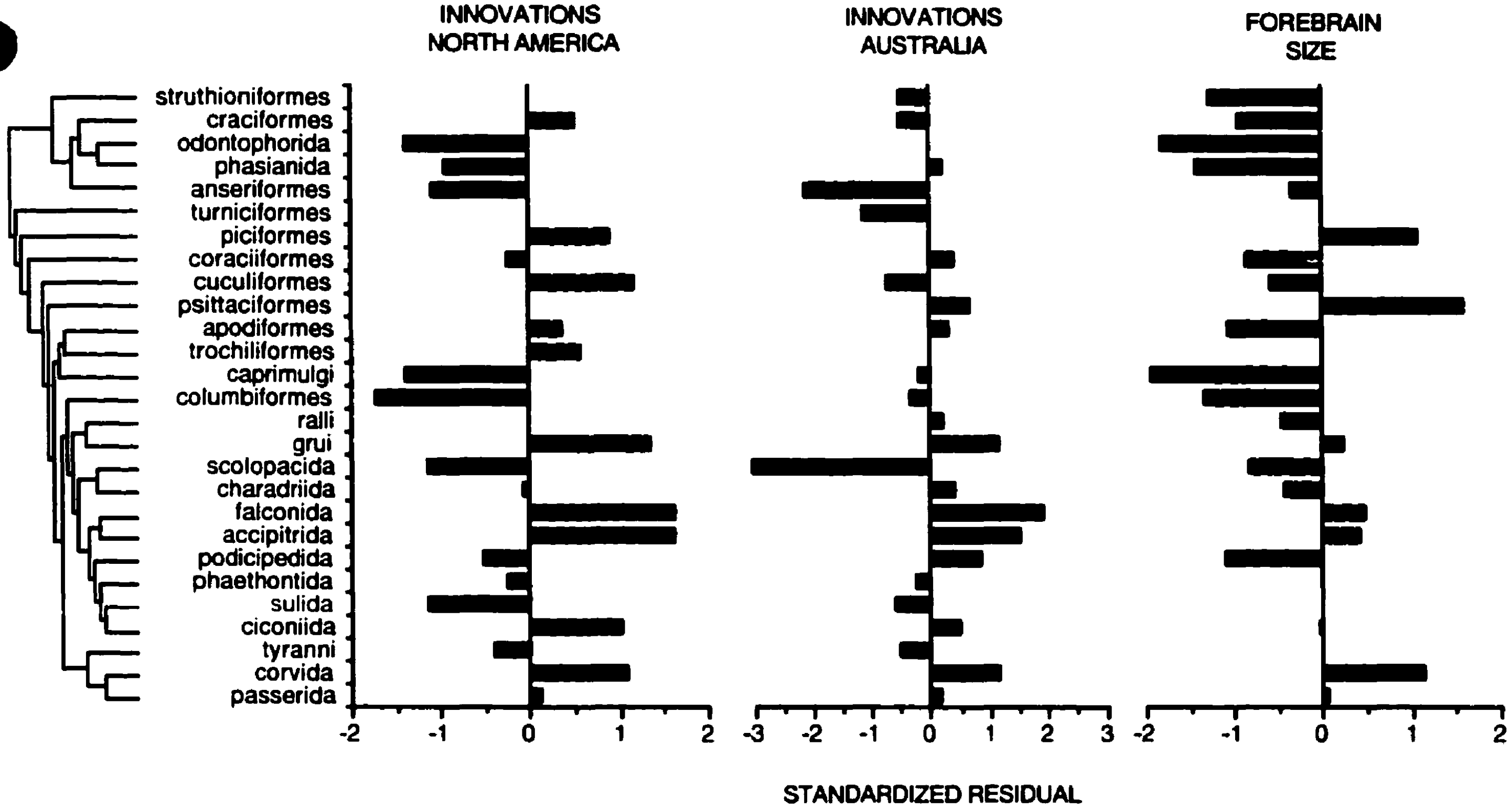
[b] Innovations found in all other North American journals.

