Cognition in an Ever-Changing World: Climatic Variability Is Associated with Brain Size in Neotropical Parrots

Cynthia Schuck-Paim a  Wladimir J. Alonso b  Eduardo B. Ottoni a

a Laboratory of Cognitive Ethology, Department of Experimental Psychology, Institute of Psychology, University of Sao Paulo, Sao Paulo, Brazil; b Fogarty International Center, National Institutes of Health, Bethesda, Md., USA

Key Words
Brain size · Cognitive ability · Encephalization · Intelligence · Climate · Environmental variability · Behavioral flexibility · Parrots

Abstract
Research on the conditions favoring the evolution of complex cognition and its underlying neural structures has increasingly stressed the role of environmental variability. These studies suggest that the ability to learn, behave flexibly and innovate would be favored under unpredictable variations in the availability of resources, as it would enable organisms to adjust to novel conditions. Despite the growing number of studies based on the idea that larger-brained organisms would be better prepared to cope with environmental challenges, direct testing of the association between brain size and environmental variability per se remains scant. Here we focus on Neotropical parrots as our model group and test the hypothesis that if relatively larger brains were favored in climatically variable environments, larger-brained species should currently tolerate a higher degree of environmental uncertainty. Although we show that there are also other factors underlying the dynamics of brain size variation in this group, our results support the hypothesis that proportionally larger-brained species are more tolerant to climatic variability, both on a temporal and spatial scale. Additionally, they suggest that the differences in relative brain size among Neotropical parrots represent multiple, recent events in the evolutionary history of the group, and are particularly tied to an increased dependence on more open and climatically unstable habitats. As this is the first study to present evidence of the link between brain size and climatic variability in birds, our findings provide a step towards understanding the potential benefits underlying variation in brain size and the maintenance of highly enlarged brains in this and other groups.

Introduction

For many years, comparative research on cognitive evolution has been driven by a quest to understand those conditions that favor the evolution of complex abilities (such as the capacity to plan, innovate and use tools) as well as the underlying neural substrates for these behaviors. Within this perspective, much of what is currently known is focused on the role of the brain and its structures as substrates for the development of cognition, and is often permeated by the implicit assumption that neural volume and cognitive capacity are related [Clutton-Brock and Harvey, 1980; Macphail and Bolhuis, 1982, 2001; Byrne, 1993; Striedter, 2004]. The general idea is that proportionally larger neural structures would have a higher information processing capacity to be used in cognitive functions, a notion supported by evidence showing that the relative size of the brain (corrected for differences in
body size) and its parts is positively associated with various measures of behavioral complexity [Biegler et al., 2001; Reader and Laland, 2002; Byrne and Corp, 2004; Lefebvre et al., 2004; Shultz and Dunbar, 2006]. In the case of birds, for instance, several studies have suggested that the degree of behavioral flexibility of a species (as measured by their reported frequencies of behavioral innovation, tool use and social learning) is highly correlated with the relative size of the whole brain, the forebrain and two areas within the forebrain: the nidopallium and the mesopallium [Lefebvre et al., 1997, 2002, 2004; Nikolakakis and Lefebvre, 2000; Timmermans et al., 2000]. The same results were obtained for primates [Reader and Laland, 2002] in that species with larger relative brain and isocortex sizes [see also Deaner et al., 2007] demonstrate higher rates of innovation, tool use and social learning.

One of the main hypothesized advantages of larger brains relates to the putative association between environmental variability and cognition. It suggests that the evolution of the ability to learn and to behave in a plastic manner would be favored in those environments subject to unpredictable variations in the availability of resources [Stephens, 1991; Ancel, 2000], hence preventing the genetic fixation of rigid behaviors. Thus the evolution of relatively larger brains would be associated with the need to adapt to ever changing conditions. This would enable organisms to learn solutions to new problems, explore new resources, and increase their probability of survival when faced with environmental change [Allman et al., 1993; Lee, 2003; Piersma and Drent, 2003; Lefebvre et al., 2004]. Such claims also extend to proposals that increases in the degree of cognitive complexity observed along the evolutionary history of some groups provided these organisms with a selective advantage in increasingly variable environments. For example, Richerson and Boyd [2001] point out that the development of complex cognitive abilities in some lineages of mammals (as measured by increases in brain size which persisted until the Pleistocene) coincides with increases in the environmental variability during the period. Similar hypotheses were also proposed to explain the evolution of the human brain: increases in the breadth of our ecological niche and degree of behavioral flexibility would have been favored in those periods of higher climatic variability [Potts, 1998; Richerson and Boyd, 2001].

The basic assumption at the core of these studies is that behavioral flexibility enables organisms to better cope with temporal and spatial fluctuations in the availability of resources and adjust to novel conditions, counteracting or minimizing the potentially deleterious effects of environmental heterogeneity [Jones, 2005]. For example, a series of studies have recently demonstrated that those birds with proportionally larger brain volumes are more likely to successfully establish themselves in new environments, both on a regional and global scale [Sol and Lefebvre, 2000; Sol et al., 2002, 2005a]. Similarly, there is some evidence that in the case of parrots a higher level of ecological flexibility (e.g., broader diets) is associated with an increased likelihood of success in the invasion of new environments [Cassey et al., 2004b]. Using data of avian mortality rates in natural populations, Sol et al. [2007] have also shown that bird species with relatively larger brains experience lower mortality rates, suggesting that enlarged brains would increase survival probability by enabling the production of flexible cognitive responses that buffer individuals against environmental stresses.

Despite the growing number of studies based on the idea that larger-brained organisms would be better prepared to cope with environmental challenges, direct testing of the association between brain size and environmental variability per se remains scant. In fact, to our knowledge, there are only two studies that directly investigated the association between behavioral flexibility/brain size and climatic variability, but the results were contradictory. MacDonald [2002] found a positive association between climatic variability and innovation rate in African primates, but Reader and MacDonald [2003] found no association between climatic variability and either brain size or behavioral flexibility. Thus, whether relative brain size is indeed associated with environmental variability remains largely unknown.

