

Original Article

Are innovative species ecological generalists? A test in North American birds

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Foraging innovation occurs when animals exploit novel food sources or invent new foraging techniques. Species vary widely in their rates of innovation, and these differences can be quantified using counts of novel behavior observed in the wild. One of the assumed benefits of innovativeness is that it allows species to exploit a wider variety of habitats and foods, enhancing survival when resources are in shortage or when individuals invade new environments. However, the relationship between innovation propensity and ecological generalism lacks firm empirical support. Moreover, innovativeness does not only imply benefits but may also lead to higher risks incurred in the wide array of habitats exploited. In this study, we test whether innovative species exploit a wider variety of habitats and food types as well as face the potential risk of more predators as a consequence of their ecological generalism. Using data for 193 North American bird species in a phylogenetically informed analysis, we find a significant positive relationship between innovation rate and habitat generalism, but not diet breadth. Although habitat generalism is also associated with exposure to a wider variety of predators, there is no direct relationship between innovation rate and predation. Our results suggest that although innovators use a wider variety of habitats, they are not necessarily diet generalists, challenging the classic view that feeding generalism is equivalent to feeding flexibility. **Key words:** cognition, diet breadth, ecological generalism, foraging, innovation. [*Behav Ecol* 22:1286–1293 (2011)]

INTRODUCTION

Behavioral innovation, defined as the ability of animals to invent new behaviors or adjust old behavior to new problems (Kummer and Goodall 1985; Reader and Laland 2003), has long been hypothesized to confer advantages to individuals exposed to novel or altered environmental conditions (Klopfer 1962; Mayr 1965; Morse 1980). Selective advantages for innovativeness have proved difficult to demonstrate, however, in part because of the difficulty of operationally quantifying innovativeness in comparative analyses. The frequency of novel or unusual behaviors reported in the literature can provide a quantitative measure of taxonomic differences in innovation propensity (Lefebvre et al. 1997, 2004; Reader and Laland 2002; Lefebvre 2010) and is a useful index for testing hypotheses on the ecology and evolution of behavioral flexibility (Sol, Duncan, et al. 2005; Sol, Lefebvre, et al. 2005; Garamszegi et al. 2007).

One of the hypothesized benefits of innovativeness is that it allows animals to exploit a wide variety of resources (Reader and MacDonald 2003), which may be useful when resources are in shortage or when individuals invade a new environment. It follows that an innovative species should more easily expand its ecological niche, becoming a greater

ecological generalist in both diet and habitat than a less innovative species. A positive relationship between innovation/flexibility and generalism has been assumed in much of the animal cognition literature, but the evidence for this relationship is mostly indirect (reviewed in Sol 2003). For example, innovation (Sol et al. 2005a) and generalism (Cassidy et al. 2004) are associated with invasion success in birds, but there is no direct test of the relationship between innovation and generalism.

Generalism is not only thought to be associated with innovation but has also been implicated in the evolution of learning and enlarged brain size. Johnston (1982) proposed that the resource variability that leads to generalist foraging (Gray 1981) might favor the evolution of learning (see also Rozin and Schull 1988). Evidence in support of better learning in generalists than in specialists comes from studies on rodents (Daly et al. 1982) and insects (Lavery and Plowright 1988). The greater amount of information that needs to be processed by a generalist compared with a specialist is also thought to contribute to selection for enlarged brains (Harvey and Krebs 1990), an idea supported by data on rodents (Mace et al. 1980) and bats (Ratcliffe et al. 2006). The predictions on innovativeness, enlarged brains, and learning are not independent; the 3 traits are intercorrelated (innovativeness and enlarged brains: Lefebvre et al. 1997; Reader and Laland 2002; innovativeness and reversal learning: Lefebvre et al. 2004; Reader et al. 2011).

