

## BEHAVIORAL DRIVE OR BEHAVIORAL INHIBITION IN EVOLUTION: SUBSPECIFIC DIVERSIFICATION IN HOLARCTIC PASSERINES

DANIEL SOL,<sup>1,2</sup> D. GRAY STIRLING,<sup>1</sup> AND LOUIS LEFEBVRE<sup>1</sup>

<sup>1</sup>*Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montréal, Québec H3A 1B1, Canada*

**Abstract.**—Behavioral changes have long been hypothesized to be an important driver of evolutionary diversification in animals, as they expose individuals to new environmental pressures and thus favor evolutionary divergence. There have been few empirical tests of this hypothesis, however, and the mechanisms linking behavioral changes and diversification processes remain controversial. We show here that Holarctic passerines with large brain size relative to body size, a character correlated with a high propensity for behavioral changes, generally have experienced more extensive subspecific diversification. This effect appears to be largely independent of other well-known mechanisms thought to promote diversification. As suggested by path analysis, relative brain size seems to affect diversification directly rather than indirectly through its presumed effect on range expansion, which is consistent with the original formulation of the behavioral drive hypothesis. Thus, the results support the long-held, intuitive hypothesis that behavioral changes facilitate evolutionary diversification.

**Key words.**—Behavioral flexibility, evolutionary diversification, geographical speciation, passerines, subspecies.

Received April 11, 2005. Accepted September 13, 2005.

In evolutionary biology, behavior is classically viewed as an important driver of evolutionary change (e.g., Baldwin 1896; Miller 1956; Mayr 1963; Wyles et al. 1983; Bateson 1988; Fitzpatrick 1988; Wcislo 1989; West-Eberhard 1989; Greenberg 1990; Futuyma 1998; Futuyma and Moreno 1998). The idea is that changes in behavior can allow animals to enter new adaptive zones and that this can then favor divergent selection on morphology, physiology, and/or behavior. Mayr (1963, p. 604), for example, argued that “behavioral changes in habitat and food selection are necessary in the shift to new adaptive zones, with structural changes in morphology acquired secondarily.” Wyles et al. (1983, p. 4396) expressed a similar view when they wrote that “As a consequence of adopting a new habit, the species faces a new set of selection pressures favoring those mutations that improve the individual’s effectiveness at living in the new way.” The concept that adaptation to a new niche is initiated by behavioral changes is implicit in influential models of population diversification leading to speciation (e.g., Miller 1956; Mayr 1963, 1969; Smith and Skúlason 1996; Schluter 2000), yet it has been the subject of surprisingly few empirical tests (Huey et al. 2003; Price et al. 2003; Dukas 2004).

Evidence that behavior affects the course of evolution is not only scarce, but the presumed mechanisms are also controversial. On one side, behavior may potentially affect the course of evolution by mechanisms other than a greater exposure of individuals to novel selective pressures. Mayr (1963, 1965, 1969), for example, suggested that behavioral adjustments may help species invade new regions and expand their range, which may increase the chances of population divergence through genetic drift, subdivision across geographical barriers, and/or increased persistence over evolutionary time (see also Rosenzweig 1995). On the other side, if individuals are able to respond to new ecological challenges by means of behavioral modifications, it is not obvious why they should be subject to directional selection (Bogert 1949;

Lynch 1990; Robinson and Dukas 1999; Huey et al. 2003; Price et al. 2003). In particular, Bogert (1949) hypothesized that if behavioral responses are enough to move a population close to a new adaptive peak, this may hide genetic variation from natural selection and hence inhibit evolutionary change (the Bogert effect; reviewed in Robinson and Dukas 1999; Huey et al. 2003; Price et al. 2003).

One approach to investigating the relationship between behavior and evolution is to compare lineages varying in their propensity for behavioral shifts and relate these differences to some measure of evolutionary diversification (Wyles et al. 1983; Lynch 1990; Nicolalakis et al. 2003). In their development of the “behavioral drive hypothesis,” Wyles et al. (1983) noted that the apparently rapid evolutionary radiation in birds and mammals compared to other vertebrates coincides with their relatively larger brains. Larger brains allow animals to process, integrate, and store more information about their environment, enhancing the capacity of individuals to modify or invent new behaviors in flexible ways (Jerison 1973; Barton 1996; Marino 1996; Lefebvre et al. 1997, 2004; Allman 2000; Kaas 2000; Madden 2001; Reader and Laland 2002; Byrne and Corp 2004). Because it is less subject to measurement error or context-dependent biases than are observational measures of cognition (Kamil 1994), brain size has proved a particularly appropriate method to quantify behavioral flexibility in comparisons among species having different lifestyles (e.g., Sol et al. 2005). To date, however, only two studies have examined variation in diversification rates between clades differing in brain size. Lynch (1990) found no evidence that morphological evolution has been faster in mammalian lineages with larger brains, but in birds Nicolalakis et al. (2003) showed that brain size is positively associated with the number of species per clade.

Here, we use a comparative analysis to explore the relationship between brain size and subspecific diversification in birds from the Holarctic region. We are particularly concerned with mechanisms, and this requires examination of recent evolutionary events, where evolutionary processes can be detected more clearly (Magurran 1999; Schluter 2000;

<sup>2</sup> Present address: Center for Ecological Research and Forestry Applications (CREAF), Autonomous University of Barcelona, E-08193 Bellaterra, Catalonia, Spain; E-mail: d.sol@creaf.uab.es.

Losos 2001). The analysis of subspecies differentiation within species may be particularly useful for this purpose. The subspecies concept was developed as a taxonomic device for classifying geographically variable species (Mayr 1969) and, as noted by Rensch (1960), the same characters that are typically used to identify species are generally used to define subspecies. This has led to the suggestion that subspecies represent a stage in the evolutionary process between the population and species level (Miller 1956; Rensch 1960; Dillon 1966; Mayr 1969; Ricklefs and Cox 1972; Roselaar 1995; Møller and Cuervo 1998; Belliure et al. 2000; Mayr and Diamond 2001; Newton 2003). Indeed, if speciation is an ongoing process, then we should find the different stages of speciation represented in nature (Mayr and Diamond 2001; Newton 2003). At the same time, concerns have been raised about the reality of subspecies as biological entities on the ground that subspecific designations may sometimes be arbitrary and do not necessarily match with genetic differentiation (Zink 2003). While the existence of inconsistency in some subspecies designations may obscure evolutionary patterns, the extent of subspecific diversification in particularly well-studied taxa may still provide valuable information for investigating differentiation processes that require examination of recent evolutionary events on a wide array of species (Møller and Cuervo 1998; Belliure et al. 2000; Mayr and Diamond 2001; Newton 2003).