Here, we focus our analysis on Neotropical parrots and test the hypothesis that if relatively larger brain sizes were favored in climatically variable environments due to the selective advantages they provided, extant larger-brained species should tolerate a higher degree of environmental uncertainty. Parrots are known for their highly inquisitive nature, sharing with corvids [Emery and Clayton, 2004; Kacelnik et al., 2006], cetaceans [Marino, 2002] and primates [Tomasello and Call, 1997] many of the features believed to be associated with advanced cognitive processing, such as high levels of sociality and life history traits marked by high longevity, slow development and a long period of parental investment. Large relative brain sizes are also a distinctive feature of parrots, in some cases comparable in size to those of nonhuman primates [Iwaniuk et al., 2005]. Nevertheless, brain size is highly variable among species in the order even when only Neotropical species are considered, with the small-
est brain more than 25 times smaller than the largest, thus making the group a good model for the comparative analysis of hypotheses on brain evolution. Brain size differences in parrots also predicts more than 95% of the variation in forebrain size [Iwaniuk et al., 2005], a structure usually associated with higher cognitive and multimodal integration functions (e.g., memory, concept formation and social intelligence). The more than 150 species of Neotropical parrots are also widely distributed across South and Central America (fig. 1) – with species inhabiting habitats as diverse as the Amazonian rainforest, the high altitudes of the Andes, the Atacama desert and the cold climates of Patagonia – thus enabling the assessment of the effect of climatic variability on brain size across a wide range of conditions, while controlling for life-history traits previously shown to be associated with variation in brain size in birds [Bennett and Harvey, 1985b; Iwaniuk and Nelson, 2003].

To determine whether those proportionally larger-brained species are more tolerant with higher levels of environmental variability, we conducted a careful and very extensive review of the geographic distribution of all Neotropical parrot species; and by using geographic information systems we extracted from the locality records the climatic parameters describing each species’ tolerance to variability in measures such as temperature and rainfall. Variation in warmth and wetness has indeed been shown to be the main climatic controls of net primary productivity of ecosystems [see e.g., Boisvenue and Running, 2006, for a review]. Moreover, such factors are known to act directly upon the phenology of plant species (e.g., by determining the rate of development of fruits and flowers) and prey populations. For example, high levels of humidity are needed for the appropriate functioning of several metabolic processes in insects; high temperatures associated with high levels of humidity tend to

Fig. 1. Map of the geographic distribution of all Neotropical parrots species in South and Central America, as registered for the period from 1783 to 2004. Sources and references for locality data are on supplementary material 1 (www.karger.com/doi/10.1159/000119710).
increase their longevity, causing an increase in their population density available for insectivorous birds. As a consequence, climatic variability in temperature and precipitation should directly affect the availability of resources to the parrot populations. If facing such fluctuations in the availability of feeding resources is cognitively demanding, enhanced cognitive abilities and more developed neural structures should be found in more variable environments.

Material and Methods

Brain and Body Size

We obtained brain measurements for a total of 468 adult individuals, belonging to 100 Neotropical parrot species (supplementary material 1, www.karger.com/doi/10.1159/000119710). Endocranial volumes previously shown to be highly correlated with brain mass in psittaciformes [predicting 98% of its variance; Iwaniuk and Nelson, 2002] were obtained from the literature [Iwaniuk et al., 2005], as well as measured from non-fractured adult skeletal specimens by adopting the same methods described by Iwaniuk and Nelson [2002]. In brief, we filled the skull cavities with lead shot (50:50 mix of sizes 9 and 10) via the foramen magnum, being careful to prevent the formation of air lacunae. The lead shot was then decanted into graduated cylinders to enable the measurement of brain volume. Corresponding body weight measurements of adult individuals were taken from the literature and measurement of brain volume. Corresponding body weight measurements of adult individuals were taken from the literature and from notes in labels of museum collections (supplementary material 2 (www.karger.com/doi/10.1159/000119710)). In those cases where information on the body size of a given species was available from multiple sources, a weighted average (with weights corresponding to the sample sizes used by each source) was calculated. In 4 cases where only body length was available (Amazona agilis, A. brasiliensis, A. pretrei and A. xanthops) body weight was estimated using the regression of body weight against body length for the corresponding genus.

Geographic Distribution

We searched for well-defined locality records characterizing the geographic distribution of all Neotropical parrot species by conducting a very extensive literature review as well as by examining records in museum catalogues and collections (supplementary material 2 for sources and references). The locality records comprised the period from 1783 to 2004. Each record was georeferenced (i.e., latitude and longitude coordinates were attributed to the locality) using maps, databases and gazetteers. For the historical records and those localities that had their names characterized by the presence of synonyms, by cases in which one species was split into two or more species, and by the clustering of two or more species into a single one. Here we use the taxonomic nomenclature currently adopted by the American Ornithologists’ Union, having reviewed and changed the nomenclature of the original records accordingly (supplementary material 3, www.karger.com/doi/10.1159/000119710). A total of 23,937 locality records representing 150 Neotropical parrot species were obtained and transferred to a database including the species cited name and its current taxonomic nomenclature, the name of the locality and its respective geographic position (city or nearest location, state/province/department, country), latitude, longitude, year of observation when available, museum number and collector (when available or appropriate) and source of information. Only those species for which we had measures of brain and body size were considered for analysis.

Climatic Variables

The environmental variables were obtained from worldwide climate maps [CRU TS 2.1; Mitchell and Jones, 2005] generated by the interpolation of climatic information obtained from ground-based meteorological stations. The mean climate surfaces were available for the period from 1901 to 2002, with a monthly temporal resolution (yielding 1,224 monthly means – i.e., 102 years × 12 months – for each locality) and a 0.5° (latitude) by 0.5° (longitude) spatial resolution [Mitchell and Jones, 2005]. We used the entire data-set, as we were interested in as much information as available about the climatic variability faced by a species. As mentioned previously, the climatic variables used were precipitation and temperature. All environmental parameters (means of climatic variables as well as measures of variability as described below) were extracted for each of the 23,937 locality records from the climatic database by using scripts written in Matlab® specifically for this purpose. The climatic information extracted was thoroughly checked for consistency before analysis.