Taxonomy is according to Sibley and Ahlquist (1990).

Table 2. Correlations between innovation frequency and the independent variables in simple regressions and p values in simple and multiple regressions

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

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


INNOVATIONS NORTH AMERICA
INNOVATIONS AUSTRALIA
FOREBRAIN SIZE
struthioniformes
craciformes
odontophorida
phasianida
anseriformes
turniciformes
piciformes
coraciiformes
cuculiformes
psittaciformes
apodiformes
trochiliformes
caprimulgi
columbiformes
ralli
grui
scolopacida
charadriida
falconida
accipitrida
podicipedida
phaethontida
sulida
ciconiida
tyranni
corvida
passerida
-2
-1
0
1
2
-3
-2
-1
0
1
2
3
-2
-1
0
1
2
STANDARDIZED RESIDUAL

Introduction to Chapter 3

In chapters 1 and 2, I demonstrated three things. First, feeding innovation rate is a valid way of measuring behavioral flexibility in birds because the relationship between number of innovations per taxon and relative forebrain size is independent of confounding variables. Second, the relationship is general: it holds in northwestern Europe, North America and Australia. Third, in the absence of species number per taxon, the confounding variable used in previous work, research effort is the best variable to remove the unwanted effects that can inflate innovation frequencies in certain taxa. Having validated the innovation measure in the previous chapters, I can now use it with confidence in the following chapter to test the link between behavioral flexibility and richness implied in Wyles, Kunkel and Wilson's (1983) behavioral drive hypothesis.

Richness, however, results from a balance between speciation and extinction rates and it is worth determining whether the number of species is attributable to the rate of species production or the rate at which they are lost. In chapter 3, therefore, I also examine the relationship between flexibility and extinction risk. In both cases, I use two measures of flexibility, the behavioral measure, feeding innovation rate, and a neuroanatomical measure, relative brain size, which is available for about 740 species.

Chapter 3

Behavioral drive revisited: innovation rate predicts species richness in birds, but not extinction risk

Abstract

The number of species varies greatly among taxa. In birds, for example, the parvorder Passerida contains 3556 species while the Odontophorida (New World Quails) 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 behavioral drive hypothesis, behavioral 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 richness. In this paper, we test the behavioral drive hypothesis by examining the link between behavioral 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. However, 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 behavioral flexibility predicts richness but not extinction risk in birds.

Introduction

The number of species varies greatly among taxa. In birds, for example, the parvorder Passerida (Sibley and 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 and 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 behavioral plasticity may be responsible for the success of the group (Fitzpatrick 1988).

The view that behavioral 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 behavioral drive hypothesis. They argued that behavioral 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 behavior expose themselves to new selection pressures that may favor 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 through allopatry, to the formation of a new species. A famous illustration of a new behavior being propagated throughout a large population involves British tits (Fisher and Hinde 1949). When a few birds started opening milk bottles in the

1920s, the behavior 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.

Another way in which behavioral flexibility can enhance speciation rates is by conferring species with a greater ability to invade new habitats (Mayr 1965; Greenberg 1990; Sol and Lefebvre 2000; Sol and Lefebvre submitted). Though not stated in the behavioral drive hypothesis, the possibility to enter new adaptive zones may lead to evolutionary divergence and favor the emergence of reproductive isolation between populations.

