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ABRAÃO DE BARROS LEITE

PADRÕES MACROEVOLUTIVOS DO TAMANHO DO
CÉREBRO E TIPOS DE NINHOS EM PASSERIFORMES

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ABRAÃO DE BARROS LEITE

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TIPOS DE NINHOS EM PASSERIFORMES**

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais do Centro de Ciências Biológicas e da Saúde, Universidade Federal de São Carlos/SP, como parte dos requisitos necessários para obtenção do título de mestre em Ecologia e Recursos Naturais, Área de concentração: Ecologia e Recursos Naturais.

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“Há uma tendência na natureza à progressão contínua de certos tipos de variedades que estão cada vez mais se afastando da classe original”

Alfred Russel Wallace

RESUMO

Aves e mamíferos aumentaram a capacidade cognitiva e forças seletivas que favorecem habilidades comportamentais complexas são consideradas importantes impulsionadores da evolução cerebral. Uma maneira tratável de inferir sobre as vias evolutivas moldando a complexidade cerebral é comparar tamanhos cerebrais entre grupos de organismos com diferentes características comportamentais e ecológicas. A construção de ninhos fechados é uma das mais notáveis habilidades das aves, mas sua relação com o tamanho do cérebro permanece inexplorada. Aqui usamos dados de 538 aves para testar se as espécies que constroem ninhos fechados têm cérebros maiores em comparação com aquelas que constroem ninhos abertos. Buscamos relações que controlam os efeitos do tamanho do corpo e outros fatores já conhecidos por afetar o tamanho do cérebro. Através de uma abordagem Bayesiana com controle filogenético, revelamos que cérebros desproporcionalmente aumentados não estão relacionados com a construção de ninhos fechados, contrariando assim o pensamento atual de que a arquitetura de ninhos fechados é mais complexa em relação a ninhos abertos. Sendo que esta falta de significância sugere a existência de variações quanto a complexidade tanto em ninhos fechados quanto ninhos abertos, além de efeitos da alometria negativa que ocorreram ao longo da evolução de passeriformes. Devido a distribuição desigual de ninhos fechados e abertos dentro dos clados, houve um alto efeito filogenético e assim reduzindo a significância do parâmetro tipo de ninho nos modelos Bayesianos. Apesar de nossos resultados não mostrarem um efeito do tipo de ninho, a ideia de que, em média, ninhos fechados podem estar associados a cérebros maiores não deve ser prontamente descartada, não excluindo assim a necessidade de investigações adicionais envolvendo um número maior de clados com informações completas do tamanho do cérebro. Assim, uma vez que uma quantidade tratável de dados do tamanho do cérebro se tornar disponível, as análises devem se concentrar, por exemplo, em famílias específicas que apresentem o maior número possível de transições independentes do tipo ninho.

Palavras-chave: Aves, Arquitetura de ninhos, Análise Bayesiana, Controle filogenético.

ABSTRACT

Birds and mammals have increased cognitive abilities and selective forces favoring complex behavioral skills are considered important drivers of brain evolution. A tractable way to infer about evolutionary pathways shaping brain complexity is to compare brain sizes between groups of organisms with different behavioral and ecological characteristics. The construction of closed nests is one of the most remarkable abilities of birds, but its relationships with brain size remains unexplored. Here we use data from 538 bird species to test whether species that build closed nests have larger brains compared to those that build open nests. We also controlled to the effects of body size and migration, both known to affect brain size. Through a Bayesian approach with phylogenetic control, we reveal that the construction of closed nests is not correlated to disproportionally enlarged brains, thus contradicting the current thought that the architecture of closed nests is more complex in relation to open nests. This lack of significance suggests the existence of variations in the complexity of both closed nests and open nests, in addition to the effects of negative allometry that occurred throughout the evolution of the passerines. Although our results do not show a nest type effect, the idea that, on average, closed nests may be associated with larger brains may not be readily ruled out. Thus, once a treatable amount of brain size data becomes available, analyses should focus, for example, on specific families that have as many nest-independent transitions as possible.

Keywords: Birds, Nest Architecture, Bayesians Analysis, Phylogenetic Control.

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BPMs- Bayesian Phylogenetic Mixed Models

CIs- credibility intervals

IC- Confidence Intervals

GLMs-Generalized Linear Models

MCMC- Markov Chain Mont Carlo

MCMCGLMM- Markov Chain Mont Carlo Generalized Linear Mixed Models

Rbmass- Relative brain mass

SE- Standard Errors

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1 INTRODUÇÃO GERAL

As aves pertencem a um ramo evolutivo que obteve grande sucesso, tendo conquistado todos os continentes e os mais variados habitats terrestres (POUGH et al., 2008). Estima-se que existam em torno de 11.000 espécies, sendo a Ordem Passeriformes a de maior número, com um total de 137 famílias e mais de 6.000 espécies (OLIVEROS et al., 2019). Nos diferentes habitats, as comunidades de aves exercem importantes papéis ecológicos, como a dispersão de sementes, polinização, predação e a necrofagia, contribuindo assim com o contínuo funcionamento dos processos ecossistêmicos que mantêm a integridade dos biomas (MENDONÇA; ANJOS, 2003; FRANCISCO et al., 2007; HELENO et al., 2011; GALETTI et al., 2013)

1.1 Capacidade cerebral das aves

A ampla irradiação destes organismos, bem como as diversificações de seus modos de vida, exigiu das aves uma ampla capacidade cerebral, que ao longo da evolução resultou em um complexo desenvolvimento neuronal e habilidades cognitivas que podem ser comparadas até mesmo com aquelas dos mamíferos. Como mostrado por uma extensa revisão feita por Emery (2006), que mostrou a superioridade da inteligência de algumas aves como os corvídeos e papagaios pode se comparar até mesmo a algumas espécies de primatas. Além disso, Olkowicz et al. (2016), usando modernas técnicas laboratoriais, mostrou que a densidade neuronal em certas aves pode ser maior do que em alguns mamíferos.