Data Analysis

Temporal Variation

To determine the degree of tolerance of each species to changes in climate with time, three measures of temporal variability were calculated for each locality and climatic variable (temperature and rainfall). The first measure was the coefficient of variation along the entire period, namely the ratio of the overall standard deviation – computed considering the entire time series (i.e., 1,248 monthly means) – divided by the overall mean of these values. A second measure was the degree of seasonal variation experienced, namely the amplitude of climatic variation during a year. As an example, to calculate the seasonal variation for temperature we determined the mean temperature for each month, then proceeded by subtracting the lowest from the highest of the twelve means. It is important to note that for rainfall, the difference between, for instance, 10 and 50 mm of rain does not have the same impact on ecosystem production (and thereby food availability) than a difference between 510 and 550 mm. Therefore, we initially log-transformed the monthly means and then subtracted the lowest from the highest mean (which is effectively the same as calculating the ratio of the highest over the lowest

mean and log-transforming the result). Thirdly, we analyzed the mean monthly coefficient of variation, that is, a measure of the mean variability experienced along one month. It was computed by calculating the mean climatic value and standard deviation for each of the twelve months and determining the twelve corresponding coefficients of variation. A mean CV (mean of the twelve CVs) was subsequently computed.

Each of the parameters was determined for each of the localities, but because each species was distributed in many localities (e.g., species A would have 80 values for each climatic measure if present in 80 geographic localities), it was necessary to establish, for each climatic parameter, a single value representing the species’ tolerance to variability. This was done by calculating a graphically weighted average of all localities, corresponding to a measure of the mean climatic variability tolerated. As the simple arithmetic mean of all localities would be biased due to spatial autocorrelation in the climatic values (values from close localities tend to be more similar than values from distant localities), we weighted the values of each locality by the sum of the distances (measured in pixels, properly converted from the latitude and longitude coordinates) from that locality to every other locality. In other words, the value of the climatic measure of variability corresponding to each locality was multiplied by its weight (corresponding to the sum of the distance of that locality to every other locality where a species occurred), and the sum of all weighted values was divided by the sum of all weights. In this way, clustered localities received a lower weight, whereas distant localities had a proportionally higher weight. This procedure resulted in an average value for each climatic parameter equivalent to one in which all localities of occurrence of a given species were evenly spaced.

Although temporal variation in climatic variability might be overcome through behavioral flexibility and the ability to innovate [Sol et al., 2005b], it is also possible for individuals to migrate to other, more favorable, regions when faced with periods of climatic stress and resource shortage. Within this perspective, it is possible that the degree of environmental variability experienced by individuals is lower for migratory than resident birds, hence any putative association between brain size and temporal climatic variability would be weaker in the former group. On the other hand, by having to survive and deal with food resources in several different environments migrating birds might, conversely, experience more environmental variability than resident birds. To account for the putative effect of migration and distinguish between these two possibilities we also examined whether the association between relative brain size and the three measures of temporal variability previously described depended on the migratory status of the species. Similarly to the classification adopted by Cassey et al. [2004a], the degree of migration undertaken by each species was classified as: (0) if they were permanent residents with local movements only; (1) if they were generally resident but there was confirmed evidence of irruptive altitudinal or seasonal movements; and (2) if the species was known for regular seasonal and altitudinal movements. Information on migration status was taken from Juniper and Parr [1998] and del Hoyo et al. [1997].

Spatial Variation
We also determined, for each climatic variable, the spatial heterogeneity in the climatic conditions experienced by each species across its geographic range (variation between locations rather than between months and years within a location) to examine its potential to predict variance in relative brain size. Two measures reflecting the range of conditions tolerated by the populations of each species were calculated: (1) the amplitude in the actual climatic values tolerated across the species’ geographic range. This was determined by computing the means of each of the twelve months for each locality and subtracting the value of the month with the lowest mean from the value of the month with the highest mean. For example, if the highest monthly mean of species A corresponded to January in the city of Salvador (42°C) and the lowest to July in the city of Porto Alegre (6°C), then the amplitude of temperature experienced by the species would equal 42–6 = 36°C. As justified before, in the case of rainfall we initially log-transformed the monthly means before performing the subtraction; (2) the coefficient of variation in the climatic variable across localities (the ratio of the standard deviation of the means of all localities – with each locality contributing with one mean – divided by the overall mean of all localities considered together).

Habitat Type
It is possible that climatic change affects the productivity of an ecosystem only after a given threshold. For example, Cowling and Shin [2006] conclude that the Amazonian rainforest is, within certain limits, resilient to environmental change, particularly decreases in temperature and rainfall. Similarly, Levey and Stiles [1992] suggest that forest interiors – home to many New World parrot species – can be buffered against large fluctuations in temperature and humidity. If the effect of climatic variability is weaker in dense tropical forests, the association between climatic variability and brain size should be weaker for those species occurring in forests. To test this possibility we classified all species into two groups, depending on whether they were distributed exclusively on dense forests or depended partially or completely on more open habitats (e.g., savannas, crops, urban environments, drier and more open terrain). A species was considered to rely on open landscapes if depending on any kind of resource (e.g., food, nests) from these habitats, even if only in a restricted part of its geographic range.