Since the association between flexibility and richness was originally proposed by Wilson and his colleagues nearly 20 years ago, it has yet to be tested. In this paper, we test the behavioral drive hypothesis by attempting to show that there is a positive correlation between behavioral flexibility and the number of species in avian taxa. We estimate flexibility with relative brain size and a behavioral 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 behavior and adapt to the novel environmental conditions or by giving them the possibility to leave and colonize new areas (Sol and Lefebvre 2000; Sol and Lefebvre submitted). The second hypothesis we therefore 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 behaviors 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 which are intensively studied by researchers (see chapters 1 and 2 and Reader and Laland 1999). 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 neo-cortex and striatum has also been demonstrated in primates (Reader and Laland 1999), indicating that the link between innovation and neural substrate size is 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. In fact, 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 behaviors, 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, 1990). 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 1996) and is the area that increases the most in size in birds with relatively large brains (Rehkämper and Zilles 1991), relative size of the whole brain can be a good estimate of Neo/HV size. In fact, the variance in brain size accounts for 95% of the variance in hemisphere size, which in turn predicts 99.1% of the variance in Neo/HV size (Timmermans 1999).

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 Appendix 1) 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 northwestern Europe; the entire innovation corpus is available upon request. The innovations from the first 11 European journals (see Appendix 1) are the same as those in Nicolakakis and Lefebvre (2000). Those from the first four Australian and first seven North American journals are similar to those in Lefebvre et al. (submitted). The Indian innovations are the same as those in Timmermans et al. (2000). The remaining innovations, as well as those from Southern Africa, were gathered by LL and Mathieu Filion.

A behavior 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 fecal 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 (0.835 to 0.926, all $p < 0.001$; Lefebvre et al. 1998; Nicolakakis and Lefebvre 2000).

The number of innovations per taxonomic group was tabulated using Sibley and 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 ANOVAs (STATISTICA, 1999) on the non-transformed 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; submitted) 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 and Lefebvre (2000) and Lefebvre et al. (submitted), 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 data from published papers were not considered since they cannot yield innovation reports; zoological surveys that simply catalog the species present in a particular area were excluded as well since they focus on identification, not behavior, 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, which average out to 0.415 when weighed by the respective innovation sample sizes (224, 57, 176 and 237) of the four zones.

Relative brain size

Out of a total of 767 species, all 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 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 (1989 a, b, c, 1990) and fresh brain weights the author obtained from the literature (Armstrong and Bergeron 1985; Rehkämper et al. 1991; Boire 1989). 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 and Monroe (1990). Data on extinction risk was provided by the IUCN Red List of Threatened Animals (Baillie and 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 or extinction were tested with multiple regressions (Systat, 5.2) in which feeding innovation rate and relative brain size were the independent variables and number of species, 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, 3556 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 and 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 and Monroe's (1990) phylogeny, currently the most comprehensive molecular phylogeny of the class Aves (Sibley and Ahlquist 1990; Barraclough et al. 1995) and obtained DNA-DNA hybridization distances from Sibley and 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) occurs 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 is 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 appears to increase with the number of innovations gathered in each region.

The number of species per taxon is significantly correlated with relative brain size ($r = 0.418, p = 0.015$) and feeding innovation rate ($r = 0.558, p = 0.001$). However, only innovation rate remains 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 is excluded from the multiple regression due to its association with innovation rate ($r = 0.570, p = 0.001$). The innovation-richness relationship holds even after the removal of 12 taxa belonging to the two most speciose avian lineages, the Passeriformes and the Ciconiiformes ($r = 0.525, p = 0.015$; 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, is strongly related to the number of species per taxon ($r = 0.885, p < 0.001$); richness explains 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 (fig. 3). Innovation rate is positively correlated with extinction risk (partial $r = 0.447, p = 0.009$) but this relationship is an artifact of the richness-innovation link; innovation rate drops out of the multiple regression when species number is included (overall r^2 of the multiple regression = 0.725, $F_{1,36} = 94.885, p < 0.001$).

The number of species per taxonomic group that went extinct in the past 400 years is correlated with the richness of the group ($r = 0.563, p = 0.001$), but more so with the number of species at risk ($r = 0.721$, $p < 0.001$) which, in itself, explains 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 is added to the number of species at risk, richness ($r = 0.861$, $p < 0.001$) is 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 is significant in the simple regression (partial $r = 0.431$, $p = 0.012$) but drops out of the final model due to its association with richness.