Devido a este importante fato evolutivo, nas últimas décadas iniciou-se um grande aumento no interesse por parte dos ornitólogos em entender a dinâmica dos fatores ecológicos e biológicos que possam ter contribuído para a evolução desta alta capacidade cognitiva das aves. Considerando-se a escassez de informações sobre as diferentes partes do cérebro para a maioria das espécies, e considerando-se também que o tamanho cerebral frequentemente pode ser correlacionado com o desempenho de comportamentos complexos, os estudos se concentraram na busca por comportamentos que pudessem estar correlacionados com o tamanho cerebral (OVERINGTON et al., 2009; SOL, 2009; NOMURA; IZAWA, 2017). Estes comportamentos poderiam oferecer pistas sobre os tipos de pressões seletivas que teriam levado ao aumento da

capacidade cognitiva das aves, bem como sobre a origem dos diferentes padrões de tamanho cerebral. Atualmente, diversos fatores correlacionados com o tamanho cerebral já foram apontados, enquanto alguns outros potenciais fatores ainda necessitam ser melhor explorados.

1.2 Tamanho cerebral e o efeito alométrico

Já nos primeiros trabalhos foi notado que o efeito alométrico era bastante forte neste grupo de organismos. Mlikovsky (1989a, 1990) analisou 4344 cérebros de 766 espécies de aves pertencentes a 116 famílias e através de um cálculo de regressão entre massa corporal *versus* massa cerebral, mostrou que havia uma forte relação entre estas características. Ainda nesta linha de abordagem, buscando entender as relações alométricas entre tamanho corporal e tamanho cerebral, Franklin et al. (2014), analisou 504 espécies de aves australianas e evidenciou a importância de se considerar o efeito alométrico em estudos que buscam correlacionar caracteres comportamentais com características cerebrais.

Porém, Ksepka et al. (2020) mostraram fortes evidências de que ao longo da radiação das Neoaves, também houve alometria negativa, ou seja, em alguns grupos de aves que sofreram pressão de seleção para miniaturização, a redução do tamanho do corpo foi mais rápida do que diminuição do tamanho cerebral, o que levou a algumas linhagens de aves pequenas a apresentarem cérebros proporcionalmente maiores. Com isto ficou evidenciado a importância de se considerar além do efeito alométrico positivo, também o efeito alométrico negativo nas conclusões dos estudos que buscam entender o efeito dos fatores ecológicos e biológicos na história evolutiva das características cerebrais relativas em aves.

As observações destas correlações foram importantes porque evidenciaram a necessidade do controle do efeito alométrico em todas as modelagens estatísticas que buscam correlacionar características ecológicas ou comportamentais com o tamanho cerebral. Nos trabalhos que utilizam o tamanho cerebral como variável resposta, duas maneiras de controle têm sido utilizadas (SOL et al., 2007): i) o uso dos resíduos do tamanho cerebral obtidos de uma regressão linear entre as métricas do corpo e do cérebro logaritmizados (R_{bmass}), ou II) o uso do valor logaritmizado das medidas cerebrais como variável resposta e a inclusão dos tamanhos corporais logaritmizados entre as variáveis preditoras. É importante ressaltar também que as medidas mais comumente utilizadas para representar os tamanhos cerebrais e corporais são a massa

(SHULTZ; DUNBAR, 2010; SAYOL et al., 2016; VINCZE et al., 2015; MINIAS; PODLASZCZUK, 2017)

1.3 Características cerebrais e ecologia comportamental

A busca pelo entendimento dos comportamentos das aves que estão mais relacionados com o tamanho relativo do cérebro, tem levado os pesquisadores a testarem diferentes aspectos comportamentais das aves como; comportamento alimentar, reprodutivo e migratório (IWANIUK; NELSON, 2001; IWANIUK; ARNOLD, 2004; SOL et al., 2010).

Como exemplo, Garamszegi et al. (2002), analisou a co-evolução entre tamanho cerebral e tamanho dos olhos e a influência destas variáveis no sucesso de captura de presas por aves noturnas. Os resultados sugeriram uma forte relação co-evolutiva entre o tamanho relativo do olho e o tamanho relativo do cérebro, primariamente em resposta a atividade noturna e depois ao comportamento de captura de presas móveis por estes animais.

Em um contexto de comportamento reprodutivo Iwaniuk e Nelson (2003), com uma amostra 1400 espécies de aves, encontrou uma relação significativa entre tamanho cerebral e as seguintes variáveis: tempo de incubação, idade de saída dos filhotes do ninho, duração do cuidado parental após a saída do ninho, e período total de cuidado parental. No entanto, não houve nenhuma relação significativa entre tamanho cerebral relativo e a idade do primeiro voo. Concluiu, portanto, que as diferenças nos padrões de desenvolvimento dos filhotes das aves estão fortemente correlacionadas com os tamanhos dos cérebros.

Shultz e Dunbar (2010), usando 135 espécies de aves, fizeram uma abordagem comparativa entre a ocorrência de *pair-bonding*, ou seja, o grau de fidelidade do casal após o acasalamento *versus* o tamanho cerebral, tendo como covariáveis, tipo de dieta, migração, tipo de desenvolvimento do filhote, forrageio, presença ou ausência de cuidado bi-parental e sistema de acasalamento. Os resultados foram significativos apenas para as variáveis migração e cuidado parental, e não significativo para os demais parâmetros. Com isto, concluíram que há uma relação entre a ocorrência de um maior investimento no cuidado parental através do *pair-bonding* e o aumento cerebral.

