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Ecological constraints on the evolution of avian brains

Received: 2 April 2004 / Revised: 27 April 2004 / Accepted: 29 April 2004 / Published online: 15 June 2004
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Abstract

Birds have brains that are comparable in size to those of mammals. However, variation in relative avian brain size is greater in birds. Thus, birds are ideal subjects for comparative studies on the ecological and behavioral influences on the evolution of the brain and its components. Previous studies of ecological or behavioral correlates in relative brain size were mainly based on gross comparisons between higher taxa or focused on the relationships between the sizes of specific brain structures and the complexity of different tasks. Here we examine variation in dimensions of the braincase, relative overall brain size and size of its components, in reference to one general ecological and behavioral task: migration. We used data from three lineages of closely related species (14 Acrocephalines, 17 Sylvia and 49 parulid warblers). Within each group, species vary in their migratory tendencies. We found that species migrating long distances have lower skulls and smaller forebrains than resident species. We discuss four hypotheses that could explain smaller forebrain sizes, and suggest relevant taxa to use in comparative analyses to examine each of these hypotheses:

– Brain size is energetically constrained. Contrasts can be made not only between migrants and residents, but also between birds in habitats with high and low levels of available food.
– Brain size is developmentally constrained; birds with short growing periods should have smaller forebrains. Comparisons need to be made between birds living in habitats with long and short breeding seasons.
– Bill adaptations for foraging constrain braincase dimensions. Further analyses would need to be done on groups with high variation in bill dimensions and foraging modes.
– Birds with small brains have to migrate to compensate for low behavioral flexibility. Contrasts between members of families containing tropical residents and migrants need to be made. We also raise the question of whether only those parts of the brain are reduced that are most dispensable and whether brain size reduction limits foraging skills and social competence.

Keywords Behavior · Constraints · Forebrain · Migration · Warblers

Introduction

Birds are known to have relatively large brains for their body size with great variation among families in the allometric relations between brain size and body mass (Mlíkovsky 1989a, 1989b, 1989c, 1990; Nealen and Ricklefs 2001). Residual variance of these relations is open to functional explanations. This residual size of the whole brain or certain parts may reflect their functional significance, an aspect that has been discussed particularly in the context of song learning and food storing (e.g. Sherry and Duff 1996; Macphail 2002; Nowicki et al. 2002; Jacobs 2003). Other behavioral skills, such as inventing new feeding techniques, tool use, and complexity of bower construction, have also been related to brain size (Lefebvre et al. 1997, 2002; Nicolakakis and Lefebvre 2000; Timmermans et al. 2000, Madden 2001). A few other ecologically significant relationships have
also been described (Bennett and Harvey 1985; Healy and Guilford 1990; Abbott et al. 1999; Nicolakakis and Lefebvre 2000; Garamszegi et al. 2002; Kalisinska 2003). All these studies attempt to demonstrate that brain size or the relative size of a specific brain component increases as an evolutionary response to a certain demand and decreases if a function is not needed. Virtually no consideration has been given to the constraints on overall brain size, and resultant trade-offs among brain functions. Besides the negative effects of domestication and captivity (Rehkämper et al. 1991, 2000; Smulders et al. 2000), the only natural factor so far discovered to give rise to such constraints seems to be migration (Winkler and Leisler, 2004). The ability to become migratory may be a key feature in the evolution not only of birds (Berthold 1999; Winker 2000), but also in other organisms (Dingle 1996). Recent studies of the evolution of avian migration (summarized by Pulido and Rappole, 2004) have revealed the flexibility and evolutionary lability of migratory traits and migratory status (e.g. Helbig 2003) and a variety of ecological conditions favoring the evolution of migration or residency. So far, studies have shown that brain size of migratory birds is smaller than in residents (Burish et al. 2004; Winkler and Leisler 2004), and that the height of the braincase is lower in migrants (Leisler and Winkler 2003; Winkler and Leisler 2004). It is also known that, in general, brain size variation in birds, after the allometric relationship between body size and brain size has been accounted for, is due to variation in forebrain size, specifically neostriatum (nidopallium according to the new nomenclature; Reiner et al. 2004) and hyperstriatum (mesopallium; Rehkämper et al. 1991, 2000; Nicolakakis et al. 2003).

The current evidence for the relation between brain size and forebrain size rests on data of very few species, mostly residents (Rehkämper et al. 1991, 2000; Timmermans et al. 2000). The relationship between skull dimensions and migration appeared in a multiple regression of several morphological variables, and its relation with brain size was not established directly (Leisler and Winkler 2003; Winkler and Leisler 2004).