The first specific goal of our study is to test whether and how subspecific diversification is related to relative brain size. A positive relationship would support the hypothesis that behavioral flexibility has enhanced morphological diversification in birds, whereas a negative relationship would lend credence to the Bogert effect. Because subspecies richness may also depend on phylogeny, time since speciation, geographical range size, and other factors (Møller and Cuervo 1998; Barraclough et al. 1999; Belliure et al. 2000; Bennett and Owens 2002), we also examine how subspecies number is related to brain size while controlling possible effects of these other factors. Finally, we use path analysis to test the sign, significance, and independence of relative brain size and range size on subspecific diversification. Multivariate models assume that each of these factors has a direct effect on subspecies number. As already mentioned, however, flexible behavior might indirectly affect subspecies number through its effect on range expansion. This idea is implicit in Mayr's geographical model of diversification (Mayr 1963, 1969), but remains to be tested.

## METHODS

### *Subspecies Number as an Evolutionary Measure of Intraspecific Diversification*

Bird subspecies are defined by consistent differences between populations in plumage color and the size and/or shape of morphological structures, and generally more than one of these criteria is used in defining a subspecies (see for example Cramp et al. 1988–1994). For example, in the grasshopper sparrow (*Ammodramus savannarum*), the subspecies *pratensis* is larger billed, darker above, and brighter than subspecies *perpadillus* (Vickery 1996).

In using subspecies richness as a measure of morphological

diversification, we are assuming that a species with many subspecies is morphologically more diverse than another with few subspecies. We tested this assumption with data gathered from Cramp et al. (1988–1994) on wing length (the only measure for which information was available for many populations) from 367 populations of 30 Palearctic passerines. Species were randomly selected from the list of studied species, subject to the condition that data on at least four different populations were available.

We took several measures to minimize possible inconsistency in subspecies designations. First, we restricted our analyses to passerine birds, a well-studied and relatively homogeneous group in terms of size and shape. Passeriformes is particularly suitable for a study like ours because it represents the most speciose evolutionary radiation in birds (Sibley and Ahlquist 1990). Second, we used the most recent taxonomic information (Clements 2000 and online updates, <http://www.ibispub.com/updates.html>). Third, we tested our predictions with data from the two most extensively studied regions of the world, the Palearctic and Nearctic regions. Finally, we compared subspecies richness and relative brain size at both the species and the family level. At the family level, subspecies number was averaged among species from the same family, reducing the influence of individual errors in recognizing too many or too few subspecies.

### *Brain Size*

We obtained information on passerine brain size from Mlíkovský (1989a,b,c, 1990), DeVoogd et al. (1993), Székely et al. (1996), Garamszegi et al. (2002), Iwaniuk and Nelson (2002), and Iwaniuk (2003). We used actual brain mass when available, but we also included cranial endocast measures, converted to mass by multiplying the reported value by 1.036 g/ml (density of fresh brain tissue; see Iwaniuk and Nelson 2002). In four cases, we used telencephalon volumes reported in DeVoogd et al. (1993) and Székely et al. (1996), which were transformed to brain mass using regression techniques. Brain mass measurements are highly repeatable across methods (Iwaniuk and Nelson 2002) and literature sources (Garamszegi et al. 2002). Information on brain size was available for 199 passerine species occurring in the Palearctic and/or Nearctic (see Electronic Appendix available online only at <http://dx.doi.org/10.1554/05-196.1.s1>).

Larger species tend to have larger brains, and this allometric effect needs to be accounted for before any comparison can be made. Following previous studies (e.g., Bennett and Harvey 1985; Lefebvre et al. 1997), we calculated the residuals of a log-log regression of brain mass against body mass (Dunning 1993; Garamszegi et al. 2002; Iwaniuk 2003). These residuals (hereafter termed “relative brain size”) were then used to test for an association between brain size, adjusted for body size, and subspecies number. Although both brain and body mass may differ between sexes and vary among seasons, Garamszegi et al. (2002) found larger variance among than within species in both variables ( $P < 0.001$  in both cases), thus validating the use of brain and body mass in comparative analyses.

### *Alternative Explanations*

In birds, the number of subspecies covaries with migratory habits, geographical range size, dispersal distance, and sexually selected traits (Møller and Cuervo 1998; Belliure et al. 2000). Thus, we also tested how these other variables influenced the relationship between relative brain size and the number of subspecies. A species was considered a long-distance migrant when it was a trans-Saharan (Palearctic) or Neotropical (Nearctic) migrant and a resident or short-distance migrant when it did not meet these criteria (Belliure et al. 2000). Resident and short-distance migrants were pooled together in the same category (following Belliure et al. 2000), as they did not differ in subspecies number and this simplification did not change the percentage of variance explained by the variable (see Crawley 1993). Geographical range size was estimated as the total number of latitudinal degrees in which each species is found breeding (see also Møller and Cuervo 1998). This geographical measure is correlated with other measures of range size (D. Sol, D. G. Stirling, and L. Lefebvre, unpubl. data), but it is less constrained by the limits of continents and provides a better description of the range of environmental and ecological conditions encountered by each species. Moreover, our preliminary analyses suggested it was more strongly correlated with relative brain size than other measures. The sexually selected trait we examined was plumage dimorphism (Barraclough et al. 1995), categorized as dimorphic or monomorphic. The data for all these variables were extracted from Rappole et al. (1983), Cramp et al. (1988–1994), Ehrlich et al. (1988), and National Geographic (1999). Information on natal and breeding dispersal distance, estimated with banding data from the British Trust for Ornithology, was obtained from Paradis et al. (1998). Both measures of dispersal gave qualitatively similar results, so we present here the analyses based on breeding dispersal as it was available for more species.