Em um interessante levantamento da literatura a respeito do uso de ferramentas por aves, Lefebvre et al. (2002), mostrou que as aves são frequentes usuários de

ferramentas, permitindo a estes animais uma exploração dos recursos alimentares de maneira mais eficiente. Mostrou também que este comportamento complexo evoluiu juntamente com o aumento cerebral em várias ordens de aves, como por exemplo, nos Passeriformes. Esta tendência foi corroborada por Cnotka et al. (2008), ao estudar *Corvus moneduloides*, uma espécie de corvídeo que usa frequentemente ferramentas a fim de explorar os recursos alimentares. Os autores encontraram um alto nível de encefalização nesta espécie em relação *Corvus c. corone*, *Pica pica*, *Garrulus glandarius* e *Passer domesticus*, que usam menos as ferramentas. Concluíram, portanto, que por *C. moneduloides* desenvolver estas habilidades complexas, foi necessário ter porções cerebrais aumentadas referentes ao *mesopallium* e *nidopallium*, levando assim a uma maior massa cerebral total.

Além disso, Iwaniuk e Hurd (2005), ao analisarem 104 espécies de aves definiram cinco tipos de cérebros baseando-se em métricas de alguns componentes cerebrais como o nidopálio, o mesopálio, o complexo estriatopalidal, o telencéfalo, o cerebelo e o diencéfalo, e mostraram que variações nos tamanhos destes componentes cerebrais estavam correlacionadas com o modo de vida das espécies, ou seja, se são caçadoras, se são presas, ou se são solitárias ou sociais. Com isto, ficou claro que a relação entre comportamento e medidas cerebrais relativas é bastante variável nas aves, podendo depender de múltiplos aspectos comportamentais, assim como tem se mostrado também em mamíferos (ALLMAN; CLAUGHLIN; HAKEEM,1993; BURISH; KUEH; WANG,2004; DUNBAR; SHULTZ, 2007; PÉREZ-BARBERÍA; SHULTZ; DUNBAR, 2007; ASHWELL; SCOFIELD, 2008; BENSON-AMRAM, et al.,2016;MARUGÁN-LOBÓN;WATANABE;KAWABE,2016;MINIAS;PODLASZCZUK,2017; NOMURA; IZAWA,2017).

1.4 Capacidade de inovação e exploração dos recursos

A capacidade de inovação das aves quando estão em situações desafiadoras para sua sobrevivência, também tem se tornado um importante parâmetro considerado nos estudos ornitológicos que buscam entender as relações evolutivas entre as características cerebrais.

Sol et al. (2005), trabalhando com 134 espécies de aves da região Paleártica, buscou entender o efeito do cérebro no comportamento migratório das espécies, tendo concluído que espécies residentes têm cérebro maior, possivelmente porque necessitam

de uma maior capacidade de inovação para a sobrevivência durante o inverno quando ocorreu uma maior escassez de recursos.

Também Sol et al. (2007), a fim de testar a hipótese de que uma melhor capacidade de sobrevivência das aves frente a estresses ambientais é facilitada pela flexibilização da resposta cognitiva, analisou a massa cerebral relativa de 236 espécies de aves e mostrou que espécies com maior massa cerebral simplesmente tiveram uma menor taxa de mortalidade em relação aquelas com uma menor massa cerebral relativa.

Overington et al. (2009), ao classificar 2182 técnicas de inovação realizadas por 76 famílias de aves, também corroborou a hipótese levantada anteriormente por Sol et al. (2007), concluindo que a capacidade de inovação está intimamente relacionada com o aumento do tamanho cerebral relativo nas aves.

Trabalhos mais recentes continuam testando relações cerebrais e corporais em aves através de abordagens laboratoriais e de ferramentas estatísticas mais modernas (SAYOL et al., 2016), como técnicas de escaneamentos 3-D do telencéfalo de aves (FUCHS et al., 2014), ou ainda com estatísticas como análise Bayesiana com abordagem de Cadeia de Markov em Modelos Mistos (MCMCGlmm) (SAYOL; SOL; PIGOT, 2020) ou através de Modelos dos Mínimos Quadrados Generalizados com controle filogenético (Pgl) (VINCZE, 2016), onde o efeito da filogenia pode ser controlado. Desta forma, através destas abordagens inovadoras, pode-se aplicar inferências mais confiáveis a respeito da co-evolução entre características cerebrais relativas, *versus* a capacidade cognitivas das aves em explorar os recursos ou ainda quando exercem comportamentos sociais como reprodução, forrageio e migração (NOMURA; IZAWA, 2017; KSEPKA et al., 2020; SAYOL et al., 2020).

1.5 Complexidade dos ninhos e capacidade cerebral

Embora mesmo com todo este arcabouço teórico de importantes correlações, principalmente entre aspectos ecológicos e tamanho cerebral, as relações da complexidade dos ninhos com o desenvolvimento neuronal ainda é algo pouco explorado. Os ninhos para as aves assim como em anfíbios e répteis, têm uma importante função, que seria de garantir proteção para os ovos e filhotes contra predadores e fatores climáticos (MEHLMAN; DORAN, 2002; ANGILLETTA; SEARS; PRINGLE, 2009).

Mainwinring et al. (2014), em uma completa revisão das características dos ninhos de aves, conclui que os mesmos são estruturas multifuncionais, que variam grandemente quanto a sua localização e formato. Além de que, muitas vezes o ninho pode ter a função de seleção sexual, pois em espécies em que os ninhos são construídos pelos machos, durante a busca por parceiros, as fêmeas verificam a qualidade dos ninhos.

Com isso, a construção e arquitetura dos ninhos foram importantes para a irradiação das aves, havendo os mais variados tipos de ninhos entre as espécies, desde aqueles onde os indivíduos utilizam apenas gravetos para a construção de plataformas rudimentares, até aquelas mais elaborados, principalmente quando se trata de ninhos fechados (SICK, 1992; SICK, 2007; PRICE; GRIFFITH, 2017).