Statistical Tests
All brain and body measures were log-transformed before analyses. To remove the effects of body size in the analysis, relative brain size was calculated as corresponding to the residuals of a log-log least-squares linear regression between brain and body size [Bennett and Harvey, 1985b]. Brain and body size were highly and significantly associated (F1,99 = 1,555, p < 0.0001, r2adj = 94%), and the residuals uncorrelated with body size (F1,99 = 0.00, p = 1.00, r2adj = 0.0%). Inspection of the distribution of relative brain size across the 100 species revealed the presence of an outlier, 3.5 standard deviations larger than the mean relative brain size. The outlier corresponded to the brain measurement of a single specimen of Pyrrhura molinae (see supplementary material 1). Given the extremely high deviation from the mean and the impossibility to determine how representative this measure was of the brain size of the species, we excluded this species from analyses (although its inclusion does not change the results). Considering recent evidence suggesting that absolute measures of brain size can best predict variation in general cognitive ability in primates [Deaner et al., 2007], we also tested for the association between absolute brain size and climatic variability.
Stepwise regression procedures were then employed to select those climatic measures most likely to predict variance in relative and absolute brain size. Two sets of regressions were conducted: one considering all measures of temporal variability and another where the predictors were the spatial measures of variability previously described. Alpha values for the stepwise regression were set at 0.05. The variables selected were included as factors in a multiple regression to estimate the extent to which each climatic variable was associated with brain size independently of the others, as well as how much of the total variance in relative brain size was explained by the model. Bivariate correlation matrices were used to examine possible effects of multi-collinearities among the climatic variables. We tested the main effect of climatic variability on brain size as well as the effect of the interaction between climatic variability and habitat type on brain size. To test whether the potential association between brain size and temporal climatic variability depended on whether a species was migratory or resident, ‘migration status’ was subsequently included in the model and the interaction between it and the variables selected in the stepwise procedure tested. We also explored potential non-linear trends in the association between relative brain size and climatic variability to examine the possibility that relatively larger brain volumes were associated with intermediate levels of climatic heterogeneity by testing the association between brain size and the polynomial terms of the climatic variables.

Based on previous work [Iwaniuk and Nelson, 2003], we additionally tested for the association between brain size and developmental period by regressing brain size against both incubation period and age at fledging. Both factors were significantly associated with body mass \( F_{1,98} = 50.2, \ p < 0.0001, \ r^2_{adj} = 33.4\% \) and \( F_{1,98} = 199, \ p < 0.0001, \ r^2_{adj} = 67\% \) for incubation period and age at fledging, respectively, so we used the residuals of the regression of each factor against body mass as a measure of relative incubation period and relative age at fledging. In those cases where the association between brain size and a developmental measure was significant, we additionally conducted all analyses controlling for this measure.

Finally, we examined the possibility that a species occurring over an area with a wider range of climatic regimes might split into a higher number of subspecies, each specialized in one regime. If this possibility were confirmed, along with a positive association between brain size and tolerance to climatic variability, it would reinforce and help explain previous findings showing an association between brain size and the polynomial terms of the climatic variables. The randomization tests conducted to examine the presence of phylogenetic signal in the variables measured (namely, a tendency for related species to more closely resemble each other) by using a randomization procedure in which the variance in the standardized contrasts of brain size against the standardized contrasts of body size \( F_{1,98} = 230, \ p < 0.0001, \ r^2_{adj} = 70\% \). Relative incubation period and age at fledging were calculated similarly, as the residuals of the regression between the contrasts of incubation period and of age at fledging against the contrasts of body size. We also tested for the presence of phylogenetic signal in the variables measured (whether a species was migratory or resident, ‘migration status’ was subsequently included in the model and the interaction between it and the variables selected in the stepwise procedure tested. We also explored potential non-linear trends in the association between relative brain size and climatic variability to examine the possibility that relatively larger brain volumes were associated with intermediate levels of climatic heterogeneity by testing the association between brain size and the polynomial terms of the climatic variables.

Phylogenetic independent contrasts [Garland et al., 1999; Garland and Ives, 2000] were calculated for brain and body size and for the developmental and environmental variables (existing data indicate that environmental factors do often exhibit significant amounts of phylogenetic signal, hence the use of contrasts is more appropriate [Garland et al., 1992; Freckleton et al., 2002]) by inputting these variables into PDTREE, a program within the PDAP package [Garland et al., 1999]. Unresolved nodes were assumed to be soft polytomies, with branch lengths between internal nodes set to zero [Purvis and Garland, 1993]. As estimates of divergence times are not available for most species, we tested three models of arbitrary branch lengths to create the contrasts: all branch lengths set equal to one [Diaz-Uriarte and Garland, 1998], Pagel’s [1992] and Grafen’s [1989] arbitrary branch length models. Inspection of the data showed that the contrasts were most properly standardized by Pagel’s model, which sets all internode branch lengths equal to one and constrains tips to be contemporary, so branch lengths were computed by following his method. All regressions involving contrasts were forced through the origin [Garland et al., 1992]. Relative brain size was calculated as the residuals of the least-square linear regression between the standardized contrasts of brain size against the standardized contrasts of body size \( F_{1,98} = 230, \ p < 0.0001, \ r^2_{adj} = 70\% \). Relative incubation period and age at fledging were calculated similarly, as the residuals of the regression between the contrasts of incubation period and of age at fledging against the contrasts of body size. We also tested for the presence of phylogenetic signal in the variables measured (namely, a tendency for related species to more closely resemble each other) by using a randomization procedure in which the variance in the standardized contrasts of the original phylogenetic tree is compared to that when the tip data have been randomly permuted (1000 random permutations) across the tips of the tree [Blomberg et al., 2003]. The tests were implemented by using PD RANDOM and PDERROR, two programs within the PDAP package [Garland et al., 1999].

Results

The randomization tests conducted to examine the presence of phylogenetic signal in the variables (whether traits were randomly distributed across the phylogeny or clustered according to relatedness, see data analysis) indicated that the morphological (brain and body size), developmental and environmental variables, as well as migratory status, exhibited highly significant phylogenetic signal \( p < 0.01 \) in all cases. Hence, unless stated otherwise the analyses below focus on the phylogenetically independent contrasts.