We attempt here to tie up some of the loose ends and analyze the relationships between skull dimensions and brain size in several groups of birds, demonstrate how those traits of the skull that are connected to brain size relate to migratory distance, and finally show which parts of the brain are reduced in migrants. In contrast to all previous studies, we rely on examples of low taxonomic rank with well known phylogenetic relationships.

**Methods**

**Birds**

We used species of two “warbler” radiations for our analysis: Old World Sylviid warblers, which are not a monophyletic assemblage (Sibley and Ahlquist 1990; Barker et al. 2001) and North American parulids. Specifically we studied 17 species of Sylvia (including Parisoma – for selection of species see Leisler and Winkler 2003) and 14 species of the genera Acrocephalus and Hippolais, which form the monophyletic group of Acrocephalines (Leisler et al. 1997; the same 13 species as listed in Leisler and Winkler 2003 plus A. orientalis). Sylvia and Acrocephalines are only distantly related; for the family-name issue between Timaliidae and Sylviidae see Cibois (2003). For parulids we deal with the same set of species studied by Ostroff (1986) and Austen (1988), except Icteria virens (i.e. 49 species).

**Morphometrics**

Measurements on skeletons were taken as described in Leisler and Winkler (1985, 2003). We measured a total of 151 Sylvia skeletons (mean 9, 2–15). Mean sample size for Acrocephalines is 8 (2–15). Parrulid skeletal characters were measured on 20 adults, 10 of each sex, for most species (Ostroff 1986; Austen 1988). Information about body mass was taken from the handbooks (listed in Leisler and Winkler 2003), Dunning (1992) and labels on the study skins.

Migration distances were calculated as stated in Leisler and Winkler (2003).

**Brains**

As part of an ongoing study of brain structure in migrants and residents, several Acrocephalus and Sylvia species were collected and compared to Parus species. Animals were sacrificed using prolonged anesthesia and subsequently perfused with 25 ml 0.1 M PBS (phosphate-buffered saline) and 35 ml 4% PFA (paraformaldehyde) in PBS at room temperature. Brains were removed and post-fixed in the same solution for another 24 h. The brain volume was determined by weighing the replaced water-volume after passive immersion on a standard digital balance. With the specific weight of the replaced liquid as 1, this gives 1 g for 1 ml (1 cm³) volume, resolved into 1 mg precision. Linear extension of selected brain components were measured using an absolute digimatic caliper to 0.01 mm precision. All landmarks for the linear extensions are easily accessible and the measurements are non-invasive, without disrupting the brain and defined as follows: three maximum forebrain orthogonal extensions (lateral, dorso-ventral and anterior-posterior projections), two tectal extensions (dorso-ventral and rostro-caudal), and three cerebellar extensions (anterior-posterior, dorso-ventral and lateral). ‘Projection-planes’ were defined and calculated by the product of two orthogonal projections taken along the maximum extension of the basically convex brain structures. Specified in this way, ‘projection planes’ (e.g. the forebrain frontal plane in Fig. 2) provide the area of the smallest square containing the
frontal projection of the corresponding convex structure. This frontal projection also coincides largely with the definition of a ‘frontal section’ within the stereotaxic coordinates of the canary brain. The angle of the frontal section thereby becomes perpendicular to a horizontal axis that forms a 45° angle with the horizontal skull axis and ‘bill plate’ (Stokes et al. 1974).

Recently, an updated avian brain nomenclature has been recommended (Reiner et al. 2004) so we refer to the new nomenclature (given in parentheses) as well as the old.

Statistical analysis

Statistical analyses were mainly based on various regression methods. Allometric relationships, mainly those with body mass as predictor, were analyzed with linear regression (Model I; Sokal and Rohlf 1995) of log-transformed data. Analyses of the association between migration distance and brain related data were analyzed in the following way. First, the log-transformed brain or skull measurements were regressed on body mass to obtain residual values. These residuals were regressed on migration distance using locally weighted regression (LWR) with a tricubic weight function (Cleveland and Devlin 1988), and the smoothing parameter optimized according to the unbiased Akaike criterion outlined in Hurvich et al. (1998). This allows accounting for possible non-linear relationships and robust data fitting. These analyses were used to produce the corresponding figures. The formal test of the relationships was done with ordinary linear regression (OLR). When the locally weighted regression analysis indicated a significant deviation from a linear relationship, we added a quadratic term to the predictor. Previous experience showed (Leisler and Winkler 2003; Winkler and Leisler 2004) that phylogeny does not influence the results perceptibly, because analyses based on star or bush like phylogenies produce the same results as conventional statistical analysis (Garland et al 1999).