In this paper, we test the prediction that innovation rate and residual brain size are positively associated with ecological generalism in birds. We focus on North American species because detailed information on their ecology is available from a single standardized source, the Birds of North America monograph series published by the American Ornithologists' Union (BNO; Gill 1992–2002). We operationalize generalism as the diversity of the foods and habitats that a species exploits

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(Bennett and Owens 2002). In addition to diet and habitat diversity, we also consider a potential ecological cost of generalism: exposure to a wider diversity of predators. Because a higher level of predation leads to higher mortality, predation might be an obvious cost of foraging innovativeness. At the same time, exposure to a diversity of predators might also contribute to selection for traits that mitigate this increased risk. For example, higher rates of innovation (Garamszegi et al. 2007) and larger brains (Møller et al. 2006) seem to involve a higher cost of endoparasitism in birds but also lead to enlarged immune organs. In the case of predation, we predict a positive association between residual brain size and the higher predator diversity potentially associated with ecological generalism. The novel predators encountered by innovative foragers are more likely to be dealt with via learning than by genetically preprogrammed recognition and avoidance for the simple reason that novelty does not provide the long term, repeated encounters which select for genetic variants that help individuals survive attacks by specific predators (Chiappe and MacDonald 2005). Instead, individual and social learning offer more flexible mechanisms to cope with rare encounters and frequent change (reviewed by Griffin 2004).

METHODS

Brain and innovation data

We gathered data on brain and body mass for 193 North American bird species from 2 major sources (Figure 1). We use actual brain mass, where available (Garamszegi et al. 2002), but also include cranial endocast measures (Iwaniuk 2003) converted to mass by multiplying endocranial volume by the density of fresh brain tissue (1.036 g/ml). A study comparing these 2 measures found that endocranial volume explains almost all of the variance in fresh brain mass ($R = 0.99$; Iwaniuk and Nelson 2002). Inclusion of brain size data from multiple sources does not bias studies of innovation and yields identical conclusions to data from a single source (Overington et al. 2009).

Brain mass and body mass are highly correlated ($R = 0.94$ in our global database of 1966 species). To introduce both variables as predictors into our model, as has been suggested as an alternative to the use of residuals (Darlington and Smulders 2001; Garcia-Berthou 2001), could create problems of collinearity given the number of variables in our analyses. We controlled for this relationship by calculating the residuals from a regression of (log) brain mass and (log) body mass (Bennett and Harvey 1985).

For our innovation measure, we used an extended version of the North American database collated by Lefebvre et al. (1997). To compile these data, the short notes sections of 30 ornithological journals published between 1960 and 1998 were exhaustively searched. In this study, as in earlier work by Lefebvre et al. (1997, 1998), an innovation was defined as the ingestion of a new food type or the use of a new foraging technique, based on the use of keywords like “unusual,” “opportunistic,” “unknown,” “rare,” “first report,” or “not noted before” in the short notes (e.g., see tables in Lefebvre et al. 1997, 1998). If numerous species were mentioned in an account, each one was attributed an innovation, but if the same innovation was found more than once for the same species, only the first record was retained. As in previous work by Lefebvre and colleagues (Nicolakakis and Lefebvre 2000; Timmermans et al. 2000; Sol, Duncan, et al. 2005), we corrected for research effort, given that the number of innovations noted by ornithologists is higher for more intensely studied groups of birds. Research effort was operationally defined as the number of published papers on each species found in the online version of “The Zoological Record”

(1978–2002). We included innovation measures for all species in our brain data set, including those with zero innovations, given that we corrected for research effort as described above, allowing for some interpretation of the zero measure (i.e., whether it was expected given the low research effort for the species). We repeated analyses with a reduced data set of the species for which we had at least one innovation, and the results were qualitatively the same. We therefore report the results of our full analyses here.

Ecological variables

We used a categorical measure of diet generalism, where a species using a greater number of food types is considered to be more generalist than a species eating a smaller number of food types. We defined food types using 6 categories based on the classification scheme of Bennett and Owens (2002): vertebrate carrion, vertebrate prey, invertebrate prey, nectar or pollen, fruit or seeds, and leaves or stems. We measured diet generalism by counting the number of food categories consumed by adults of each species as noted in the BNO monographs for 193 species. We only included foods that were under the heading “main foods taken” in the species monograph to avoid any overlap between foods included in our measure of diet generalism and new foods included in innovation rate. Diet generalism scores for each species ranged from 1 to 6 categories (Table 1).

Similarly, we quantified habitat generalism based on the total number of habitats used by each species during the breeding season. We chose this season because information on the migratory and winter habitats of North American birds is sometimes poor, particularly for less-studied species. Habitats were placed into 8 categories based on the categorization scheme of Bennett and Owens (2002): forest; woodland; scrub; tundra, moorland, and mountain; grassland, steppe, savannah, and agricultural; marine; marshland, freshwater habitats; and urban and suburban habitats. For each species, habitat generalism was calculated by counting the total number of habitat categories. Habitat generalism scores ranged from 1 to 8 habitat types (Table 1).