Relative Brain Size

Relative brain size was significantly associated with the degree of seasonal variation in temperature experienced by the parrots, and the effect of temperature variability on brain size strongly depended on habitat type.
Specifically, changes in relative brain size along the phylogenetic tree were accompanied by changes in the same direction in the species’ tolerance to the degree of annual seasonality in temperature (fig. 2a). Figure 2b shows that the significance of the relationship is due to those contrasts representing a transition from forest to open landscapes. These contrasts are located predominantly on the upper right corner of the graph, and represent evolutionary increases in relative brain size and tolerance to temperature variability occurring simultaneously with the transition from forested to open terrain in the phylogenetic tree. The trend line in figure 2b also suggests that during this transition larger increases in brain size were accompanied by respectively larger changes in the degree of tolerance to climatic variability. Temporal climatic variability and habitat type explained approximately 20.8% ($r^2$ adj) of the variance in relative brain size. Of the two developmental measures considered, relative brain size was significantly associated with relative age at fledging ($F_{1,96} = 16.14, p < 0.0001$). We therefore conducted the analyses again controlling for this parameter, as well as testing the effect of migration. This refined model accounted for approximately 26.6% of the variance in relative brain size, with a positive and significant effect of relative age at fledging ($F_{1,91} = 9.5, p < 0.01$), habitat type ($F_{1,91} = 5.7, p = 0.019$) and again the interaction between temperature variability (as represented by the degree of annual seasonality) and habitat type ($F_{1,91} = 3.7, p = 0.05$).
Neither the direct effect of migratory status on relative brain size nor the interaction between migratory status and the degree of seasonal variation in temperature were significant ($F_{1,91} = 0.33, p = 0.56$ and $F_{1,91} = 0.32, p = 0.57$, respectively). There was no significant association between the contrasts of relative brain size and the quadratic or cubic terms of any of the variables ($p > 0.05$ in all cases).

Of the two measures of spatial heterogeneity in the climatic conditions experienced by each species, relative brain size was significantly and positively associated with the coefficient of variation in precipitation ($F_{1,94} = 8.12, p < 0.01$) and, similar to the pattern found for variability in temperature seasonality, the effect of precipitation CV strongly depended on habitat type (main effect of habitat type and interaction with precipitation CV, respectively: $F_{1,94} = 6.3, p = 0.01$ and $F_{1,94} = 13.9, p < 0.0001$; $r^2_{adj} = 27.9\%$). This means that evolutionary increases in relative brain sizes were accompanied by an expansion in the distribution of the species across a wider range of precipitation regimes (fig. 3a). The contrasts representing the transition to those open landscapes, more vulnerable to the effects of climatic oscillations, also concentrate on the upper right corner of figure 3b, and represent those instances in which increases in relative brain size occurred simultaneously with the presence of the species in a wider range of precipitation conditions. The relationship between precipitation variability and relative brain size was not significant for the contrasts representing the occupation of more densely vegetated habitats (fig. 3c). Interestingly, there also seems to be a positive trend between brain size and precipitation variability in the absence of

Fig. 3. Association between the standardized contrasts of relative brain size and the coefficient of variation in precipitation when considering a all contrasts, b only those contrasts representing a transition from a dependence exclusively on dense forests to more open terrain, c only those contrasts representing a transition from more open landscapes to a life exclusively in forests and d no habitat transition.
habitat changes (fig. 3d). Inspection of the key contrasts responsible for the positive trend (in bold) in the upper right corner shows that they are restricted exclusively to those species depending on open landscapes, and characterized by an expansion of their geographic range. The proportion of variance in relative brain size explained increased to 34.7% when relative age at fledging was included in the model (effects of age at fledging, precipitation CV, habitat type and the interaction between precipitation CV and habitat type, respectively: $F_{1,93} = 10.84$, ...
p < 0.001; F₁,93 = 8.96, p = 0.004; F₁,93 = 4.73, p = 0.032 and F₁,93 = 11.3, p = 0.001; r²_adj = 34.7%). There was no significant association in our study between relative brain size and the polynomial terms of the spatial parameters of measured climatic variability (p > 0.05).

The bar graphs in figures 4b–d represent, respectively, relative brain size, seasonal variation in temperature and precipitation CV experienced by each of the 99 species analyzed (averages for each species, not corrected for phylogenetic relatedness), with each individual bar corresponding to the species depicted in the accompanying topology in figure 4a. As shown in the figure, there were strong correlations between relative brain size (fig. 4b) and seasonal variation in temperature (fig. 4c, black bars) within some monophyletic groups. The pattern observed for the macaws and conures in figure 4c (corresponding to the groups Ara (‘AR’) to Aratinga (‘AT’) in fig. 4a) is interesting, with the association between brain size and climatic variability in temperature stronger (r²_adj = 0.43) for the macaws (Ara, Primolius, Orthopsittaca and Cyanopsitta) and progressively weaker when the two groups of Aratinga (‘AT/ND’ and ‘AT’) and Anodorhynchus (‘AN’, along with ‘DI/GU’) are included in the analysis (r²_adj = 0.33, r²_adj = 0.20 and r²_adj = 0.11, respectively; p < 0.05 in all cases). A similar pattern is observed for the association between relative brain size and precipitation CV, respectively: F₁,97 = 12.06, p = 0.001, r²_adj = 0.10 and F₁,97 = 5.46, p = 0.022, r²_adj = 0.04), as species with a higher number of subspecies were present in a wider range of climatic regimes. However, the contrasts in subspecies number were not associated with the contrasts of relative brain size (F₁,97 = 0.35, p = 0.55, r²_adj = 0.00), nor was the association between subspecies number and brain size dependent on habitat type (F₁,94 = 0.3, p = 0.5). When subspecies number was included as an additional independent variable in the model to explain variation in brain size, the association between relative brain size and climatic variability remained strongly significant.