Multiple regressions on independent contrasts yield similar results to those prior to phylogenetic correction. Relative brain size ($r = 0.403$, $p = 0.022$) and innovation rate ($r = 0.495$, $p = 0.004$) are the main correlates of richness, with innovation rate explaining 24.5% of the variance in the final model (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 ($r = 0.914$, $p < 0.001$) are 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 is the number of species, which accounts for 83.6% of the variance (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 behavioral 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 behavior. 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 behavioral 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 vs. 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 behavioral drive hypothesis, which predicts accelerated rates of evolution in animals with the capacity for both behavioral innovation and the transmission of the novel behavior 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 favor 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 and Laland (1999) demonstrated an association between neural substrate size, innovation rate and social learning, thereby satisfying the key assumption of the behavioral drive hypothesis. Taken together, the two studies indicate that behavioral flexibility may be a trait that can accelerate evolution. 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; Vermeij 1988; Fitzpatrick 1988) has been replaced by a study directed at the entire avifauna with, at its center, a more general explanation of evolutionary success based on behavioral differences and the capacity for innovation.

In addition, by validating the behavioral drive hypothesis, the present study emphasizes the role of behavior in explaining unequal richness among taxa. Traditionally, asides from work on sexual selection and mating behavior (Barraclough et al. 1995; Mitra et al. 1996; Møller and Cuervo 1998), most attempts to account for richness have focused on ecological and/or abiotic factors, often overlooking the importance of behavioral attributes. This study clearly adopts a behavioral perspective and argues that the ability to produce new behaviors may be important in driving the production of species by exposing individuals to new situations and allowing the expression of mutations favorable to the new circumstances. Though there has been some skepticism about how learnt behaviors 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.

Though behavioral 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 explains 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 can easily be coded, i.e. the species, genus or family, but where variance in flexibility is low. The second was to choose a level that maximizes the variance explained in the variables that are important for the hypothesis, the parvorder, but where many confounds are 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 behavioral 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 is 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, though it should be noted that the exponent of the relationship is less than one (fig. 3). 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 and 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 and Groombridge 1996). 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 four years, Temple 1986) which differs markedly from the natural situation millions of years ago.

Though 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 and 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. 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 behavioral 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 behavioral drive hypothesis (accelerated rates of evolution in flexible species), but it also has a major theoretical implication. It shows 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.

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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			
Northwestern 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

Figure 1. Log transformed number of species versus feeding innovation rate in 33 avian taxa, as defined by Sibley and Monroe (1990). $Y = 4.6149 + 1.0777X$, $r^2 = 0.267$, $p = 0.001$