Information on predation was not available for all of the species for which we had innovation, brain, and generalism data. We collated information on the predators of 155 North American bird species, amounting to a total of 83 predator species. In an initial analysis, we included all predators regardless of whether they were reported to prey on adults, nestlings, or eggs. In a second analysis, we included only predation that affected adult birds. In this analysis, our sample size was reduced to 99 species. We report results for analyses using both predator diversity measures.

We were interested in understanding whether innovation exposes animals to a behaviorally broader range of predators rather than to a greater number of predator species per se. Consequently, we quantified predator diversity in terms of behavioral variation. We used 2 approaches to measure this. First, each bird species' predators were placed into categories according to the predator's hunting technique. We then counted the total number of predator categories for each species in order to obtain a species-specific operational estimate of predator diversity. Second, we quantified the number of predator categories from the prey's point of view. We assumed that the variety of a species' antipredator behaviors should reflect the behavioral diversity of the predators to which it is exposed. Therefore, we grouped each species' responses into categories and obtained species-specific operational estimates of antipredator behaviors by counting the total number of response categories for each species.

To measure predator diversity according to the predator's hunting technique, diurnal raptors, nocturnal raptors, and

Table 1
Description of ecological variables used in this study

Variable name	Description	Range of values
Predator diversity	1) Number of predator categories known to prey on adults, young, and eggs of a given species or 2) Number of predator categories known to prey only on adult birds for a given species	From 1 to 7
Antipredator behaviors	Number of antipredator behaviors recorded for a species	From 1 to 6
Habitat generalism	Number of habitat types used during the breeding season	From 1 to 8
Diet generalism	Number of food types in regular diet	From 1 to 6

fleeing, freezing, and alarm calling constituted 3 separate categories. Distraction displays, active attacks on predators, and coordinated evasive maneuvers constituted 3 additional categories, yielding between 1 and 6 antipredator behaviors (Table 1).

Statistical analyses

We used a phylogenetic generalized least squares (PGLS) approach (Grafen 1989; Freckleton et al. 2002) to ensure that the results were not affected by pseudoreplication arising from common ancestry. This method is based on the estimation of a parameter λ , which measures the degree to which the variance/covariance matrix follows the Brownian model of evolution. We used an R code kindly provided by R. P. Freckleton. Our phylogenetic hypothesis to the genus level was that suggested by Sibley and Ahlquist (1990; Figure 1), with branch lengths estimated based on DNA hybridization. This phylogeny is considered to be the most comprehensive and is widely used in comparative analyses of birds (Rolland et al. 1998; Brändle et al. 2002). We further resolved relationships at the species level using a supertree assembled by Katie Davis at the bird supertree project (Davis 2008). Diagnostic plots were examined in order to check for outliers, heteroschedasticity, and nonnormal errors.

RESULTS

In the first model, we included innovation as the response variable and our 2 measures of generalism as predictors. Research effort was included in every model with innovation. Innovation rate was positively correlated with habitat generalism (PGLS: $F_{4,193} = 2.65$, $P = 0.009$, Table 2, Figure 2A), but there was no relationship between innovativeness and diet breadth ($F_{3,193} = 1.45$, $P = 0.148$, Table 2, Figure 2B). Habitat generalism and diet breadth were not significantly correlated with one another ($F_{2,193} = 0.17$, $P = 0.68$).

We ran a second set of analyses with our predation measures as predictors and habitat generalism or diet generalism as the response variable. As predicted, habitat generalists are exposed to a wider diversity of predators, measured as hunting categories of predators (PGLS: $F_{1,148} = -2.231$, $P = 0.027$; with adults only PGLS: $F_{1,99} = -2.017$, $P = 0.05$), but dietary gen-

eralists are not ($F_{4,111} = 0.14$, $P = 0.89$). Neither measure of generalism was associated with the number of antipredator responses (PGLS: habitat: $F_{2,131} = 0.192$, $P = 0.85$; diet: $F_{2,131} = 0.420$, $P = 0.68$). There was no significant relationship between innovativeness and predator diversity, whether this was quantified as the number of predator types (PGLS: $F_{2,155} = 0.66$, $P = 0.510$, Figure 2C) or the number of antipredator categories (PGLS: $F_{2,132} = 1.69$, $P = 0.095$). Excluding nest predation and thus focusing only on situations where a foraging adult might encounter predators did not change the results (PGLS: $F_{2,99} = 0.56$, $P = 0.578$).