Os ninhos das aves estão entre as estruturas mais complexas da natureza e de uma maneira geral, as habilidades necessárias para se construir o ninho são herdadas geneticamente (COLLIAS, 1964; COLLIAS, 1997; FANG; TUANMU; HUNG, 2018) e envolvem várias etapas, como a escolha do local, a escolha do material apropriado e a habilidade para tecer o material, sendo uma das atividades que mais utiliza a capacidade cognitiva (COLLIAS 1964; COLLIAS 1997)

Até o momento, Hall et al. (2013), foi o primeiro e único que buscou entender a capacidade cognitiva das aves no contexto de construção de ninho. Foram utilizadas informações a respeito dos níveis de foliação cerebelar de 64 espécies (17 ordens) que não construíam ninhos, espécies que construíam plataformas rudimentares, e aquelas espécies que construíam ninhos em forma de taças. Por fim, os autores concluíram que há uma relação positiva entre o número de foliações e a complexidade dos ninhos.

1.6 Justificativa

Diante do referencial teórico apresentado acima e considerando-se o fato de que a construção de ninhos exige habilidades complexas, podendo estas serem resultantes de altas capacidades cognitivas (COLLIAS, 1997; HANSELL, 2000; HALL; STREET; HEALY, 2013; FANG; TUANMU; HUNG, 2018) buscamos entender se espécies que constroem ninhos fechados, teoricamente mais complexos do que ninhos abertos (COLLIAS, 1997; HANSELL, 2000), teriam tamanhos cerebrais relativos maiores.

Para isto foram realizadas modelagens com abordagem Bayesiana com o intuito de controlar o efeito filogenético como fator aleatório (MCMCGLMM). Foi utilizado

um amplo volume de dados já disponível na literatura e outros fatores que têm efeito determinante para o tamanho cerebral também foram controlados, como a massa corporal e a capacidade migratória. Ao testar esta correlação, espera-se contribuir com a literatura atual de trabalhos em ecologia reprodutiva de aves, e acrescentar conhecimento científico na relação entre capacidade cognitiva das aves e seus comportamentos reprodutivos no contexto de construção de ninho.

2 OBJETIVOS

Diante disto, o objetivo deste trabalho foi testar se a construção de ninhos fechados em Passeriformes é um comportamento correlacionado com tamanhos cerebrais maiores em relação à construção de ninhos abertos em forma de taça, utilizando para isto uma amostragem de 538 espécies de aves.

3 CAPÍTULO 1

Do passerine birds constructing enclosed nests
have bigger brains?

3.1 ABSTRACT

Selective forces favoring complex behavioral skills are thought to be important drivers of brain size. The construction of enclosed nests is one of the most remarkable bird skills, but its relationship with brain size remains unexplored. Here we used data from 538 passerine birds to test whether species constructing enclosed nests have larger brains compared to those constructing open nests, controlled to other important variables known to affect birds' brain sizes. Although a significant correlation between nest type and brain size was obtained with traditional generalized linear modeling approaches (GLMs), this difference disappeared with the use a Markov Chain Monte Carlo Bayesian Procedure that included phylogeny as a random effect term. It suggested that nest types and brain size evolution is not independent from phylogeny, and that passerine species can construct enclosed nests independently of their relative brain sizes. Potential explanations are: enclosed nests are not more complex and their constructions are not more cognitively demanding than open nests; small passerine birds have enlarged brains, independently of nest type, due to the effect of the negative allometry, or the parts of the brain involved in nest construction can experience increases in complexity that do not impact brain size. We reveal that disproportionately enlarged brains are not a prerequisite for enclosed nest construction by passerine birds, but our study do not precludes the need for further investigations. Our analyses involved about 8% of the passerine species and as a tractable amount of brain size data becomes available, analyses should focus, for instance, on specific families presenting as many independent nest type transitions as possible.

Keywords: Birds, Nest Architecture, Bayesians Analysis, Phylogenetic Control.

3.2 INTRODUCTION

Selective pressures favoring complex behavioral skills are thought to contribute to the evolution of organisms with increased cognitive capacity (DUNBAR; SHULTZ, 2007; SHULTZ; DUNBAR, 2007; PÉREZ-BARBERÍA; VINCZE et al., 2015; BENSON-AMRAM et al., 2016) As the evolution of such cognitively-demanding abilities is often accompanied by augments in parts of the brain (NOMURA; IZAWA, 2017), comparing relative brain sizes between groups of organisms with different behavioral and ecological characteristics has been an important way to infer about the potential evolutionary forces that have molded the brains of the different taxa

(IWANIUK; NELSON, 2001; EMERY, 2006; PÉREZ-BARBERÍA; SHULTZ; DUNBAR, 2007).

In birds, understanding the causes of brain size variations is important for both evolutionary and conservation purposes, as it is correlated to many life history traits (NOMURA; IZAWA, 2017; SAYOL; SOL; PIGOT, 2020), and it affects the way the different species respond to environmental disturbances (SHULTZ et al., 2005; SOL et al., 2007; OVERINGTON et al., 2009; MAKLAKOV et al., 2011). It was evidenced for instance, that species with larger brains were more prone to thrive in new habitats, including farmlands (SHULTZ et al., 2005; SOL; LEFEBVRE; RODRÍGUEZ-TEIJEIRO, 2005), and urban environments (MAKLAKOV et al., 2011; SAYOL; SOL; PIGOT, 2020); were more capable to occupy habitats with higher seasonality and fluctuations in resource availability (SAYOL et al., 2016), and showed higher adult survival rates in nature (SOL et al., 2007). All these findings provide support to the "cognitive buffer hypothesis" which predicts that large brains are more capable to store and to process information, facilitating the responses to new situations, which in turn increases survival and longevity (SOL et al., 2007; MINIAS; PODLASZCZUK, 2017). While these studies revealed the posterior adaptability of species that already had disproportionally larger brains to a changing world, a number of works have addressed the associations between brain sizes and variations in cognitively-demanding abilities and life history traits that were present along the evolutionary trajectories of the taxa. Although correlation do not represent the causal relationships, these works provided insights about the potential selective forces that molded avian brains (SOL; LEFEBVRE; RODRÍGUEZ-TEIJEIRO, 2005; SHULTZ; DUNBAR, 2010; NOMURA; IZAWA, 2017).