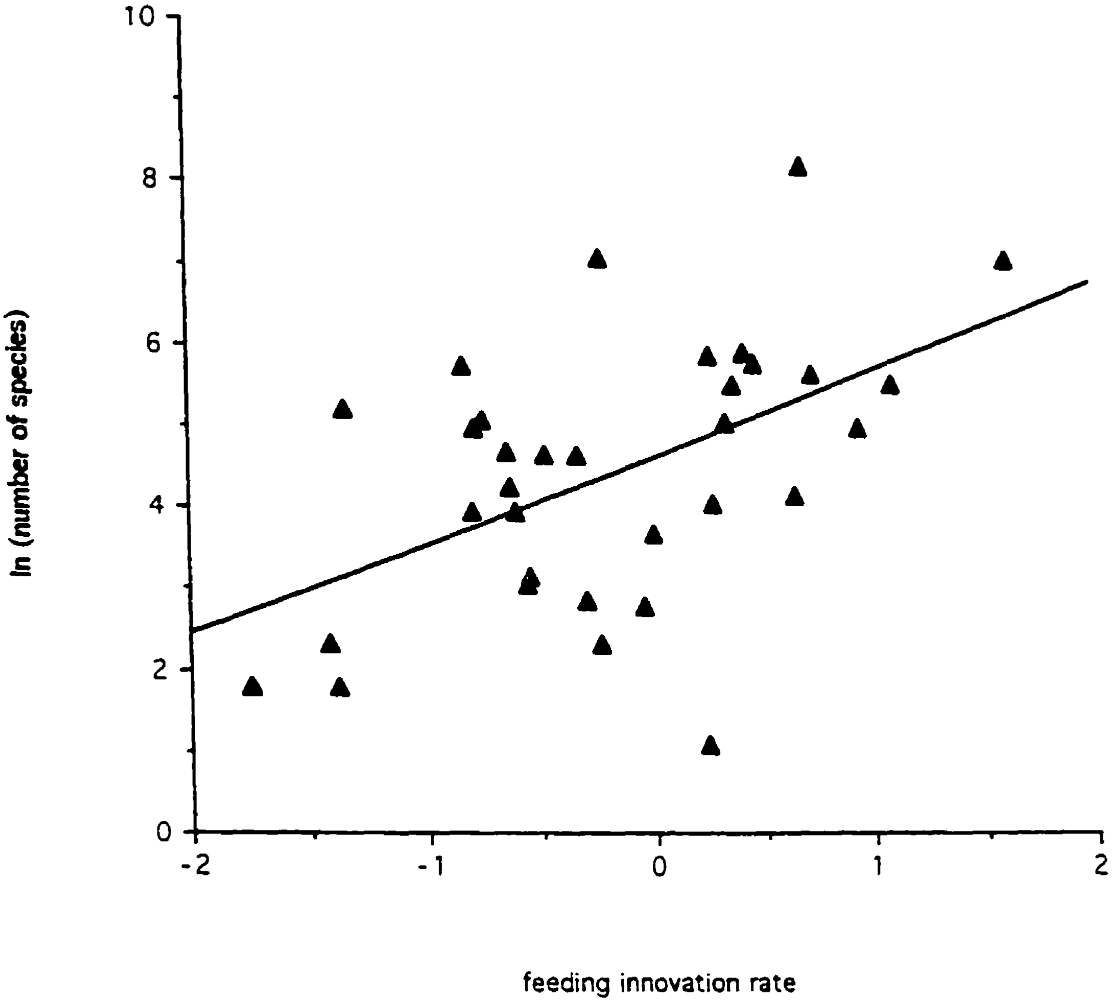

10
8
6
4
2
0
ln (number of species)
-2
-1
0
1
2
feeding innovation rate

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. $Y = 4.6076 + 0.99175X$, $r^2 = 0.275$, $p = 0.015$