We corrected for research effort in all of our analyses with the number of innovations per species, but research effort could also impact the number of recorded food types, habitat types, or predators for a species. We therefore tested each of these separately and found no significant relationship between research effort and number of food types (General Linear Model: $F_{1,192} = 0.231$, $P = 0.635$), habitat types ($F_{1,197} = 1.543$, $P = 0.216$), or number of predators on adults and young ($F_{1,154} = 0.2889$, $P = 0.592$).

There was a positive relationship between innovation rate and residual brain size (PGLS: $F_{3,193} = 5.45$, $P < 0.0001$). However, brain size was unrelated to diet breadth ($F_{3,193} = 1.46$, $P = 0.15$), habitat breadth ($F_{3,193} = 1.51$, $P = 0.13$), or number of predator categories, no matter how predator diversity was quantified (PGLS, number of predators on adults and young: $F_{2,155} = -1.33$, $P = 0.184$; adults only: $F_{2,99} = -0.916$, $P = 0.184$; antipredator responses: $F_{2,132} = -1.55$, $P = 0.125$).

DISCUSSION

In this study, we tested the relationship between innovativeness and ecological generalism in North American birds. We predicted a positive relationship between these measures and found that innovative species are habitat, but not diet, generalists.

One of the hypothesized advantages of innovativeness is that it allows animals to deal with challenges in the environment by expanding their behavioral repertoire. Several studies support this hypothesis indirectly: in a study of over 600 introduction events in birds, Cassey et al. (2004) found that habitat generalism of species increased the degree of success when introduced to a new habitat. Sol et al. (2005a) found that innovativeness contributed to introduction success rates. Shultz et al. (2005) demonstrated that population declines of farmland bird species in Britain were negatively correlated with niche position and relative brain size. Our study links these studies by demonstrating a positive relationship between innovativeness and habitat generalism. Given all of these results, it may be that innovators are able to thrive in a wide variety of habitats—including novel ones—because they are able to expand their feeding behavior to exploit (novel) available resources, despite the fact that they are not diet generalists in their native habitats.

Table 2
Results of PGLS models of number of innovations as a function of ecological variables and research effort

Term	Estimate	Standard error	T value	P
Diet breadth	0.286	0.197	1.45	0.148
Habitat breadth	0.407	0.154	2.65	0.009
Research effort	0.004	0.001	6.56	<0.001