Studies using phylogenetic reconstructions and path analyses evidenced that bird species with bi-parental care, long-term pair bonding, and stable relationships tended to exhibit larger brains, which was attributed to the need of negotiation and coordinate cooperation between partners (SHULTZ; DUNBAR, 2010). Levels of complexity of the arenas constructed by the bower birds were also associated to brain size in the bowerbirds (DAY et al., 2005), while levels of cooperative breeding among crow species (IWANIUK; ARNOLD, 2004), and diet in a large range of species were not correlated to brain sizes (GARAMSZEGI; MØLLER; ERRITZØE, 2002; IWANIUK; ARNOLD, 2004; DAY; WESTCOTT; OLSTER, 2005; CNOTKA et al., 2008; OVERINGTON et al., 2009; SOL, 2009; NOMURA; IZAWA, 2017; SAYOL; SOL; PIGOT, 2020). Migration, on the other hand, was demonstrated to constrain brain size,

likely because of the energetic costs of the movements among others. (SOL et al., 2010) but alternatively, large-brained species could become resident because they have higher capacity to innovate in foraging abilities during the winter (SOL et al., 2005). However, addressing the relationships between birds' behavioral and ecological aspects with relative brain sizes is not straightforward because of the strong allometric effect, not only because much of the brain size variation is explained by body size (JERISON, 1985; MILOKVICK, 1989a, 1990; FRANKLIN et al., 2014; KSEPKA et al., 2020), but also because body size is a labile character and in some bird lineages body size changes can outpace changes in brain sizes (negative allometry) (KSEPKA et al., 2020).

One of the most remarkable and likely cognitively demanding bird abilities is nest construction (COLLIAS, 1997; HANSELL, 2000), yet its relationship with brain size is not fully comprehended. Nest construction is supposed to be correlated to brain characteristics because: i) this behavior is present in all avian families, ii) nests are highly variable in levels of complexity, iii) the construction of certain types of nests seem to demand high cognitive capability (FANG; TUANMU; HUNG, 2018), and iv) nest construction has important adaptive components, as nest loss is the main cause of bird mortality and nests can provide not only support to the eggs and young, but also protection against predators and thermal insulation (MARTIN et al., 2016). Hall et al. (2013) found that levels of cerebellar foliation from 64 species belonging to 17 different Orders was higher in birds constructing cup nests than in birds that do not construct nests or construct simple platform nests. Differently from open nests, that are open above, enclosed nests have a roof and a limited entrance (COLLIAS, 1997; HANSELL, 2000; PRICE; GRIFFITH, 2017). They are not only bigger, because they have to accommodate the whole body of the incubating individual, but theoretically they demand more complex woven skills (COLLIAS, 1997; HANSELL, 2000; PRICE; GRIFFITH, 2017). Enclosed nests are present in about half of the passerine families and have emerged independently several times, which demonstrates its importance (MARTIN et al., 2016).

Here we expand the investigations on the relationships between nest type and birds' brain sizes by addressing enclosed versus open nests, controlled to body size and migration. We restricted our work to the Passeriformes because this is the Order in which the vast majority of closed-nester species is concentrated (MARTIN et al., 2016, FANG; TUANMU; HUNG, 2018). Our work is based on the assumption that enclosed

nests are more complex and require higher cognitive abilities than open nests to be constructed, which might be associated with relatively bigger brains.

3.3 MATERIAL AND METHODS

3.3.1 Brain size data

Brain size has been often expressed by endocranial volume or brain mass. For details on the laboratorial procedures by which these estimates are obtained, see, for instance, (IWANIUK; NELSON, 2003). Endocranial volumes can be transformed into brain masses by multiplying them by the density of the brain tissue (1.036 g/ml) (KRETSCHMANN; WINGERT, 1969; IWANIUK; NELSON, 2001). This is a reliable procedure as these two types of measures are highly correlated within the Passeriformes (IWANIUK; NELSON, 2002). Here we used either direct or transformed average brain mass data from 538 passerine species worldwide (see electronic supplementary material for complete excel file), obtained from the literature (MLIKOVSKY, 1990; SOL et al., 2007; MAKLAKOV et al., 2011; FRANKLIN et al., 2014; SAYOL et al., 2016). When the same species was present in more than one reference the values were averaged.

While using whole brain size for comparative studies have been criticized (HEALY; ROWE, 2007) a number of evidences indicate that it is still a reliable parameter. When specific brain regions become larger, the whole brain size should become larger too (FRANKLIN et al., 2014). Besides, sizes of specific brain areas are available for only a few species (HALL; STREET; HEALY, 2013; SAYOL; SOL; PIGOT, 2020). The brain area though to affect complex motor and manipulative abilities in birds is the cerebellum, and levels of cerebellar surface foliations were previously correlated to nest type complexity. Even for this organ, increases in foliations were correlated to the volume of the entire *cerebellum* (HALL; STREET; HEALY, 2013), which is an indicative that it should also affect the whole brain size. According to this reasoning, several studies after (HEALY; ROWE, 2007) have used brain size and it was correlated to cognitive abilities (SOL; LEFEBVRE; RODRÍGUEZ-TEIJEIRO, 2005; SOL et al., 2007; SAYOL et al., 2016; NOMURA; IZAWA, 2017; SAYOL; SOL; PIGOT, 2020). Thus, while our study will not detect which brain area will grow larger, it will indicate lineages to look in order to find the brain regions related to the ability to build enclosed nests.

3.3.2 Body size and migration information

Body mass information was also obtained from the same references we used to extract brain size data, and again, when a species was present in more than one reference, average value was used of this variable. Because migration was evidenced to constrain brain size (SOL; LEFEBVRE; RODRÍGUEZ-TEIJEIRO, 2005; SOL et al., 2010) we performed tests for all species together using migration (yes/no) as a covariate, and also for migratory and non-migratory species separately, with local movements not considered as migration. All data migratory status was obtained from the Handbook of the Birds of the World online (DEL HOYO et al., 2016).