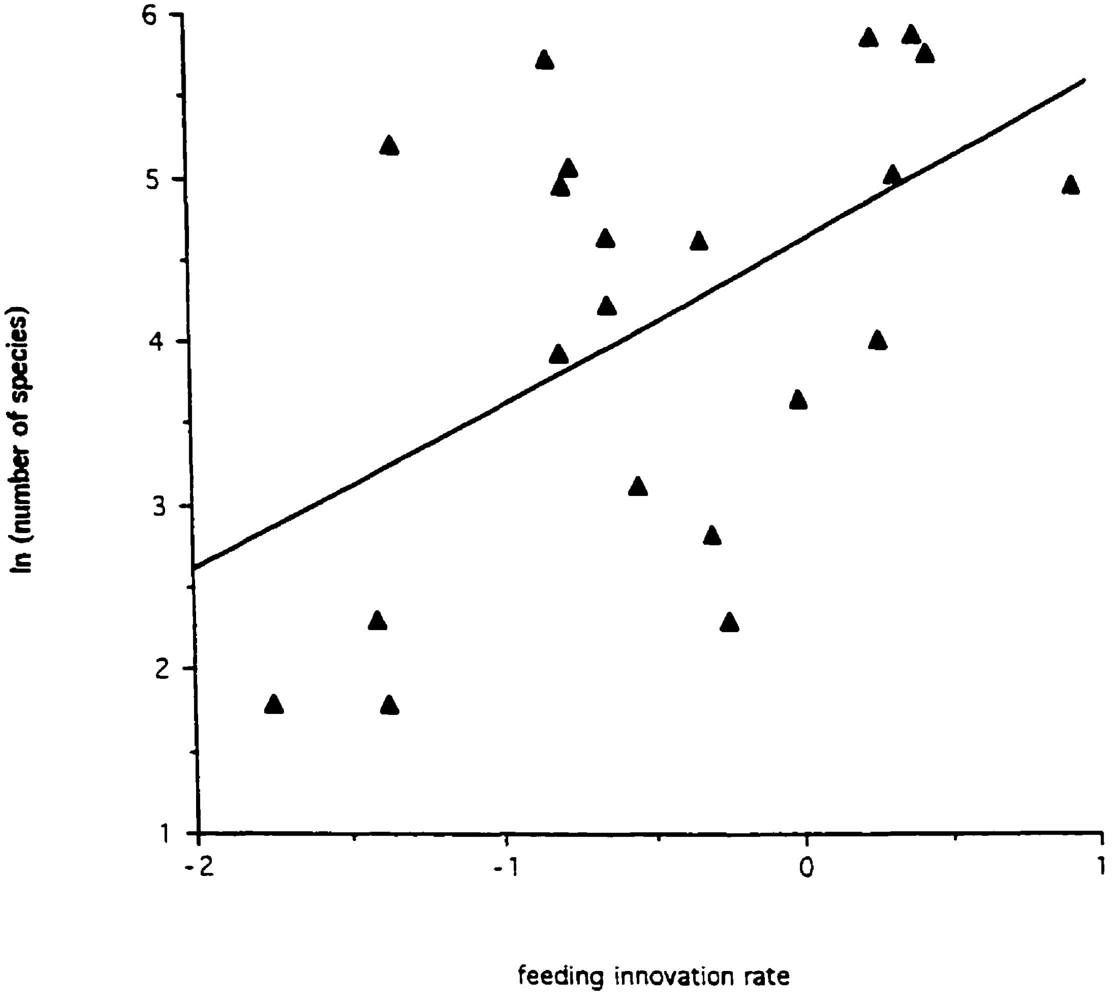