Finally, we examined three additional variables not considered in previous analyses: body size, taken from Dunning (1993) and measured (whenever information was available) as female mass to reduce the influence of sexually selected dimorphism; latitude of the geographical range, measured as the midpoint between the northern and southern limits of the species' range; and time of origin of the species, estimated using mitochondrial DNA genetic distances among sister species and taken from Klicka and Zink (1997). Time of origin and dispersal distance were not known for most species used in our analyses, so these variables were analyzed separately.

### *Statistical Approach*

First, we examined whether variation in subspecies richness could be explained by chance alone by testing its distribution against that predicted by an evolutionary model based on the geometric distribution (Nee et al. 1992; Owens et al. 1999).

Second, we used a nested ANOVA (Bell 1989; Harvey and Pagel 1991) to partition variation in subspecies number throughout the taxonomy (species, genus, family, superfamily, and parvorder, following Sibley and Monroe 1990). This allowed us to identify the appropriate level(s) of analysis (Bennett and Owens 2002; see below) as well as quantify

the degree of taxonomic autocorrelation contained in this variable. The number of subspecies within a species must have evolved since the origin of that species and therefore is independent from the number of subspecies in any other species. It is nevertheless possible that the propensity to evolve subspecies varies among taxa due to other characters that are inherited phylogenetically. Because we found little phylogenetic inertia in subspecies number (see Results), we did not use phylogenetically based methods in comparisons between species, but we did account in our models for variation found at the family level (see below).

Third, we investigated the relationship between subspecies number and relative brain size with generalized linear mixed models (GLMM). The number of subspecies per species was strongly left-skewed and could not be normalized by transformations. Thus, we implemented models with Poisson error and log-link, as recommended by Crawley (1993). Even though subspecies is largely a species-level characteristic, we also found some variation in subspecies number at the family level (see Results). To account for this nonindependence of the data, we specified a variance component model with the GLIMMIX macro in SAS (Goldstein 1995; Littell et al. 1996), including family as a random effect (see Blackburn and Duncan 2001). The taxonomic variable acted as a control for unmeasured traits that might vary among families and ensured that significance tests for the fixed-effect predictors (i.e., relative brain size and confounding variables) were not biased by nonindependence of species from the same family (Duncan et al. 2001). One important assumption of the GLMM approach is that the taxonomy reflects phylogenetic relationships; we thus employed the taxonomy of Sibley and Monroe (1990), which is based on a molecular phylogeny (Sibley and Ahlquist 1990). We also coded the zoogeographical region (Nearctic, Palearctic, multiregion) as a random effect, which allowed us to simultaneously analyze all species while controlling for differences in the environment in different regions (see Blackburn and Duncan 2001).

Fourth, we studied the importance of the alternative explanations (range size, latitude, body size, sexual selection, migration, and dispersal ability) by incorporating them in a multivariate GLMM to statistically control for their effect on variation in subspecies number. Interactions between relative brain size and the confounding variables were also tested, but none were significant and are therefore not reported.

Fifth, because we found some variation in subspecies number at the family level, we examined our hypothesis at this taxonomic level. This is justified because relative brain size shows significant variation at the family level (47%; see also Sol 2003), in addition to that found at the species level (30%). We estimated the average value of both subspecies number (log-transformed) and relative brain size for each family. These variables were compared with least-square regression. Mean subspecies richness may be phylogenetically autocorrelated, a possibility that could not be statistically validated with only 18 families. As a precaution, we controlled for common ancestry with independent standardized linear contrasts (Felsenstein 1985). Our phylogenetic hypothesis was that proposed by Sibley and Ahlquist (1990) based on DNA hybridization, with branch lengths estimated as genetic dis-

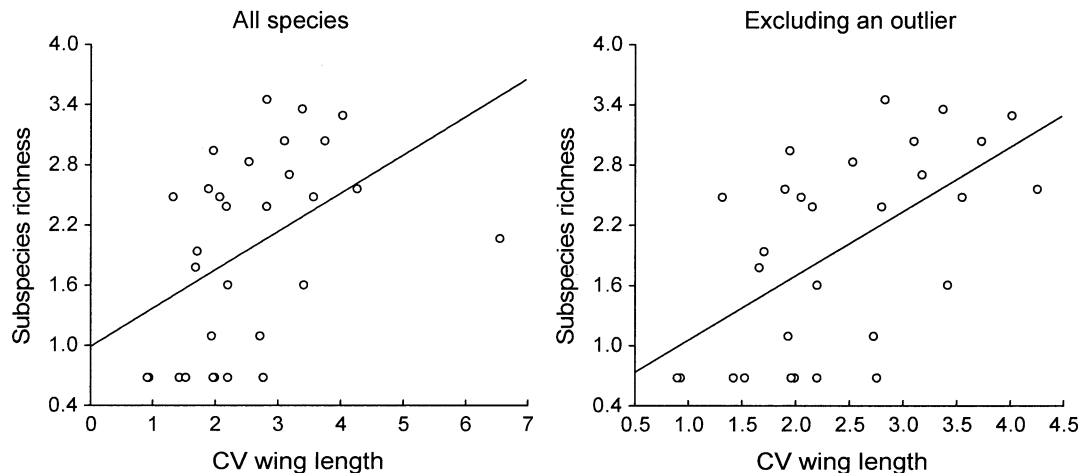


FIG. 1. Covariation between subspecies richness and morphological variation (coefficient of variation [CV] in wing length) in a random sample of Palearctic passerines (see text for details).

tances. We calculated the contrasts with the program Compare 4.6. (Martins 2004) and analyzed them with a regression forced through the origin.

Finally, we used path analysis to deconstruct the causal relationships between subspecies number, behavioral flexibility, and the geographical variables (range size and mid-latitude) at the species level. A path model predicts the direction and strength of hypothetical causal relationships between a set of variables (Li 1975). If a path model exactly predicts the size of the observed correlations and the variance explained, then the causal hypothesis is consistent with the observations. The difference between expected and observed correlations, as well as the variance explained, scales the reliability of each causal model (Li 1975). We used ordinary regressions to estimate the standardized partial regression coefficients (see Li 1975), but we do not report  $P$ -values because of the nonnormal distribution of subspecies number.

## RESULTS

### *Test of Assumptions*

Subspecies richness was positively correlated with the degree of morphological variation (CV) observed in the species ( $r = 0.46$ ,  $F_{1,28} = 7.34$ ,  $P < 0.011$ ; Fig. 1A). This relationship improved considerably when we removed an outlier (Fig. 1B). Thus, our assumption that a species with many subspecies is morphologically more diverse than another with a few subspecies seems to be reasonable.