Results

Brain size and skull dimensions

Data on brain mass on each of eight sylviid and parulid species were available from the literature (Milkovsky 1990; Graber and Graber 1962, 1965). With these, we could investigate how brain mass is related to body mass and skull height. If the skull height describes more than just allometric size relations we expected that it would explain the brain data better than body mass. This was true in both cases. All data were log-transformed and the allometric relations were obtained with linear regression. In the parulids, the correlation coefficient between brain mass and body mass was 0.943, between skull height and brain mass 0.966 ($P < 0.0001$). The residuals of both skull height and brain mass on body mass correlated positively as well ($r = 0.632, P < 0.1$). When the outlying black-and-white warbler (*Mniotilta varia*) is removed (its brain mass is much lower than expected for its size) the correlation is much better with $r = 0.937$ ($P < 0.002$). We obtained similar results with the sylvid data. The correlation coefficient between brain mass and body mass was 0.967, and between skull height and brain mass 0.968 ($P < 0.0001$). The residuals of both skull height and brain mass on body mass correlated with $r = 0.623, P < 0.1$). This shows that in both groups skull height is a reasonably good predictor of brain size. Similarly, Brooke et al. (1999) found that skull measurements can be used to predict eye sizes. However, the magnitude of the body mass – brain mass residuals is close to the accuracy of the measurements. So, significant results are to be expected to require larger sample sizes especially when very small birds are involved.

The relative skull height of 14 *Acrocephalus/Hippolais* species increased with decreasing migration distance in a non-linear way (Fig. 1a). The LWR fit was excellent (smoothing parameter $f = 0.929, \chi^2_{11.3} = 1.971, P > 0.99$); but the comparison with a ordinary linear equation revealed a significant deviation from linearity ($F_{1.1,11.3} = 5.704, P < 0.05$). Therefore, we entered both migration distance and its square into an OLR. Both the
Akaike information criterion and the Bayesian information criterion (Schwarz 1978) suggested only to retain the square of the migration distance in the final regression which resulted in a high correlation ($r = -0.924$; $F_{1,47} = 70.3$, two-sided $P < 0.00001$).

The corresponding analysis for 17 species of *Sylvia* warblers also showed a negative relationship of skull height with migration distance (Fig. 1b). The LWR fit was satisfactory (smoothing parameter $f = 0.889$, $\chi^2_{14} = 12.620$, $P > 0.5$); and the comparison with an ordinary linear equation did not show a deviation from linearity ($F_{1,2,14} = 0.225$, $P > 0.6$). Thus, we could apply OLR with which we found a weakly significant negative correlation ($r = -0.449$; $F_{1,15} = 3.791$, two-sided $P < 0.1$).

The New World wood-warblers (Parulini) belong to a radiation of passerines commonly known as nine-primaried oscine birds (Lovette and Bermingham 2002). They are in many ways convergent to Old World sylvids, especially the *Phylloscopus* warblers, and species analyzed here are somewhat smaller than those in the preceding analyses. As expected, error variance was higher, but the larger sample size of 49 species could compensate for this and the results were analogous to the preceding ones, showing again a negative relationship of residual skull height with migration distance (Fig. 1c). The LWR fit was excellent (smoothing parameter $f = 0.961$, $\chi^2_{46,1} = 32.32$, $P > 0.9$); and there was no deviation from linearity in the relation ($F_{1,4,46,1} = 0.546$, $P > 0.5$). We obtained with OLR a highly significant correlation ($r = -0.567$; $F_{1,47} = 22.226$, two-sided $P < 0.00005$).

**Brain dimensions**

In Fig. 2, the frontal forebrain projection plane was chosen as the response variable to the overall brain volume. The reason for this choice is because changes in volume of hyperstriata (mesopallium) and neostriata (nidopallium) can be expected to be reflected by changes of either dorso-ventral or lateral or both linear extensions, whereas extensions along the anterior-posterior axis will largely remain unaltered for a given encephalization type (the dorso-frontal type of passeriform birds; Rehkämper et al. 1991). These telencephalic measures were compared to dorsal met- and mesencephalic subdivisions such as cerebellum and optic tectum because these components appear to be less conservative (and thus more ‘sensitive’) from a volumetric point of view when compared to changes in brainstem structures across different orders of birds (Boire and Baron 1994). As expected, our within-order comparison shows that brain weight is a good predictor for the relevant telencephalon size in the subset of songbirds studied (regression slope $P < 0.001$, correlation $r = 0.913$). A subsequent morphometric study of telencephalic composition (focusing on the relative volume of hyperstriata [total mesopallium], neostriatum [total nidopallium] and paleaostriatum [striatum mediale, laterale and globus pallidus]) supported the view, that an increase in forebrain size is due to an increase in hyperstriatum and neostriatum in passeriforms (Rehkämper et al. 1991), and secondly revealed that the relative composition of forebrain striata may differ between congeneric migrants and residents (Bernroider et al. in preparation).