3.3.3 Nest type classifications

We characterized nest type considering only two broad categories (open and enclosed nests) that could be easily differentiated in their levels of complexity. Open nests are those without a roof-like structure, and for passerines, they are predominantly cup-shaped nests. Although the Jays (Corvidae) construct robust nest basis of sticks, resembling many platform nests, they actually have deep cup-shaped incubatory chambers made of finer materials, being more complex than the simple platform nests constructed, for instance, by some non-passerines birds, i.e. egrets, doves, and many marine birds. Then, further subdivisions such as the ‘no nests’ and ‘platform nests’ categories adopted in the multi-Orders study of (HALL; STREET; HEALY, 2013) were not used here. We considered as enclosed nests the globular structures constructed by the parental individuals, with a limited, often lateral entrance (COLLIAS, 1997; MARTIN et al., 2016). Excavators, or species nesting in pre-existent cavities (hole-nesters) were not considered because they were too few to form a category (see also MEDINA, 2019), but those constructing nests in sites protected by overhead cover, such as cliff faces, under rocks, and depressions on banks were maintained. Species constructing nests more often in branches, and rarely in three roles were kept (*Lamprotornis superbus*, *Melanodryas cucullata*, *M. vittata*, *Petroica multicolor*, *Machetornis rixosa*), but those constructing nests more often in cavities and facultatively on trees were eliminated (i.e. *Myiodinastes maculatus* and *Gnorimopsar chopi*). Domed nests, characterized by the presence of a roof but with a less restricted entrance, were considered as enclosed nests, but only partially domed nests, showing an intermediate pattern between open and enclosed, were eliminated (*Phylloscopus sibilatrix* and *Megalurus gramineus*). Two species that could construct both types of nests (open or enclosed) were also eliminated (*Cisticola exilis* and *Rhinomyias gularis*). Pouch nests, hung by its rims were considered as open nests, but

for four species constructing deep pensile pouches, with a remarkably restrict top entrance, nests were considered as enclosed (*Smicromnis brevirostris*, *Icterus galbula*, *Epinecrophylla fulviventris*, *Cercomacra tyrannina*). We also eliminated the bower birds from our analyses, species for which males construct elaborated structures to attract females, which, however, do not serve as nests (*Chlamydera maculata*, *C. nuchalis*, *Prionodura newtoniana*, *Amblyornis macgregoriae*). Information on nest type for each species was obtained from the Handbook of the Birds of the World Alive and therein references (DEL HOYO et al., 2016).

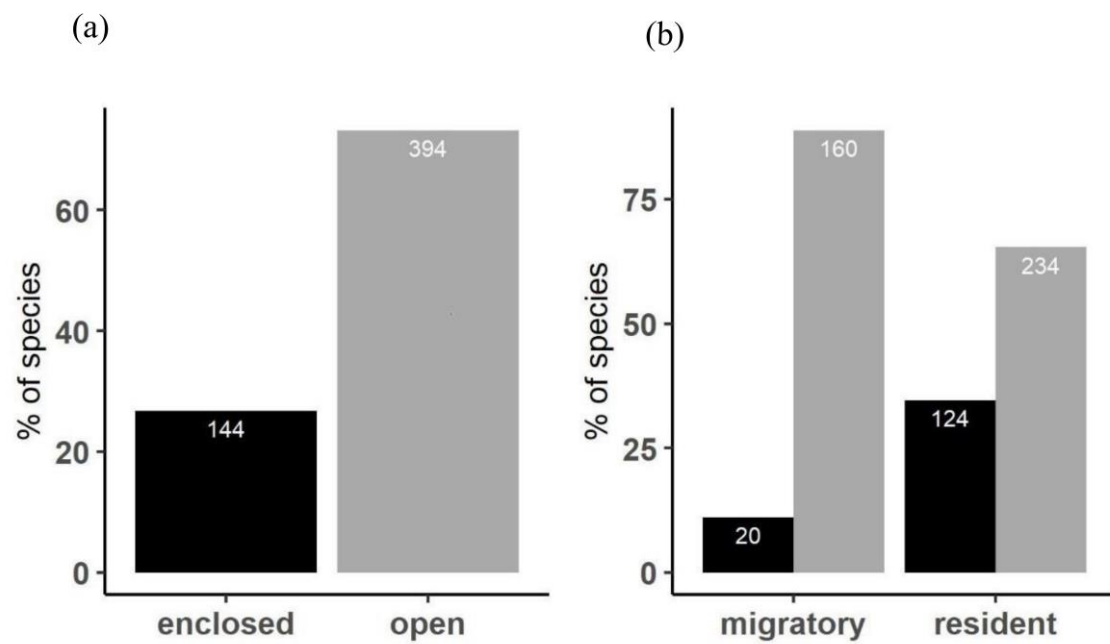
3.3.4 Statistical analyses

To test the correlation between nest types and brain size, we first performed conventional Generalized Linear Models (GLMs), using the R-Package Stat, with a gaussian distribution and identity link-function. Two different procedures have being commonly applied to account for the allometric effect in studies involving brain size correlations. The simplest procedure is the use of log-transformed brain size as the response variable and the inclusion of log-transformed body mass among the explanatory variables. Another procedure is the use of the brain size residuals obtained from a log-log least-squares linear regression (Rbmass) as the explanatory variable (SOL et al., 2002; SAYOL et al., 2020), eliminating the need for body mass to be included among the explanatory variables (FRANKLIN et al., 2014). Then, our first model had log-transformed brain mass as the response variable, and nest type (enclosed/open), migratory behavior (yes/no), and log-transformed body mass as explanatory variables. As enclosed nests are more common among the smaller passerines (Martin et al. 2016), the interaction log-body mass vs. nest type was also included as a explanatory variable. The second model included Rbmass obtained with phylogenetic control using the phylo.resid function from package Phytools (REVELL 2012), as the response variable, and nest type (enclosed/open), migratory behavior (yes/no), and the interaction log-body mass vs. nest type as explanatory variables. As migratory behavior was always significant (see results below), in addition to global analyses, we also modeled resident and migratory taxa separately to test the correlations without the influence of migration. We report maximum-likelihood parameter estimates, their standard errors (SE), with upper and lower 97.5% confidence limits, and t-tests to verify significant variables within models.