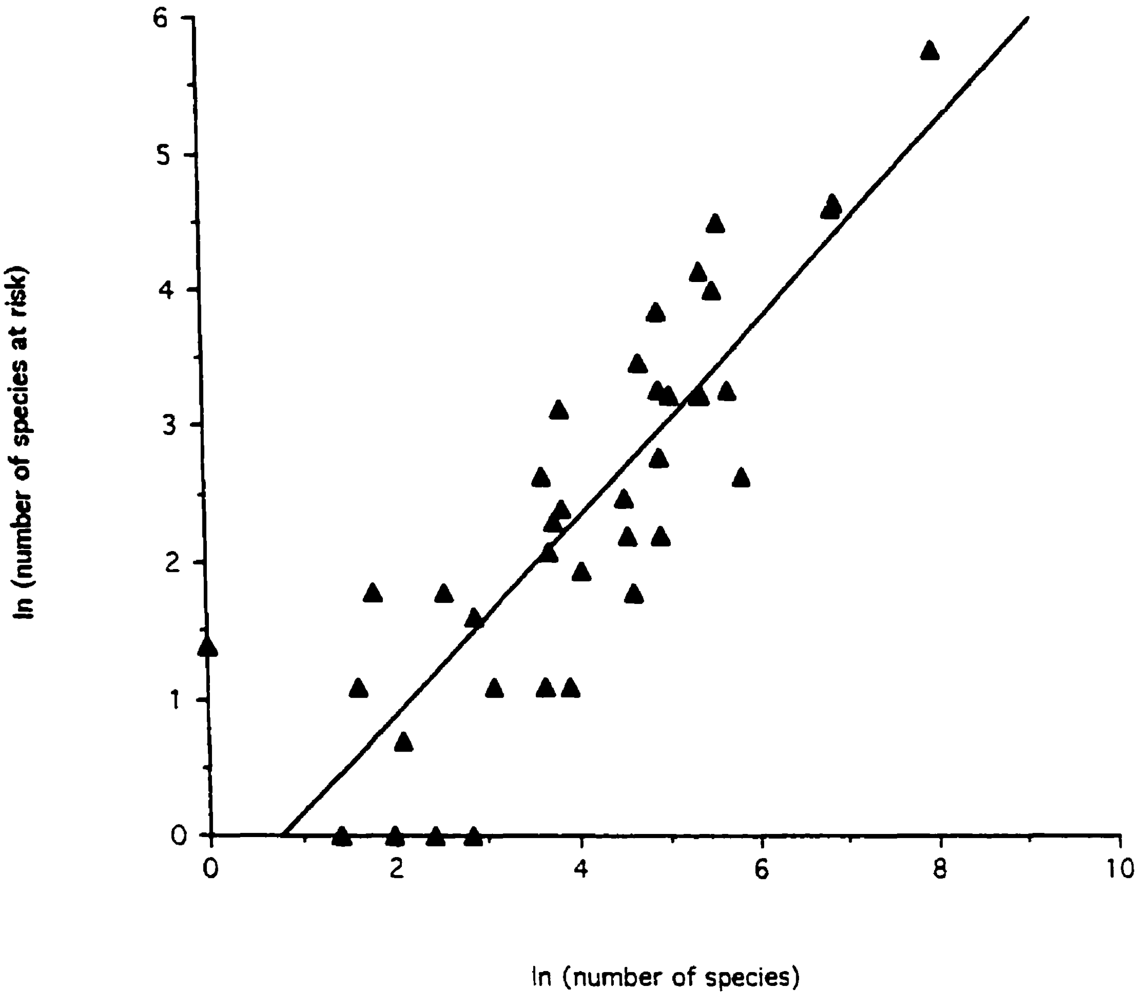