**Discussion**

**Migration and brain size**

The lower brain size in migrants (Winkler and Leisler 2004; Burish et al. 2004) is clearly also apparent in the braincase dimensions (skull height; Fig. 1). Although measurement errors and other sources of variation are relatively high, measurements of skull dimensions can serve as reasonable approximation of brain size. This could easily be explored for comparative studies on the evolution of brain size in passeriform birds because researchers can obtain the necessary data relatively easily in museum collections.

Particularly in the data on *Acrocephalines* (Fig. 1a), a non-linear relationship between migration distance and skull height appeared. It indicates that the effects of migration on brain size are proportionally stronger in long distance migrants, while short distance migrants may be not affected at all. It is clearly premature to generalize these findings. The relationships in the parulids and in *Sylvia* (Fig. 1b,c) show a similar tendency, but the deviation from a linear function is small to negligible. More accurate measurements of brains and brain sections, rather than of skulls, should help to clarify this issue. These data should come from a group of closely related birds which comprise samples of residents, short and long distance migrants. Histological studies have further advantages. One can identify the
brain sections that are responsible for overall brain size variation, and the relationships between volumetric size and neuron density can be clarified.

Previous studies have found that differences in overall brain size are mainly due to differences in the size of the forebrain, particularly the neostriatum (nidopallium) and the hyperstriatum ventrale (mesopallium, Rehkämper et al. 1991, 2000). These conclusions were mainly based on gross comparisons between a few gallinaceous and passerine birds. The fact that the quail (Coturnix coturnix), a migrant, was among the gallinaceous birds analyzed, and corvids and the house sparrow (Passer domesticus), all residents, represented the Passeriformes may have strengthened this difference. Our preliminary histological data show that the size of forebrain(regions) do in fact disproportionally grow with overall brain size, whereas other brain subdivisions do not show such a relationship. Primary, secondary and tertiary areas are a common feature of both the neostriatum and the hyperstriatum ventrale and these regions are thought to represent multimodal integrative areas (Rehkämper et al. 1991; and references therein), and the hyperstriatum/neostriatum complex (meso- and nidopallium) in birds is in many respects equivalent to the isocortex in mammals (Rehkämper et al. 1991). Behavioral flexibility, measured as the occurrence of feeding innovations in wild birds (Lefebvre et al. 1997), correlates well with laboratory studies of learning speed and reversal learning, and with the relative size of telencephalic structures (Timmermans et al. 2000).

Possible explanations for smaller relative forebrain size

The brain has high energy demands and requires a large supply of oxygen and glucose (Armstrong and Bergeron 1985). Metabolic demands therefore inevitably not only constrain its development, but also its final size. Alerstam and Hedenström (1998) and Wikelski et al. (2003) found that, over the entire migration, migrants spend double the amount of energy during stopovers that they spend for flight. Thus, it would clearly be advantageous for migrants to keep resting metabolism including brain costs low. Migrants are not the only birds that may face severe energetic constraints. Birds that live in poor habitats with low food supply may have similar problems, especially when energetic demands are high. This hypothesis would therefore predict that not only migration, but also habitats that constrain availability of energy, can have an effect on brain size.