### Absolute Brain Size

The contrasts of relative age at fledging and incubation period were not associated with the contrasts of absolute brain size but, consistent with the pattern observed for relative brain size, absolute brain size (corrected for phylogeny) was marginally associated with the degree of seasonal variation in temperature and its interaction with habitat type (effect of seasonal variation in temperature, habitat type and the interaction between the two factors, respectively: F₁,94 = 3.2, p = 0.078; F₁,94 = 0.17, p = 0.68 and F₁,94 = 3.8, p = 0.05; r²_adj = 6.7%). Similarly, absolute brain size was associated with precipitation CV and its interaction with habitat type (effect of precipitation CV, habitat type and the interaction between the two factors, respectively: F₁,94 = 7.04, p = 0.009; F₁,94 = 0.14, p = 0.7 and F₁,94 = 6.14, p = 0.015; r²_adj = 10.3%). As before, migration did not have any significant effect on absolute brain size when added to the model. Similarly, there was no association between the contrasts of subspecies number and absolute brain size (main effect of subspecies number and of the interaction between subspecies number and habitat type on the contrasts of absolute brain size, respectively: F₁,94 = 0.68, p = 0.41 and F₁,94 = 0.07, p = 0.8).

The association between absolute brain size and climatic variability could alternatively result from a putative association between climatic variability and body size, as those larger-bodied organisms might cope better with climatic oscillations through an enhanced ability to thermoregulate. Nonetheless, there was no association between climatic variability and absolute body size (association of body size with seasonal variation in temperature and precipitation CV, respectively: F₁,94 = 0.85, p = 0.35, and F₁,94 = 2.02, p = 0.15), nor was there any interaction between these variables and habitat type (F₁,94 = 1.12, p = 0.3 and F₁,94 = 0.56, p = 0.45 for temperature and precipitation, respectively). The contrasts of absolute brain size were, however, significantly correlated with the contrasts of relative brain size (F₁,94 = 40.1, p < 0.001, r² = 28.7%), raising the possibility that the significant association between absolute brain size and climate was an artifact of the association between relative brain size and...
climatic variability. To further inspect this possibility we tested (1) whether the association between absolute brain size and the two measures of climatic variability would hold when controlling for the effects of relative brain size (i.e., whether there was any variability in absolute brain size explained by climate in addition to that already explained by relative brain size) and vice-versa, namely (2) whether the previously detected association between relative brain size and the two measures of climatic variability would hold when controlling for absolute brain size. The significant association between absolute brain size and climatic variability ceased to exist when relative brain size was controlled ($F_{1,93} = 0.88, p = 0.35$; $F_{1,93} = 1.15, p = 0.3$; $F_{1,93} = 2.1, p = 0.15$ and $F_{1,93} = 0.66, p = 0.42$, for the degree of seasonal variation in temperature and its interaction with habitat type and the coefficient of spatial variation in precipitation and its interaction with habitat type, respectively). The positive association between relative brain size and climatic variability nonetheless remained significant for precipitation CV ($F_{1,92} = 3.8, p = 0.05$ and $F_{1,92} = 6.7, p = 0.01$ for precipitation CV and its interaction with habitat type, respectively) when absolute brain size was controlled, with the model explaining $46.4\% (r^2_{adj})$ of the variance in relative brain size.

### Discussion

Our results indicate that proportionally larger-brained species are more tolerant to climatic variability, as those parrots with larger brain volumes were shown to inhabit areas subject to a higher degree of seasonal variation in temperature, and to tolerate a significantly wider range of precipitation regimes. The association between climatic variability and brain size was especially strong for those contrasts representing a transition from forested to more open terrains, in which the effect of variation in climatic regimes should have a higher and more immediate impact on ecosystem productivity and thereby resource availability. The results were consistent for the various models tested, as the same measures of climatic variability were selected in each case.

In figure 4a it is possible to observe that the contrasts predominantly responsible for the significant association between relative brain size and climatic variability are relatively recent in the group’s phylogenetic history, as they correspond mostly to those within-genera nodes in the tree characterized by an expansion into more open and climatically unstable landscapes. The expectation that the effects of climatic variability should be felt more strongly in open habitats is also confirmed by the observation of a positive and significant association between relative brain size and climatic variability for the macaws and Aratinga conures, a group predominantly formed by species that are found on drier and more open areas, savannas and grasslands. Interestingly, there is evidence that the origin of those species that are today found in open landscapes coincide with the formation of these habitats in South America [Tavares et al., 2006]. More specifically, Tavares et al. [2006] suggest that the rapid and relatively recent radiation of genera in the clade formed by the macaws, conures and allies seems to have occurred via niche-diversification, as these open dry areas were colonized from forests. In the case of the parakeets from the genus Brotogeris, for which a positive and strong association between climate and brain size was also found (fig. 4b), the largest-brained species (e.g., B. tirica) are those found a in a wide range of habitats (including open ones), whereas the smallest-brained ones (B. sanctithomae and B. chrysoptera) are those species restricted to forests.

If on the one hand our results show a significant and consistent association between brain size and both temporal and spatial climatic variability, on the other they also indicate that climatic variability is not the sole or main factor underlying current variation in residual brain size among Neotropical parrots, as variability in temperature and precipitation accounted respectively for approximately 20 and 28% of the overall variance in residual brain size. The absence of a stronger association between brain size and climatic variability might indicate that selective pressures other than climatic variability could also direct or maintain present-day differences in residual brain size. Indeed, when age at fledging was controlled the temporal and spatial models explained approximately 27 and 35% of the variance in brain size, respectively. In addition to development, other factors might be potentially associated with relatively larger brains, such as trade-offs between neural and somatic growth [Aiello and Wheeler, 1995], differences in the cognitive requirements of different diets [Clutton-Brock and Harvey, 1980] and in the cognitive demands of the social environments encountered by each species [Byrne and Whiten, 1988]. Yet, there are few examples of these theories being tested in birds, with those that exist being either negative or inconclusive [Isler and Van Schaik, 2006]. For example, although two previous studies have found no association between relative forebrain size and flock size in birds [Beauchamp and Fernandez-Juricic, 2004; Iwaniuk and Arnold, 2004], Emery et al. [2007]
have recently found that those bird species that form stable lifelong pair bonds have larger relative brain sizes. Whether social complexity is positively associated with relative brain size in parrots remains to be tested when data becomes available. Social groups could also, conversely, buffer individuals against environmental change by changing their size and composition in response to environmental variability [Jones, 2005], which in turn may counteract the effects of heterogeneity in feeding conditions per se. Yet, to our knowledge this possibility has not been examined in birds.