The distribution of the number of subspecies per species was significantly different from a null model based on the geometric distribution ( $\chi^2 = 9.31$ ,  $df = 2$ ,  $P = 0.009$ ), suggesting that variation in subspecies richness is nonrandom. Nevertheless, this method assumes that all species are of similar age, which is not necessarily true. Thus, a possible explanation for the nonrandomness of the pattern is that some species have had more time to evolve than others (Owens et al. 1999). We tested this possibility using information on time of divergence in North American passerines estimated as mean mitochondrial DNA genetic distance to sister species (Klicka and Zink 1997). We found no evidence for a signif-

icant relationship between mitochondrial DNA genetic distance and subspecific diversification ( $F_{1,72} = 1.96$ ,  $P = 0.17$ ). Although the power of this test is somewhat limited, we can at least conclude that the relationship between time since speciation and subspecies number is weak for North American species.

The nonrandom pattern of subspecies richness is also difficult to explain as a result of phylogenetic inertia. A nested ANOVA (Harvey and Pagel 1991) on the different taxonomic levels (species, genus, family, superfamily, and parvorder) revealed that over 75% of variation in subspecies number was at the species level, with only 22% found at the family level. Similar low phylogenetic inertia was found using the test for serial independence (TFSI, Abouheif 1999; Reeve and Abouheif 2003; results not presented).

Thus, variation in the number of subspecies per species in the studied passerines does not appear to be random, a pure effect of time, or a consequence of phylogenetic inertia. Consequently, we proceed to test whether subspecies number is related to relative brain size or to other factors suggested to promote evolutionary differentiation.

### *Brain Size and Subspecific Diversification*

Relative brain size was positively associated with subspecies number (GLMM, estimate  $\pm$  standard error:  $0.273 \pm 0.085$ ,  $F_{1,177} = 10.36$ ,  $P = 0.0015$ ; Fig. 2), when both taxonomy and region were accounted for. Relative brain size may nonetheless be nonrandomly distributed with respect to a range of other variables also correlated with subspecies number (Table 1). In line with previous work (Møller and Cuervo 1998; Belliure et al. 2000), we found a more extensive subspecific diversification in species that do not undergo long-distance migrations and in those that show a larger geographical range (Table 1). When these and other potential confounding effects were accommodated in the model, relative brain size remained significantly associated with subspecies number (Table 1).

Using the subset of 47 Palearctic species for which estimates of breeding dispersal distance were available (Paradis

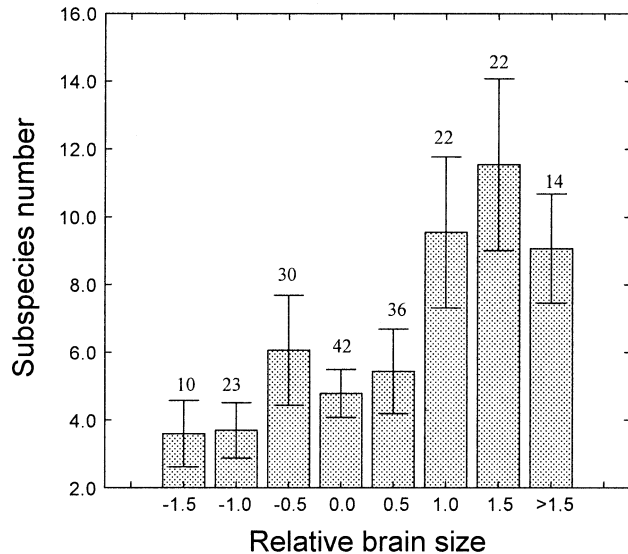


FIG. 2. Relationship between relative brain size and subspecific diversification (mean  $\pm$  SE) in passerines from the Holarctic region. Numbers on the x-axis represent upper limits of relative brain size intervals, and numbers on the top of each bar are the number of species in each category.

et al. 1998), we tested whether the link between relative brain size and subspecies number was confounded by dispersal distance. This reduced data set did not allow us to include all the possible confounding variables in our model, so we focused on range because widely distributed species tend to have lower breeding dispersal (Belliere et al. 2000). When dispersal distance was included in the GLMM, large-brained species still showed a tendency to have more subspecies than small-brained species ( $F_{1,28} = 6.06$ ,  $P = 0.02$ ). The relationship between subspecies number and range size was slightly below the 0.05 threshold for statistical significance ( $F_{1,28} = 4.60$ ,  $P = 0.04$ ), while the relationship with breeding dispersal was slightly above the threshold ( $F_{1,28} = 3.87$ ,  $P = 0.06$ ).

Finally, we examined the relationship between relative brain size and subspecific diversification at the family level, because relative brain size varies at this level (see Sol 2003), as does subspecies number. At this taxonomic level, the average number of subspecies per species was positively associated with mean relative brain size ( $t_{16} = 2.81$ ,  $P = 0.012$ ;

Fig. 3A). This relationship also held when applying independent contrast analysis to control for phylogenetic effects ( $t_{16} = 2.85$ ,  $P = 0.011$ ; Fig. 3B).

#### Mechanisms Linking Brain Size, Geographical Range, and Subspecies Number: Path Analysis

We used path analysis to disentangle direct and indirect effects linking relative brain size and range size with subspecific diversification (Fig. 4). Midlatitude was included in the model as a precaution, because both biological diversity and range size are known to vary with latitude (Newton 2003). The best causal model revealed that the effects of range and brain size were virtually independent and the standardized partial regression coefficients (path coefficients) were almost the same size as the correlations (Fig. 4). In other words, the effect of relative brain size on subspecies number was mostly direct rather than being indirectly caused by its effect on range size (Fig. 4). This model explained the same proportion of variation in subspecies number as the multivariate model ( $R^2_{199} = 0.33$ ). The explanatory power improved when we removed eight outliers (datapoints above the third quartile,  $\sim 4\%$  of the data) and reran the analysis ( $R^2_{191} = 0.47$ ). It is noteworthy that, while midlatitude and range are negatively correlated at the scale of our study ( $r = -0.34$ ,  $P = 0.0001$ ), which is contrary to the Rapoport rule, midlatitude did not have a direct effect on subspecies number and the indirect path explained only 1% of the variance in subspecies number, even though lower latitudes have larger numbers of species (Rosenzweig 1995; Blackburn and Gaston 1996).