Changes in overall brain size strongly affect the relative size of particular brain components because of allometric relationships. Which structure is bigger or smaller depends on the conservative order in neurogenesis. It has therefore been argued that (in mammalian brains) variation in most regions is simply a consequence of a functionally driven change in one or very few other regions, with a disproportionately large growth occurring in late-generated parts (Finlay and Darlington 1995; Finlay et al. 2001). These byproducts of neurogenetic changes may set the ‘frame’ that can be utilized by various behaviors, which in turn may modify the neurogenetic substrate. The duration of brain development is thus central to the understanding of the relative size of certain brain regions. Altricial birds retain a high potential for brain growth after hatching (Portmann and Sutter 1940; Portmann 1962; Ricklefs and Starck 1998; Schew and Ricklefs 1998). Development may slow down or become very costly in birds which either have to prepare early for migration (our data) or live in regions with a short productive period. The developmental hypothesis thus predicts that birds with short breeding seasons, like in Arctic or Alpine habitats or in desert like areas with a very short vegetation period, terminate brain growth earlier than those in more benign habitats and consequently may develop relatively small forebrains. The nutritional stress hypothesis posited by Nowicki et al. (1998) rests on similar assumptions. However, it focuses on the conditions during postnatal development rather than on the time available for growth. Nowicki et al. (2002) produced experimental results which show that swamp sparrows (Melospiza georgiana) that were fed 70% less than controls until the time of independence grew smaller song-related forebrain nuclei.

The braincase as such may be influenced by selective forces which are not related to brain development. Higher aerodynamic efficiency of flatter heads can probably be ruled out because of the very small effects involved, but this should be checked in future studies. Adaptations that pertain to the feeding apparatus and the forces that govern bill mechanics may play some role. For example, Beecher (1978) discussed cranial transformations, which are dictated by demands of increasing biting force in frugivores. Parrots and woodpeckers have to deal with very strong forces for very different reasons and with completely different mechanics, yet they are among the families with the largest brains (Portmann 1962; Bennett and Harvey 1985). So, the negative effects, if there are any, of bill mechanics on brain case volume must be rather special (see Leisler and Winkler 2003 for further discussion).

Evolutionary aspects

So far, we have implicitly assumed that the causal chain runs like this: ecological factors result in strong selective advantages for becoming a migrant (or to live in certain habitats), this in turn exerts strong pressure on brain development, namely forebrain reduction, and as a further consequence certain cognitive abilities are compromised. The prediction that one could deduce from this scenario is that all other birds that do not face such constraints would have large forebrains because multimodal integrational capacities and learning performance confer general selective advantages (e.g. Rehkämper et al. 1991). In a way, that logic
could be turned around by supposing that some (unknown) factor created variation in forebrain size and hence cognitive abilities. Less gifted birds, as it were, could do better if they evade changing and because of that highly demanding environmental conditions, and possibly also crowding, by becoming migratory. By such a strategy they would never face challenges that would require a good brain. The relationship between migration distance and brain size described in this paper are hard to explain with this hypothesis. One could expect that groups of small brained birds contain more migrants than other ones and live in more benign habitats. This expectation could be tested in a comparative analysis of lineages which contain both tropical residents and migrants.

Our findings that migrants possess smaller forebrains than residents seem counterintuitive to our image that an integrated system of several complex traits is required for migration (e.g. Rappole et al. 2003). If the brain is reduced because of energetic or developmental constraints, the question arises what associated abilities are lost. From an adaptionist’s point of view one would expect that primarily those parts are reduced that are most dispensable. Birds that escape conditions of low food supply may, for instance, not be very skilled and innovative foragers, and they would not need to be very competent in maintaining and interacting in complex social networks because they break down during migration, particularly in small nocturnal migrants, anyway. This is in accordance with the current view that migrants are (pre-)adapted to use niche dimensions common to many different locations (e.g. Rappole and Jones 2002), solitarily or in simply organized flocks, and in a rather stereotyped way. If brain size evolution is mainly a matter of rather fixed allometric relationships, losses of functions may be as unspecific as the gains discussed above. Migration or any other ecological constraint that prevents attaining a large forebrain would then have similar behavioral effects across a wide range of species.

The ideas presented here are based on only few interspecific comparisons and obviously need further testing. The next step would be to look for adaptive divergence within species with pronounced diversification of migration patterns like blackcap (Sylvia atricapilla), white-crowned sparrow (Zonotrichia leucophrys) or stonechat (Saxicola torquata) and others.

Acknowledgements We thank J. Blondel and the curators of the museums in Tring, Tervuren, Vienna, Bonn, Berlin, Munich, Stuttgart, Washington, New York, Pretoria, Cape Town, and Paris for access to and loan of specimens. Special thanks are due to K.-H. Siebenrock who measured the skulls of Acrocephalines and Sylvia warblers. We thank Samuel S-H Wang, Princeton University, and his group for giving us access to their manuscript before publication. We are also grateful to W. Hochachka, F. Pulido, and M. Winter for helpful discussion and useful criticism of an earlier version of this manuscript. Birds were collected with permission of the governments of the city of Vienna (MA22–3472/2002), and the state of Burgenland (S-N-A1007/152–2002).

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