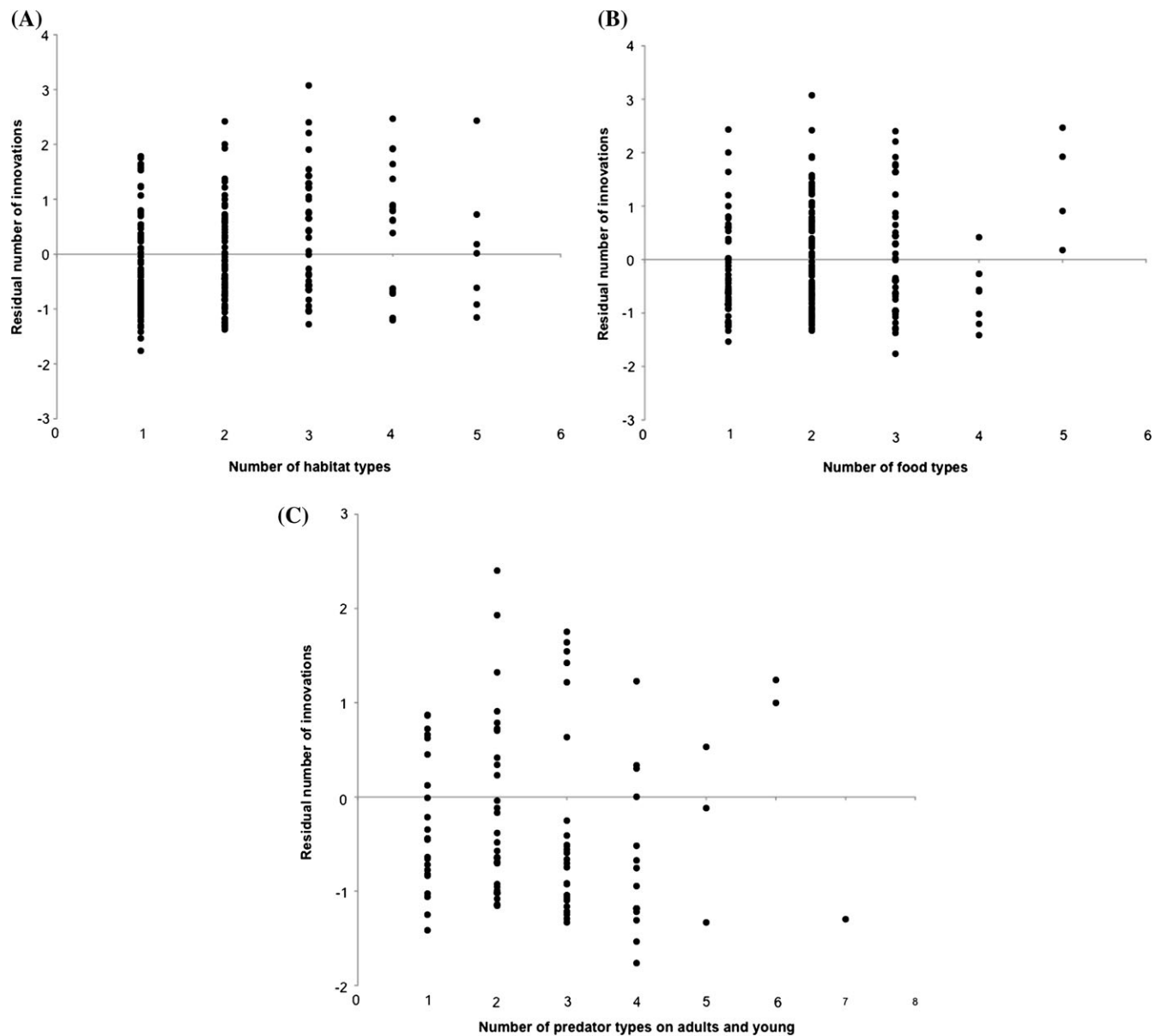


Figure 2

Residual number of innovations (from a regression of log number of innovations vs. log research effort) versus (A) Number of habitat types, (B) Number of food types, and (C) Number of predator types on adults and young for the North American bird species in our analyses. Only the relationship between innovation and habitat types was significant. Graphs show raw data, but we corrected for phylogenetic relationships in our analyses.

The lack of any relationship between innovativeness and diet generalism was unexpected. Indeed, innovation and feeding generalism are often assumed to be part of a suite of related behavioral traits (Sol 2003), and innovativeness was initially conceived partly as a measure of feeding generalism (Lefebvre et al. 1997). In our study, we chose measures of diet breadth and foraging flexibility (i.e., foraging innovation) that operated on different scales and therefore should be distinct measures: where diet breadth was based on broad categorizations of food types (e.g., leaves, vertebrate prey, etc.), a foraging innovation might be recorded when a species eats a new type of leaf, even though this falls broadly within its regular diet. We predicted a positive relationship between these measures based on the reasoning that the ability to eat novel foods and use novel foraging techniques should represent a general capacity for enlarging the diet and that this would be reflected

in the larger diet breadth of more innovative species. However, there is emerging evidence that diet breadth is not equivalent to feeding innovativeness and that the 2 measures have different relationships with brain size. For example, new foods do not contribute per se to the relationship between innovation rate and brain size, unless novel feeding techniques are also present (Overington et al. 2009). In primates, Reader et al. (2011) also fail to find a significant relationship between innovation rate and diet breadth. In their study, diet breadth falls with group size and percent fruit in the diet on a second principle component that is uncorrelated with a first, “general intelligence” component containing rates of innovation, tool use, social learning, extractive foraging, and tactical deception. The results of these studies highlight the difference between the size of the feeding repertoire (e.g., major dietary categories exploited) and the ability to expand that repertoire

through innovation. Although increased flexibility should allow species to eat a wider variety of foods when necessary, degree of generalism is also shaped by factors, such as resource availability, competition, and morphology (Futuyma and Moreno 1988). Thus, innovators may be diet specialists (e.g., the snail kite *Rosthramus sociabilis* and the osprey *Pandion haliaetus*, with 23 innovations between them) or generalists (the kites *Milvus milvus* and *M. migrans*, with 17 innovations between them), depending on the conditions at hand. Our results help interpret some previous comparative analyses that find habitat (but not diet) generalism to be relevant in important ecological and evolutionary processes, such as the invasion of novel environments (Cassey et al. 2004) and the rate of evolutionary diversification (Phillimore et al. 2007).