#### DISCUSSION

Our results reveal that Holarctic passerines with larger relative brain size generally have more subspecies than those with smaller brains. This relationship appears to be independent of other factors with previously suggested effects on subspecies number, such as dispersal potential, geographical range size, or the degree of sexual dimorphism in plumage (Møller and Cuervo 1998; Belliere et al. 2000). Assuming that subspecies richness is an appropriate proxy for intra-specific diversification, our results suggest that behaviorally flexible lineages have undergone greater evolutionary diversification than less flexible lineages. Thus, the integration of our findings with those reported by Nicolakakis et al. (2003),

TABLE 1. Variables explaining variation in subspecies number in passerines from the Holarctic region ( $N = 199$  Nearctic, Palearctic, or multiregional species). Subspecies number is modeled with a GLMM with Poisson error and log-link, with taxonomy and region included as random factors. Each fixed effect is tested when included with all other significant fixed effects.

Fixed effects		Estimate	SE	$F_{1,172}$	$P$	
Relative brain size		0.239	0.074	10.41	0.0015	
Range size		3.162	0.419	57.04	<0.0001	
Midlatitude		0.599	0.457	1.71	0.1923	
Migratory habits		-0.646	0.172	14.11	0.0002	
Plumage dichromatism		-0.031	0.127	0.06	0.8091	
Body mass		-0.146	0.182	0.65	0.4225	
Random effects		Ratio	Estimate	SE	$Z$	$P$
Family		0.025	0.094	0.064	1.46	0.0718
Region		0.007	0.028	0.039	0.72	0.2352

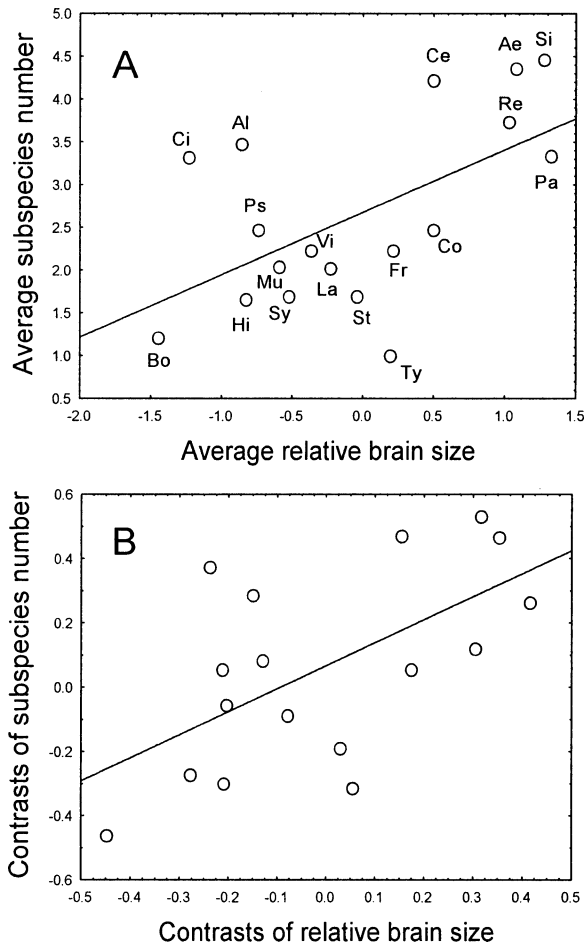


FIG. 3. Relationship between mean relative brain size and mean subspecies number at the family level in Holarctic passerines. The relationship is shown without (A) and controlling (B) for phylogenetic effects with independent contrast analysis. Family codes are as follows: Ae, Aegithalidae; Al, Alaudidae; Bo, Bombycillidae; Ce, Certhiidae; Ci, Cinclidae; Co, Corvidae; Fr, Fringillidae; Hi, Hirundinidae; La, Laniidae; Mu, Muscicapidae; Pa, Paridae; Ps, Passeridae; Re, Regulidae; Si, Sittidae; St, Sturnidae; Sy, Sylviidae; Ty, Tyrannidae; Vi, Vireonidae.

who found that avian lineages that have larger brains and exhibit a higher propensity for innovative behaviors tend to contain more species than less flexible lineages, provides consistent support for the long-held hypothesis that behavior facilitates evolutionary diversification.

Behavioral flexibility may theoretically favor evolutionary change through two main mechanisms: promoting range expansion and facilitating entry into new adaptive zones. The classic geographic model of diversification pioneered by Mayr (1963, 1969), suggests that flexible behavior in conjunction with range expansion causes diversification. The idea is that behavior helps individuals expand their geographical range, thereby causing evolutionary diversification through local adaptation, genetic drift, subdivision across geographical barriers, and/or increased persistence over evolutionary time (Rosenzweig 1995). In birds, range size is the strongest correlate of subspecies variation (Belliere et al. 2000; present study), although it is worth noting that sub-

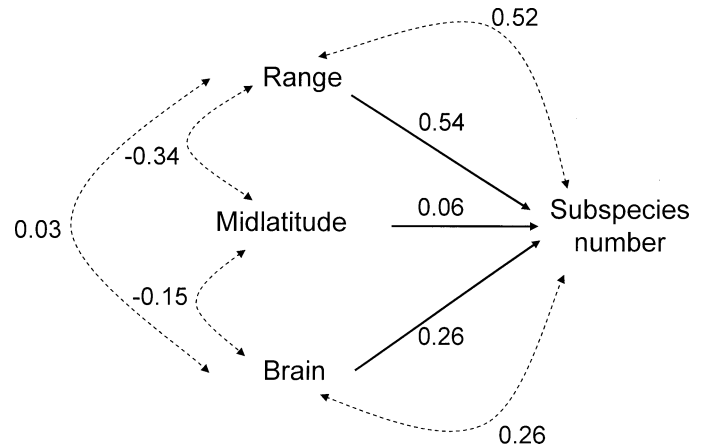


FIG. 4. Path diagram depicting the likely causal relationship between relative brain size and subspecies number (see text for details). Dashed lines with the double-ended arrow indicate a correlation and solid lines with a single arrow indicate path coefficients.

species are geographically defined, such as even a null model would predict an association between subspecies richness and range size. We find no evidence, however, that behavior indirectly affects subspecific diversification through its effect on geographical expansion. On the contrary, path analysis indicates that the effects of both range size and flexible behaviors are direct and largely independent. The independence of behavior and geographical range size is an unexpected result, given the long-held idea that flexible behaviors favor a species' establishment in new regions (Mayr 1965) and the support for this idea in recent comparative studies in birds (Sol et al. 2005). Range expansion, however, not only depends on the ability of individuals to establish themselves in novel regions but also on dispersal processes, which may be unrelated to behavioral flexibility. Moreover, we note that our results do not imply that geography plays no role in the link between brain size and subspecific diversification; rather, they suggest that the link between brain size and subspecies number does not simply result from behaviorally flexible species having larger geographical ranges than less flexible species.