6
5
4
3
2
1
-2
-1
0
1
ln (number of species)
feeding innovation rate

Figure 3. Log transformed number of species at risk versus log transformed number of species in 38 avian taxa. $Y = -0.054570 + 0.71394X$, $r^2 = 0.725$, $p < 0.001$



ln (number of species at risk)
0
1
2
3
4
5
6
0
2
4
6
8
10
ln (number of species)

Appendix 1. List of journals and years surveyed for innovation reports in six geographical areas of the world

Indian subcontinent

Journal of the Bombay Natural History Society, 1930-2000

Southern Africa

Ostrich, 1930-2000

Madoqua, 1970-2000

Bokmakierie, 1950-1989

Lammergeyer, 1962-2000

Honeyguide, 1974, 1977-1980

Cormorant, 1976-1987

New Zealand

Notornis, 1974-2000

Australia

Emu, 1940-2000

Corella, 1977-1981

Sunbird, 1970-1982

Australian Birdwatcher, 1975-1982

Canberra Bird Notes, 1968-1981

South Australian Ornithologist, 1914-1982

Tasmanian Naturalist, 1967-1973, 1981

North America

Auk, 1970-2000

Condor, 1970-2000

Wilson Bulletin, 1970-2000

Journal of Field Ornithology, 1980-2000

Ontario Birds, 1983-2000

Bird Banding, 1970-1979

Oriole, 1971-1981

Alabama Birdlife, 1971, 1977-1980, 1982

American Birds, 1971-1999

Birdwatcher's Digest, 1982-1987

Cassinia, 1970-1981

Chat, 1972-1981

Colorado Field Ornithologist, 1967-1981

Delmarva Ornithologist, 1972-1995

Florida Field Naturalist, 1975-1987

Inland Bird Banding, 1972-1981

Kansas Ornithological Society Bulletin, 1971-1981

Kingbird, 1971-1981

Loon, 1971-1984

Maryland Birdlife, 1970-1997

Migrant, 1970-1991

Murrelet, 1970-1988

North American Bird Bander, 1976-1981

Nebraska Bird Review, 1970-1981

Passenger Pigeon, 1974-1981

Redstart, 1974-1981

Northwestern Europe

Alauda, 1970-2000

Bird Study, 1970-2000

Ibis, 1970-2000

British Birds, 1970-2000

Scottish Birds, 1970-2000

Die Vogelwarte, 1970-2000

Nos Oiseaux, 1970-2000

Ornis Fennica, 1970-2000

Ornis Scandinavica/Journal of Avian Biology, 1970-2000

Ardea, 1970-2000

Aves, 1970-1981

Ornithologischen Gesellschaft in Bayern (Anzeiger), 1978-1987

Aquila, 1970-1999

Vogelwelt, 1970-1987

Der Falke, 1974-1981

Le Gerfaut, 1970-1990

Irish Birds, 1977-1991

Irish Naturalists' Journal, 1970-1987

Ornis Svecica, 1991-1994

Der Ornithologische Beobachter, 1970-1987

Ornithologische Mitteilungen, 1971-1981

Rivista Italiana di Ornitologia, 1979-1980, 1988

Nature in Wales, 1975-1981

L'Oiseau et la Revue Française d'Ornithologie, 1970-1993

General Conclusion

The first two chapters of this thesis demonstrated that the link between relative forebrain size and the corrected number of feeding innovations per taxon cannot be attributed to confounding variables such as population size, observer bias, ornithologist interest, journal source, mode of juvenile development and phylogeny. This is true in northwestern Europe (chapter 1) as well as in North America and Australia (chapter 2), and confirms the validity of feeding innovation rate as a measure of behavioral flexibility in birds. As such, chapters 1 and 2 provide a means of quantifying flexibility in the field that is ecologically relevant because it measures behaviors that occur in the natural habitat of the bird and that is available for a wide range of taxa, thereby making it useful in large-scale comparative studies, such as the one presented in chapter 3.

In chapter 3, a significant association between the number of species and both feeding innovation rate and relative brain size was found in simple regressions. In the multiple regression, however, innovation rate was the only significant predictor of richness, thereby offering support to the behavioral drive hypothesis. Relative brain size dropped out of the final model due to its association with innovation rate. This does not imply however that larger brains are more or less important in generating richness than is the capacity to innovate. It is possible that the cause of high species numbers in certain taxa is the particular ability of those taxa to adapt their feeding strategies to new circumstances, an ability favored by a larger neural substrate. Alternatively, increased brain size per se may be responsible for differences in richness by favoring a cognitive ability other than innovativeness. In any case, the use of multiple regressions does not allow us to discern between the two. In the future, it would be interesting to determine which of the two flexibility correlates is the cause of high species richness, in which case path analysis may be a more appropriate statistical approach.

Although the flexibility-richness hypothesis stated in chapter 3 was supported, the suggested relationship between flexibility and extinction risk was not. Contrary to expectations, greater flexibility did not endow taxa with a greater chance of survival. The only predictor of threat in my analysis was the number of species contained within a taxon: species-rich taxa contained more threatened species than species-poor groups. As stated in the conclusion of chapter 3, the stochastic nature of species extinctions leads to two important theoretical considerations. First, it implies that richness results from high rates of speciation rather than low rates of extinction, a result that is in agreement with the prediction of the behavioral drive hypothesis (flexible individuals should evolve faster). Second, it shows that the rate-controls of speciation and extinction are different and, therefore, that speciation and extinction are not 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.

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