Responses other than those of a behavioral or cognitive nature might also have been selected under variable climatic regimes, obscuring the relationship between residual brain size and climatic variability. For example, the impact of environmental change on populations is largely influenced by the ability of individuals to flexibly adjust important life-history events [Reed et al., 2003]. In addition to being able to explore new resources when occupying a new environment, the potential of a species to successfully expand its geographic range and colonize new habitats will also be influenced by its ability to alter physiological responses to environmental cues triggering important events, such as novel photoperiodic conditions determining the initiation of the breeding season [Coppack and Pulido, 2004]. So in addition to behavioral flexibility, physiological, developmental and morphological constraints could limit the extent to which a species is able to establish its presence at new locations. Environmental variability is also thought to affect the costs of reproduction, with evidence showing that the growth and development of altricial nestlings are shaped by extrinsic environmental forces [Remes and Martin, 2002]. For example, optimal clutch sizes may be significantly changed in variable environments as compared to optimal clutch sizes in a constant environment. If individuals produce a small fixed clutch size they might be unable to explore highly favorable environments, whereas if they produce a large (and costly) clutch size they might be able to explore highly favorable conditions [Orzack and Tuljapurkar, 2001]. Variation in clutch size is, in turn, associated with growth and developmental rates, with offspring from larger clutches presenting a slower growth rate [Ricklefs, 1968]. Because slower developmental cycles are positively associated with proportionally larger brains [Bennett and Harvey, 1985a; Finlay and Darlington, 1995; Starck and Ricklefs, 1998], by affecting optimal clutch sizes environmental variability could also influence brain size as a consequence. Through its effects on food availability, hence competition for food, differences in the degree of climatic variability might also affect nest predation rates. Nest predation has been suggested as one of the most important environmental factors determining the evolution of incubation and nestling periods in birds [Moller, 2005]: in general, the offspring of populations subject to higher predation rates grow faster and leave the nest earlier [Bosque and Bosque, 1995; Martin, 1995]. Therefore, if acting as a selective pressure favoring slower or faster life cycles, predation could simultaneously favor the fixation of relatively larger or smaller brains [Deacon, 1990; Finlay et al., 2001]. That said, it would be unlikely given the high metabolic costs of the brain tissue [Aiello and Wheeler, 1995] that increases in brain size as a byproduct of other processes were maintained without providing some net benefit to individuals [Dunbar, 2001].

The association between relative brain size and climatic variability might have also been weakened by the limitations in existing data to test this hypothesis. The first relates to the measurements of brain and body size, which in some cases were obtained from a single specimen. Therefore, deviations of the specimen from the average brain or body size of the species would add noise to the relationship and decrease the overall proportion of variance explained. Secondly, there is the uncertainty regarding the phylogenetic history of the species. Although a number of recent studies have greatly advanced our knowledge of the evolutionary history of Neotropical parrots [e.g., Ribas and Miyaki, 2004; Ribas et al., 2005, 2006; Tavares et al., 2006], their phylogeny is still not entirely resolved. Additionally, existing data on the geographic distribution of these species is still incomplete, decreasing the precision with which we estimated the climatic variability to which each species was exposed. Here we conducted the most thorough and extensive review on the geographic distribution of all Neotropical parrot species to date by collating data from a diverse range of sources (supplementary material 2). We have also included data from a long period of time, the aim of which was to reduce the recent influence of human impact on the distribution of the species. Yet the effects of habitat loss, fragmentation and traffic exploitation are known to be extensive among parrots [Collar, 1991; Wright et al., 2001], and have most certainly resulted in the absence of species from areas where they were originally present. Although anthropogenic influences are unlikely to differentially affect those species with relatively larger or smaller brain sizes (largerparrot species are more prone to extinction [Munn, 1995], but we have not found any association between residual brain size and body size), they might have caused climatic variability to be overestimat-
ed for some species and underestimated for others. Moreover, a species could be absent from specific areas simply due to historical factors, to the presence of geographical barriers, competitive exclusion and a lack of ornithological surveys. Although these factors should not add any bias to the associations tested, they add noise to the data and reduce the overall correlation between relative brain size and climatic variability.

Next, there is the question that has been raised by some critics which is whether overall brain size is an appropriate or reliable measure of an organism’s cognitive capacity [Deacon, 1990; Byrne, 1996; see also Herculano-Houzel, 2006]. One of the main arguments proposes that changes to one or more brain structures cannot be detected by measuring the whole brain, and that natural selection would act on the size of these structures, rather than on overall brain size [Healy and Rowe, 2007; but see Finlay and Darlington, 1995; Garamszegi and Eens, 2004]. However, in addition to a number of studies showing strong associations between overall brain/forebrain size and the reported frequencies of innovation rate, tool use, social learning, invasion success and mortality rate in birds, there is also evidence [Rehkamper et al., 1991, 2000] that differences in whole brain size are primarily due to differences in the size of the forebrain, more specifically the size of the nidopallium and mesopallium, the areas most strongly associated with the social and ecological variables examined in our study.