An important challenge and limitation in comparative studies of species ecology is that we rely on static quantitative measures to reflect species traits that might instead be dynamic. An interesting follow-up to our study might therefore consider the ways in which diet breadth and/or foraging innovation and the relationship between these measures could change based on an animal's current surroundings. For example, we might see an increased rate of innovation and a broader diet during the initial stages of introduction to a new environment (Wright et al. 2010), though these traits might be independent of one another when an animal is well established in a given region. A dynamic expansion of diet breadth provides another possible explanation for our findings: A greater capacity for expanding diet when entering a new environment followed by a narrowing of diet breadth once established could underlie the relationships between innovation, diet breadth, and habitat breadth we found here. The data we used from the Birds of North America monographs are based on many observations throughout species ranges and should therefore capture the full range of species behavior, with populations at different stages of range expansion. However, a finer level comparison, perhaps between populations or subspecies living in different conditions, might provide some useful insight into the degree to which the relationships between these species traits is dynamic.

Another data limitation in our study was that we considered habitats used in the breeding season only. The data on habitats used in the nonbreeding season are highly variable for North American birds, particularly for long-distance migrants, and this limitation was therefore a practical one. Depending on migration status, breeding season habitats may represent only a portion of the true variation in habitat use for a given species. However, the ability to use a wider variety of habitats during a crucial time of life should reflect something of a species' ability to adjust its behavior and should therefore capture the element of generalism that we were most interested in here. Again, a more refined study on just a few species might provide some insight into the relationship between habitat use throughout the year, diet breadth, and foraging innovation.

Although innovativeness and brain size were positively correlated, brain size was not associated with either habitat or diet generalism. This is in apparent contradiction with the widely held hypothesis that enlarged brain size is associated with broader resource use (e.g., Harvey and Krebs 1990). However, many studies that demonstrate a relationship between brain size and generalism may actually have quantified behavioral flexibility rather than breadth of resource use. For example, it has been shown that brain size is positively correlated with the variety of hunting techniques used by bat species (Ratcliffe et al. 2006). In a broader sample of mammals, species with larger brain size had greater behavioral repertoires (quantified as the number of behaviors recorded in species ethograms), a measure that focused on the breadth of

behaviors—not resources—used (Changizi 2003). The relationship between generalism and brain size, when it appears, may be indirect, with behavioral flexibility as the intervening variable. For example, path analysis of the relationship between innovation, brain size, and introduction success showed that the most likely relationship between these traits was that enlarged brain size is associated with increased innovativeness, which then leads to greater invasion potential (Sol et al. 2005a). In British farmland birds, niche position and relative brain size (in particular, the telencephalon) are negatively correlated with species declines (Shultz et al. 2005): Given the robust relationship between innovation and brain size across regions and taxonomic levels (e.g., Lefebvre et al. 1997; Overington et al. 2009), it is quite possible that enlarged brain size is associated with innovativeness in these species, which in turn plays a role in their ability to broaden their resource use and to withstand habitat destruction.

One factor that may conceal overall patterns in our sample is the phylogenetic level where cognitive and ecological traits vary. Much of the variation in brain size and innovation occurs at ancient splits in the phylogeny (i.e., the family or parvorder: Overington et al. 2009), yet there is a great deal of variation in ecological traits at the species level within families (e.g., Schuck-Paim et al. 2008). In this study, we were interested in ecological traits of species. Thus, although variation in brain size may be better captured by focusing at the family or parvorder level in birds, a study at that level would require an averaging of ecological values of species within the family, concealing variation in the traits of interest. This problem of scale should be approached empirically, with a focus on asking the same questions about the evolution of cognition across clades and at different phylogenetic levels. Indeed, the relationships between ecology and cognition may differ between taxa and between avian clades.