Then, to account for the phylogenetic non-independency of comparative data, the above models were also analyzed using Markov chain Monte Carlo (MCMC) Bayesian Phylogenetic Mixed Models (BPMMs), as available in MCMCglmm R package v2.20 (HADFIELD, 2010). For each modeling, a sample of 1,000 trees obtained from the Mega Tree of birdtree.org (JETZ et al., 2012) was used to generate a consensus phylogeny (maximum credibility tree) with Phangorn R-Package. Then, the non-phylogenetic independency of the data was addressed by including the consensus phylogeny as a random factor in the modeling. MCMC was programmed to 1010,000 iterations, with a burn-in of 10,000 and a thinning interval of 1,000 iterations, resulting in a posterior distribution of 1,000 samples. To facilitate model convergence, inverse Wishart-prior was used ($V = 1$, $v = 0.02$) (see also SAYOL et al., 2020). For each variable, we report the posterior mean and the 95% credibility intervals (CIs), and their significances were obtained by pMCMC, which is the proportion of samples in the posterior distribution non-overlapping zero. Analyses were repeated six times to check for the consistency of the significance of the results. For the whole set of species, we also calculated the posterior probability of the phylogenetic signal λ across posterior mean (mean of the posterior distribution), using either log-transformed brain mass and Rbmass as response variables, and posterior mode values of λ (values from posterior distribution) with 95% credible intervals are reported. To visualize the co-evolution of relative brain size and nest type, we constructed a phylogeny with the consensus tree obtained for the whole set of species using a consensus phylogeny (maximum credibility tree) with Phangorn R-Package. In this tree, branch colors represent the phylogenetically-corrected Rbmass, and the terminal nodes depict nest types

3.4 RESULTS

Of 581 passerine species with brain size information, 538 species distributed across 91 families were selected for the analyses, being 144 with enclosed nests and 394 with open nests. Among these species, 358 were resident and 180 were migratory, being the proportion of species with enclosed nests approximately three times bigger in the resident (35.42 %) than in the migratory taxa (11.11%) (Graphic 1). Our sampling involved about 8% of the known passerine species and their distributions across geographic regions was uneven (Figure 1).



Graphic 1. Barplots evidencing; (a) percentage of the total number of species building enclosed and open nests. (b) percentages of open and enclosed nets within migratory and resident categories. Black bars represent enclosed, and grey bars represent open nest.

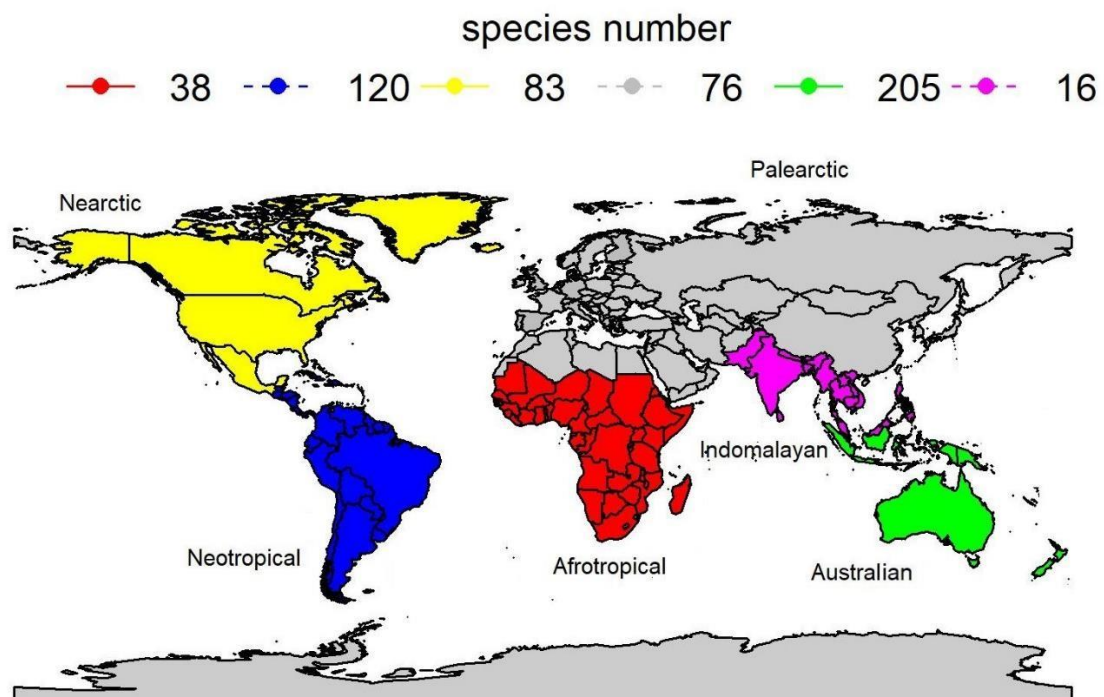


Figure 1. Numbers of species considered in the analysis (total = 538), distributed according to their reproductive biogeographic zones.