The most obvious way in which behavior might directly drive subspecific diversification is by facilitating entry into new adaptive zones (Wyles et al. 1983; Price et al. 2003), thereby favoring local adaptation in geographically defined populations. Shifts in habitat or food selection may bring individuals into contact with novel selective forces, which then may prompt subsequent evolutionary divergence in morphology, physiology, and behavior. Thus, provided variation exists in the available habitats or resources across the geographical range of a species, behavior may facilitate the diversification of a single lineage into different subspecies, each one adapted to the local habitats or resources (Grant and Grant 1989; Smith and Skúlason 1996; Orr and Smith 1998; Schluter 2000; Reznick and Ghalambor 2001). In the red crossbill (*Loxia curvirostra*) complex, for example, the diversification in bill morphology seen in the Pacific Northwest appears to be a response to alternative adaptive peaks related to cones of different conifer species (Benkman 1993).

At the macroevolutionary level, adaptation to a wide array of novel feeding opportunities appears to be a major factor in classic examples of dramatic adaptive radiations, such as the Hawaiian honeycreepers (Carroll and Dingle 1996; Lovette et al. 2001) and Darwin's finches (Grant 2001).

While our findings do not contradict the case-by-case importance of the Bogert effect on species evolution (Huey et al. 2003), they do indicate that, at least in Holarctic passerines, flexible behaviors appear to have facilitated the first stages of evolutionary diversification. The ability of individuals to respond to new ecological challenges by means of behavioral modifications may reduce the strength of natural selection on morphological, physiological, or behavioral characters but, as suggested by Price et al. (2003), selection may still be important if this response is either incomplete or involves costs. Moreover, because some stochasticity is likely in the precise behaviors that are modified, behavioral shifts may be particularly potent in exposing individuals to novel selective pressures (Price et al. 2003). Experimental evidence that behavioral change does not necessarily prevent natural selection from operating on other characters when individuals are exposed to new ecological pressures has been recently reported by Losos et al. (2004): In the Caribbean, *Anolis* lizards altered their habitat use in the presence of an introduced predator, but these behavioral shifts did not prevent the population to be subject to selection favoring larger size in females and longer legs in males.

The view that phenotypic divergence as well as speciation may be the outcome of divergent natural selection stemming from habitat or resource segregation has received increased empirical support in recent years (Schluter 2000; Losos and Miles 2002). Because a shift to new environments or resources is clearly a behavioral phenomenon, we need to explicitly consider the role of behavior in shaping adaptive processes. Thus, an obvious follow-up to our study is to test whether behaviorally flexible lineages have undergone a more extensive diversification in relevant adaptive traits than less flexible lineages. Recent developments in the comparative analysis of adaptive radiations (Schluter 2000; Losos and Miles 2002) will allow this issue to be addressed as soon as well-sampled molecular phylogenies become available.

With the increasing availability of molecular information, it will also be possible in the near future to perform large-scale analyses on genetically defined taxa. The fact that morphological differentiation between subspecies does not always match genetic differentiation (Zink 2004) is a potential problem with respect to the analyses presented here but is also an intriguing result that cannot simply be attributed to mistakes in subspecies designation or lack of resolution in some of the molecular methods used (Newton 2003). More likely, the discrepancy between morphological and molecular data may indicate that the two measures reflect different phenomena, subspecific diversification presumably representing very recent drift or adaptation of populations to local conditions and mitochondrial DNA differentiation best describing historical isolation (Questiau et al. 1998; Avise 2000; Newton 2003). Thus, the integration of morphological and genetic information is likely to provide new and important insights into the role of behavioral changes in shaping the course of evolution.

#### ACKNOWLEDGMENTS

We thank M. D. Sorenson, R. B. Huey, J. B. Losos, S. M. Reader, W. Vickery, P. R. Grant, D. Reale, J. L. Copete, J. Clavell, R. Aymí, N. Nicolakakis, C. W. Benkman, and the McGill and UQAM discussion groups for helpful comments on specific issues or early versions of the paper; E. Abouheif and T. D. Price for advice on phylogenetic analyses; T. D. Price for sending us an unpublished paper; E. Martins, J. Reeve, and E. Abouheif for making their programs available to us; and C. Pujol for her constant encouragement. This work was supported by a grant from the Québec Ministry of Education (Canada) and a "Ramón y Cajal" fellowship from the Ministerio de Ciencia y Tecnología (Spain) to DS and a grant from the Natural Sciences and Engineering Research Council of Canada to LL.