To understand the evolution of intelligence, comparative analyses must pinpoint situations where large brains and innovativeness provide a survival advantage (Sol et al. 2005a; Sol et al. 2007) as well as those where they impart costs and constraints. Innovations are inherently risky, and short notes occasionally report death or sickness in birds that ingest a novel food (Borgelt 1960; Bostic 1966; Gartrell and Reid 2007). In this study, we predicted an additional ecological cost to innovation: exposure to a diversity of predators. Contrary to our prediction, we found that although predator diversity is positively correlated with habitat breadth, it is not associated with differences in either innovativeness or brain size. This lack of a relationship is consistent with recent work demonstrating that variation in predation risk by European sparrow hawks for European passerines is not associated with brain size (Møller et al. 2006). Given the positive relationship we found between predator diversity and habitat breadth (which suggests that our method for quantifying predator diversity was meaningful), predation does not appear to be an ecological cost of innovative foraging behavior across North American birds. However, this does not suggest that predation is not a cost in some cases or within certain taxa. This study represents one of the first attempts, to our knowledge, to quantify predator diversity across such a large number of species. Given the breadth of the study, some detail may have been lost within our classifications. For example, because so few bird species were preyed on by different species of fish, snakes, or reptiles, we used a single category for these taxa. Future work might focus on one or a few species to determine the more specific, and likely dynamic, relationships between foraging innovation and susceptibility and exposure to a range of predators.

Contrary to the case for predation, there is some evidence that disease might be a major environmental risk of innovativeness. Garamszegi et al. (2007) have shown that innovative

birds have a higher blood parasite load and larger immune organs (spleen, thymus, and bursa of Fabricius) than noninnovators. Path analysis suggests that it is innovativeness that drives the increased demands on immune systems, in accordance with the idea that exposure to new foods increases exposure to new pathogens. Møller et al. (2005) found that the relationship also applies to brain size: Larger brained birds have enlarged immune organs, as one would predict from the relationship between innovation and brain size (though it should be noted that the use of spleen size as a measure of immune response remains controversial, e.g., Smith and Hunt 2004). Specific diseases such as salmonellosis (Tizard 2004), botulism (Ortiz and Smith 1994), and mycoplasmal conjunctivitis (Fischer et al. 1997) have also been linked to flexible lifestyles.

Some species are subject to much more intensive study than others, which could introduce bias into measures of ecology and behavior recorded in the literature. For instance, habitat or diet generalism might simply be a function of how much a species is studied rather than a true reflection of its ecological niche. In studies of foraging innovation, research effort (measured as the number of published papers on each species found in the online version of "The Zoological Record," 1978–2002; see METHODS) is always positively correlated with the number of innovations recorded for a taxon (Lefebvre 2010). For our measures of diet, habitat, and predation, we were fortunate to have the excellent Birds of North America monograph series to work from, where a huge research effort has gone into both collection and collation of data for each species. This was reflected in the lack of relationship between research effort and any of the ecological measures in our study.

This work provides the first direct empirical test in birds of a common assumption in the animal cognition literature, that is, that ecological generalism and flexibility are strongly and positively correlated with one another. We quantify behavioral flexibility as the number of foraging innovations observed in a given species. The strong positive relationship between residual brain size and innovation in North American birds adds to the evidence that this relationship is robust across phylogenetic levels (Lefebvre et al. 1997, 2004; Sol et al. 2005a,b) and geographical regions (Lefebvre et al. 1998). Contrary to predictions, innovativeness is not associated with diet breadth, and there is no relationship between diet breadth and habitat generalism in our sample. Further, neither diet nor habitat generalism are correlated with residual brain size. These findings lead to several conclusions: First, our measure of innovation is more than just a quantification of diet breadth of species. Second, flexibility and generalism are distinct traits and should be considered as such when we examine the ecological and evolutionary consequences of behavioral innovation. Third, "generalism" is not a unitary trait, and species may be, for example, feeding specialists and habitat generalists at the same time. Finally, our study fails to support the hypothesis that ecological generalism is associated with enlarged brain size in North American birds, raising questions about the role of diet and habitat use in the evolution of the avian brain. We hope that this work will stimulate further investigation of the complex relationships between brain, behavior, and ecology in birds and other taxa.

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