We found evidence that both absolute and relative brain size were positively associated with the degree of environmental variability experienced by each species. However, the association of climatic variability was much stronger with relative than with absolute brain size, and remained significant even after eliminating the effects of absolute brain size in the analysis (in fact, when absolute brain size was controlled the climatic model explained approximately 44% of the variance in relative brain size). In other words, those species with relatively larger brains were found to be more tolerant to climatic variability independent of the absolute size of their brains. Still, the fact that climatic variability did not explain variation in absolute brain size in addition to that already explained by relative brain size does not necessarily rule out the potential role of absolute brain size as a proxy for cognition in this group. In fact, reports of tool use in parrots (an ability supposedly requiring advanced cognitive processing) are restricted to those species with the largest absolute brain sizes in the group: the Hyacinth and Lear’s macaws [Borsari and Ottoni, 2004; Borsari, personal observation] and the black palm cockatoo [Wallace, 2000]. The brain sizes of species well known for their cognitive ability, such as Keas and African Grey parrots, are also within the largest 15% in the family. Nevertheless, because studies on cognition are limited to an extremely limited number of species, it is still not possible to further examine the putative role of absolute brain size as a potential substrate for cognitive evolution. Of course, having found an association between climatic variability and brain size does not necessarily imply that brain and forebrain size correlate with behavioral flexibility or cognitive ability per se. For example, because the correlations involve multimodal integrative areas such as the forebrain, the production of complex behaviors might also result from the presence of complex motor and sensory skills [as opposed to only advanced cognitive skills; Healy and Rowe, 2007] that could enable the exploration of a wider range of resources. The consistent and significant association does suggest, however, that relatively larger brains provide an advantage in climatically variable environments.

Another aspect of our results deserves further attention and relates to our observation that the migratory status of the species neither affected the association between residual brain size and climatic variability, nor were resident species larger-brained or more likely to tolerate higher degrees of climatic variability. On the one hand, the lack of association could be taken as evidence against the hypothesis that larger brains are primarily tied to the ability to survive under variable conditions. If environmental variability is cognitively demanding and cognitive capacity is positively associated with brain size, the association between climatic variability and brain size should be stronger for resident species that endure environmental changes without leaving their habitats. An association between brain size and residency would be also expected on the basis of the energetic constraints imposed by migration, as migrant species should also possess relatively smaller brains due to the energetic demands imposed by long distance flights. Alternatively, however, migration might also favor enlarged brains given the cognitive demands of spatial orientation [Healy and Rowe, 2007], as well as the need to process information regarding the distribution of resources in other areas. More importantly perhaps, residency seems to be favored in habitats that are more stable or where variation in food availability is more predictable, occurring in annual or sub-annual cycles [Mettke Hofmann et al., 2004]. Given the existence of such opposing pressures, average residual brain size might not differ between residents and migrants. Still, very little is known about most New World parrot species, so we feel that the current classification of
the migratory status of these parrots still lacks precision, making the detection of any relationship more difficult.

In conclusion, we have found a consistent and significant positive association between relative brain size and climatic variability, both on a temporal and spatial scale. Additionally, our study suggests that the differences in relative brain size among the species of the group represent multiple events which are relatively recent in the evolutionary history of the group, and particularly tied to an increased dependence on more open and unstable habitats. These findings also add to a growing number of studies suggesting a close link between brain size and the ability to plastically adjust to novel situations. Still, it is clear that there are other, unmeasured forces that also drive the dynamics of brain size variation in this group. Here we have argued that the unexplained proportion of the variance in brain size might have derived from limitations in the existing data to test this hypothesis, together with the presence of other selective pressures and developmental constraints which, if not accounted for, could reduce the strength of its association with climatic variability. It is also important to highlight that our analyses do not address the origin of variation in brain size among Neotropical parrots. As in any comparative study using current data to provide insight into possible selective forces acting upon a trait, the underlying assumption is that the trait analyzed would be maintained at an optimum by present-day selective pressures to serve its current function [Reeve and Sherman, 1993; Hansen, 1997]. Current selection need not reflect the selective pressures during the trait’s evolution [Gould and Vrba, 1982], so the observed association between climatic variability and brain size does not unequivocally support the past role of climate on parrot brain evolution. However, by being the first study to show evidence of the link between brain size and climatic variability, along with the coinciding increase in brain size and the occupation of more open landscapes, our results provide a step forward towards understanding the potential benefits underlying variation in brain size and the maintenance of highly enlarged brains in this and other evolutionarily distant groups.

Acknowledgements

We are grateful to Andrew Iwaniuk and two anonymous reviewers for very helpful comments on a previous version of the manuscript and to Renato Gaban-Lima, Elizabeth Hofling, Herculano Alvarenga, James Dean and O. Olson for allowing us access to their osteological collections and for logistical support. Andrew Iwaniuk, Alex Weir and Radha Nair were very kind with tips and guidance on how to measure cranial volume. We would also like to thank the following curators and collection managers for sending us data on their bird collections, from which we extracted many of the locality records used to determine the geographic distribution of Neotropical parrots: N. Rice (Academy of Natural Sciences), W. Boles (Australian Museum), T. Chesser (Berkeley Museum of Vertebrate Zoology), D.J. Long (California Academy of Sciences), R. Symonds (University Museum of Zoology, Cambridge), M. Gosselin (Canadian Museum of Nature), S.P. Rogers (Carnegie Museum of Natural History), K. Bostwick (Cornell University Museum of Vertebrates), J. Woods (Delaware Museum of Natural History), T. Webber (Florida Museum of Natural History), A. Echevarría (Instituto Miguel Lillo), E. Redding (Moore Laboratory of Zoology), C. Darrieu (Museum d’Histoire Naturelle de la Ville de Genève), R. Bruckert (Muséum National d’Histoire Naturelle), J. Hinshaw (Museum of Zoology of Michigan University), M. Robbins (Natural History Museum of Kansas University), M. Guntert (Natural History Museum Bern), S. Phibbs (Oxford Museum of Natural History), G. Schnell and A.C. Person (Sam Noble Oklahoma Museum), O. Olson, J. Dean and C. Ludwig (Smithsonian Museum of Natural History), M. Burger (Transvaal Museum), R. Corado (Western Foundation of Vertebrate Zoology). Financial support was received from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) and FAPESP (Fundação de Amparo a Pesquisa do Estado de São Paulo).

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