#### LITERATURE CITED

- Abouheif, E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. *Evol. Ecol. Res.* 1: 895–909.
- Allman, J. 2000. *Evolving brains*. Scientific American Library, New York.
- Avise, J. C. 2000. *Phylogeography: the history and formation of species*. Harvard Univ. Press, Cambridge, MA.
- Baldwin, J. M. 1896. A new factor in evolution. *Am. Nat.* 30: 441–451.
- Barracough, T. G., P. H. Harvey, and S. Nee. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. Lond. B* 259:211–215.
- Barracough, T. G., A. P. Vogler, and P. H. Harvey. 1999. Revealing the factors that promote speciation. Pp. 202–219 in A. E. Magurran and R. M. May, eds. *Evolution of biological diversity*. Oxford Univ. Press, Oxford, U.K.
- Barton, R. A. 1996. Neocortex size and behavioral ecology in primates. *Proc. R. Soc. Lond. B* 263:173–177.
- Bateson, P. 1988. The active role of behaviour in evolution. Pp. 191–207 in M.-W. Ho and S. W. Fox, eds. *Evolutionary processes and metaphors*. Wiley, New York.
- Bell, G. 1989. A comparative method. *Am. Nat.* 133:553–571.
- Belliure, J., G. Sorci, A. P. Møller, and J. Clobert. 2000. Dispersal distance predicts subspecies richness in birds. *J. Evol. Biol.* 13: 480–487.
- Benkman, C. W. 1993. Adaptation to single resources and the evolution of crossbills (*Loxia*) diversity. *Ecol. Monogr.* 63:305–325.
- Bennett, P. M., and P. H. Harvey. 1985. Relative brain size and ecology in birds. *J. Zool. Lond.* 207:151–169.
- Bennett, P. M., and I. P. F. Owens. 2002. *Evolutionary ecology of birds*. Oxford Univ. Press, Oxford, U.K.
- Blackburn, T. M., and R. P. Duncan. 2001. Determinants of establishment success in introduced birds. *Nature* 414:195–197.
- Blackburn, T. M., and K. J. Gaston. 1996. A sideways look at patterns in species richness, or why there are so few species outside the tropics. *Biodiversity Lett.* 3:44–53.
- Bogert, C. M. 1949. Thermoregulation in reptiles, a factor in evolution. *Evolution* 3:195–211.
- Byrne, R. W., and N. Corp. 2004. Neocortex size predicts deception rate in primates. *Proc. R. Soc. Lond. B* 271:1693–1699.
- Carroll, S. P., and H. Dingle. 1996. The biology of post-invasion events. *Biol. Conserv.* 78:207–214.
- Clements, J. F. 2000. *Birds of the world: a checklist*. Ibis Publishing Company, Vista, London.
- Cramp, S. K., E. L. Simmons, and C. M. Perrins, eds. 1988–1994. *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic*. 5 vols. Oxford Univ. Press, Oxford, U.K.
- Crawley, M. J. 1993. *GLIM for ecologists*. Blackwell, Oxford, U.K.
- DeVoogd, T. J., J. R. Krebs, S. D. Healy, and A. Purvis. 1993. Relations between song repertoire size and the volume of brain

- nuclei related to song: comparative evolutionary analyses amongst oscine birds. *Proc. R. Soc. Lond. B* 254:75–82.
- Dillon, L. S. 1966. The life cycle of the species: an extension of current concepts. *Syst. Zool.* 15:112–126.
- Dukas, R. 2004. Evolutionary biology of animal cognition. *Annu. Rev. Ecol. Syst.* 35:347–374.
- Duncan, R. P., T. M. Blackburn, and T. H. Worthy. 2001. Prehistoric bird extinctions and human hunting. *Proc. R. Soc. Lond. B* 269:517–521.
- Dunning, J. B. 1993. *CRC handbook of avian body masses*. CRC Press, Boca Raton, FL.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1998. *The birder's handbook: a field guide to the natural history of North American birds*. Simon and Schuster, New York.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- Fitzpatrick, J. W. 1988. Why so many passerine birds? A Response to Raikow. *Syst. Zool.* 37:76.
- Futuyma, D. J. 1998. *Evolutionary biology*. Sinauer Associates, Sunderland, MA.
- Futuyma, D. J., and G. Moreno. 1998. The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.* 19:207–233.
- Garamszegi, L. Z., A. P. Møller, and J. Erritzoe. 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proc. R. Soc. Lond. B* 269:961–967.
- Goldstein, H. 1995. *Multilevel statistical models*. Edward Arnold, Oxford, U.K.
- Grant, B. R., and P. R. Grant. 1989. Natural selection in a population of Darwin's finches. *Am. Nat.* 133:377–393.
- Grant, P. R. 2001. Reconstructing the evolution of birds on islands: 100 years of research. *Oikos* 92:385–403.
- Greenberg, R. S. 1990. Ecological plasticity, neophobia, and resource use in birds. *Stud. Avian Biol.* 13:431–437.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford Univ. Press, Oxford, U.K.
- Huey, R. B., P. E. Hertz, and B. Sinervo. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* 161:357–366.
- Iwaniuk, A. N. 2003. *The evolution of brain size and structure in birds*. Ph.D. diss. Monash University, Clayton, New Zealand.
- Iwaniuk, A. N., and J. E. Nelson. 2002. Can endocranial volume be used as an estimate of brain size in birds? *Can. J. Zool.* 80:16–23.
- Jerison, H. J. 1973. *Evolution of the brain and intelligence*. Academic Press, New York.
- Kaas, J. H. 2000. Why is brain size so important? Design problems and solutions as neocortex gets bigger or smaller. *Brain Mind* 1:7–23.
- Kamil, A. C. 1994. A synthetic approach to the study of animal intelligence. Pp. 11–45 in L. A. Real, ed. *Behavioral mechanisms in evolutionary ecology*. Univ. of Chicago Press, Chicago, IL.
- Klicka, J., and R. M. Zink. 1997. The importance of recent ice ages in speciation: a failed paradigm. *Science* 277:1666–1669.
- Lefebvre, L., P. Whittle, E. Lascaris, and A. Finkelstein. 1997. Feeding innovations and forebrain size in birds. *Anim. Behav.* 53:549–560.
- Lefebvre, L., S. M. Reader, and D. Sol. 2004. Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* 63:233–246.
- Li, C. C. 1975. *Path analysis: a primer*. Boxwood Press, Pacific Grove, CA.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. SAS Institute, Cary, NC.
- Losos, J. B. 2001. A close-up look at adaptive radiation. *Trends Ecol. Evol.* 16:265–266.
- Losos, J. B., and D. B. Miles. 2002. Testing the hypothesis that a clade has adaptively radiated: iguanid lizard clades as a case study. *Am. Nat.* 160:147–157.
- Losos, J. B., T. W. Schoener, and D. A. Spiller. 2004. Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature* 432:505–508.
- Lovette, I. J., E. Bermingham, and R. E. Ricklefs. 2001. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proc. R. Soc. Lond. B* 269:37–42.
- Lynch, M. 1990. The rate of morphological evolution in mammals from the standpoint of the neutral expectation. *Am. Nat.* 136:727–741.
- Madden, J. 2001. Sex, bowers and brains. *Proc. R. Soc. Lond. B* 268:833–838.
- Magurran, A. E. 1999. Population differentiation without speciation. Pp. 160–183 in A. E. Magurran and R. M. May, eds. *Evolution of biological diversity*. Oxford Univ. Press, Oxford, U.K.
- Marino, L. 1996. What can dolphins tell us about primate evolution? *Evol. Anthropol.* 5:81–88.
- Martins, E. P. 2004. COMPARE, version 4.6. Computer programs for the statistical analysis of comparative data. Distributed by the author at <http://compare.bio.indiana.edu/>.
- Mayr, E. 1963. *Animal species and evolution*. Belknap Press, Cambridge, MA.
- . 1965. The nature of colonising birds. Pp. 29–43 in H. G. Baker and G. L. Stebbins, eds. *The genetics of colonizing species*. Academic Press, New York.
- . 1969. *Principles of systematic zoology*. Mc-Graw-Hill, New York.
- Mayr, E., and J. Diamond. 2001. *The birds of the Northern Melanesia: speciation, ecology and biogeography*. Oxford Univ. Press, Oxford, U.K.
- Miller, A. H. 1956. Ecological factors that accelerate formation of races and species of terrestrial vertebrates. *Evolution* 10:262–277.
- Mlíkovský, J. 1989a. Brain size in birds. 1. Tinamiformes through Ciconiiformes. *Vest. Cseke Spol. Zool.* 53:33–45.
- . 1989b. Brain size in birds. 2. Falconiformes through Gaviiformes. *Vest. Cseke Spol. Zool.* 53:200–213.
- . 1989c. Brain size in birds. 3. Columbiformes through Piciformes. *Vest. Cseke Spol. Zool.* 53:252–264.
- . 1990. Brain size in birds. 4. Passeriformes. *Acta Soc. Zool. Bohemoslov.* 54:27–37.
- Møller, A. P., and J. J. Cuervo. 1998. Speciation and feather ornamentation in birds. *Evolution* 52:859–869.
- National Geographic. 1999. *Field guide to the birds of North America*. National Geographic Society, Washington, DC.
- Nee, S., A. O. Mooers, and P. H. Harvey. 1992. Tempo and mode of evolution revealed from molecular phylogenies. *Proc. Natl. Acad. Sci. USA* 89:8322–8326.
- Newton, I. 2003. *Speciation and biogeography of birds*. Academic Press, Oxford, U.K.
- Nicolakakis, N., D. Sol, and L. Lefebvre. 2003. Behavioral flexibility predicts species richness in birds, but not extinction risk. *Anim. Behav.* 65:445–452.
- Orr, M. R., and T. B. Smith. 1998. Ecology and speciation. *Trend Ecol. Evol.* 13:502–506.
- Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life history, sexual selection or ecology. *Proc. R. Soc. Lond. B* 266:933–939.
- Paradis, E., S. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. *J. Anim. Ecol.* 67:518–536.
- Price, T. D., A. Qvarnström, and D. E. Irwin. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. B* 270:1433–1440.
- Questiau, S., M.-C. Eybert, A. R. Gaginckaya, L. Gielly, and P. Taberlet. 1998. Recent divergence between two morphologically differentiated subspecies of bluethroat (Aves: Muscicapidae: *Luscinia svecica*) inferred from mitochondrial DNA sequence variation. *Mol. Ecol.* 7:239–245.
- Rappole, J. H., E. S. Morton, T. E. Lovejoy, and J. L. Ruos. 1983. *Nearctic avian migrants in the Neotropics*. Texas A & M University, Kingsville, TX.
- Reader, S., and K. Laland. 2002. Social intelligence, innovation and enhanced brain size in primate. *Proc. Natl. Acad. Sci. USA* 99:4436–4441.
- Reeve, J., and E. Abouheif. 2003. *Phylogenetic independence*. Ver. 2.0. Dept. of Biology, McGill University, Montreal, Canada.



- Rensch, B. 1960. Evolution above the species level. Columbia Univ. Press, New York.
- Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 112–113:183–198.
- Ricklefs, R. E., and G. W. Cox. 1972. Taxon cycles in the West Indies avifauna. *Am. Nat.* 106:195–219.
- Robinson, B. W., and R. Dukas. 1999. The influence of phenotypic modifications on evolution: the Baldwin effect and modern perspectives. *Oikos* 85:582–589.
- Roselaar, C. S. 1995. Taxonomy, morphology, and distribution of the songbirds of Turkey: an atlas of biodiversity of Turkish passerine birds. Pica Press, Mountfield, Sussex, U.K.
- Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge Univ. Press, Cambridge, U.K.
- Schluter, D. 2000. The ecology of adaptive radiations. Oxford Univ. Press, Oxford, U.K.
- Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and classification of birds: a study in molecular evolution. Yale Univ. Press, New Haven, CT.
- Sibley, C. G., and B. Monroe. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, CT.
- Smith, T. B., and S. Skúlason. 1996. Evolutionary significance of resource polymorphism in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* 27:111–133.
- Sol, D. 2003. Behavioral flexibility: A neglected issue in the ecological and evolutionary literature? Pp. 63–82 in S. M. Reader and K. Laland, eds. *Animal innovation*. Oxford Univ. Press, Oxford, U.K.
- Sol, D., R. P. Duncan, T. M. Blackburn, P. Cassey, and L. Lefebvre. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. USA* 102:5460–5465.
- Székely, T., C. K. Catchpole, A. DeVoogd, Z. Marchl, and T. J. DeVoogd. 1996. Evolutionary changes in a song control area of the brain (HVC) are associated with evolutionary changes in song repertoire among European warblers (Sylviidae). *Proc. R. Soc. Lond. B* 263:607–610.
- Vickery, P. D. 1996. Grasshopper sparrow (*Ammodramus sava-narum*). No. 239 in A. Poole and F. Gill, eds. *The birds of North America*. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- Wcislo, W. T. 1989. Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* 20:137–169.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* 20:249–279.
- Wyles, J. S., J. G. Kunkel, and A. C. Wilson. 1983. Birds, behavior and anatomical evolution. *Proc. Natl. Acad. Sci. USA* 80:4394–4397.
- Zink, R. M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proc. R. Soc. Lond. B* 271:561–564.

Corresponding Editor: M. Sorenson