Nest type, and also the other explanatory variables, predicted relative brain mass when we used conventional GLM analyses (Table 1), except when migratory species were addressed separately, (Table 1). However, neither nest type, nor its interaction with body size, predicted brain size when we applied the Bayesian approach with phylogenetic control, independently of the used data partition (Table 2). The phylogeny of the whole set of species evidenced a clear overall lack of association between phylogenetically-corrected Rbmass values and nest types (Figure 2). Phylogenetic signal estimated for the tree containing the whole set of species, and its credible intervals were mean $\lambda = 0.6277046$, (0.50 to 0.75) and posterior mode $\lambda = 0.6248176$ when we used Rbmass as response variables

Table 1. Estimated values, 95% confidence intervals (IC), values of t-test (t), and levels of significance (P) for predictive variables used in GLM models to account for brain size variations in the whole species dataset, and for resident and migratory taxa separately. Response variables were log-transformed brain mass (log-brain) or brain size residuals of a log-log phylogenetically-controlled linear regression (Rbmass). Predictive variables included nest type (open/closed), log-transformed body mass, and migratory behavior (yes/no).

Response variable	Partition/sample size	Model parameter	Estimate value (IC)	T value	P- value
Log(brain)	All species/ n=538	(Intercept)	-2.32 (-2.41 to -2.22)	-48.36	< 0.001
		Log (body mass)	0.67(0.64 to 0.70)	43.97	<0.001
		Migratory behavior (no)	0.09 (0.06 to 0.12)	5.95	< 0.001
		Nest (open)	-0.15 (-0.26 to -0.04)	-2.73	0.006
		Log (body mass) *Nest (open)	0.04 (0.01 to 0.07)	2.46	0.013
Log(brain)	Residents/ n=358	(Intercept)	-2.22 (-2.31 to -2.12)	-45.45	<0.001
		Log(body)	0.67 (0.64 to 0.70)	40.23	<0.001
		Nest (open)	-0.19 (-0.31 to -0.07)	-3.13	0.001
		Log (body mass) *Nest (open)	0.05 (0.01 to 0.08)	2.57	0.010

Log(brain)	Migratory/ n=180	(Intercept)	-2.44 (-2.70 to -2.18)	-18.55	<0.001
		Log (body mass)	0.69 (0.61 to 0.76)	17.05	<0.001
		Nest (open)	0.03(-0.24 to 0.30)	0.22	0.82
		Log (body mass) *Nest (open)	0.007 (-0.07 to 0.09)	0.16	0.86
Rbmass	All species/ n=538	(Intercept)	0.05 (-0.04 to 0.14)	1.09	0.27
		Log (body mass)	-0.03(-0.06 to -0.004)	-2.24	0.024
		Migratory behavior (no)	0.09 (0.06 to 0.12)	5.95	< 0.001
		Nest (open)	-0.15 (-0.26 to -0.04)	-2.73	0.006
		Log (body mass) *Nest (open)	0.04 (0.01 to 0.07)	2.46	0.013
Rbmass	Residents/ n=358	(Intercept)	0.10 (0.01 to 0.20)	2.19	0.028
		Log(body)	0.02(-0.06 to 0.002)	-1.78	0.07
		Nest (open)	-0.19 (-0.31 to -0.07)	-3.13	0.001
		Log (body mass) *Nest (open)	0.05 (0.01 to 0.08)	2.57	0.010
Rbmass	Migratory/ n=180	(Intercept)	-0.02(-0.28 to 0.23)	-0.21	0.83
		Log (body mass)	-0.01 (-0.08 to 0.07)	-0.16	0.82
		Nest (open)	0.03 (-0.24 to 0.30)	0.22	0.87
		Log (body mass) *Nest (open)	0.01 (-0.07 to 0.09)	0.16	0.86

Table 2. Models testing the effects of log(body mass) and nest type (open/enclosed) with and without interactions between these variables, and migration behavior (yes/no), on the log(brain mass) and in Rbmass. We used Phylogenetic Bayesian mixed models (MCMCGLMM) that include phylogeny as random effect. For each effect, we show the posterior mean with 95% credible intervals (CI).

Response variable	Partition/sample size	Model parameter	Posterior Mean (CI)	pMCMC
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Log (brain)	All species/ n=538	(Intercept)	-2.24 (-2.42 to -2.08)	< 0.001
		Log (body mass)	0.65 (0.61 to 0.68)	<0.001
		Migratory behavior (no)	0.07 (0.04 to 0.10)	< 0.001
		Nest (open)	-0.05 (-0.18 to 0.07)	0.41
		Log (body mass) *Nest (open)	0.01 (-0.02 to 0.05)	0.57
Log (brain)	Residents/ n=358	(Intercept)	-2.16 (-2.34 to -1.99)	<0.001
		Log(body)	0.65 (0.61 to 0.69)	<0.001
		Nest (open)	-0.06 (0.21 to 0.07)	0.35
		Log (body mass) *Nest (open)	0.01 (-0.03 to 0.05)	0.52
Log (brain)	Migratory/ n=180	(Intercept)	-2.23 (-2.59 to -1.90)	<0.001
		Log (body mass)	0.62 (0.53 to 0.72)	<0.001
		Nest (open)	-0.09 (-0.39 to 0.21)	0.51
		Log (body mass) *Nest (open)	-0.03 (-0.07 to 0.12)	0.52
Rbmass	All species/ n=538	(Intercept)	-0.31 (-0.47 to -0.14)	<0.001
		Log (body mass)	0.06(0.03 to 0.10)	<0.001
		Migratory behavior (no)	0.07(0.04 to 0.10)	<0.001
		Nest (open)	-0.05 (-0.18 to 0.08)	0.41
		Log (body mass) *Nest (open)	-0.01(-0.02 to 0.05)	0.59
Rbmass	Residents/ n=358	(Intercept)	-0.20 (-0.38 to -0.03)	0.024
		Log (body mass)	0.05 (0.01 to 0.09)	0.010
		Nest (open)	-0.06 (-0.21 to 0.07)	0.36
		Log (body mass) *Nest (open)	0.01(-0.02 to 0.06)	0.51
Rbmass	Migratory/ n=180	(Intercept)	0.01 (-0.32 to 0.37)	0.96
		Log (body mass)	-0.01 (-0.09 to 0.08)	0.89
		Nest (open)	-0.10 (-0.40 to 0.19)	0.51
		Log (body mass) *Nest (open)	0.03 (-0.05 to 0.13)	0.46

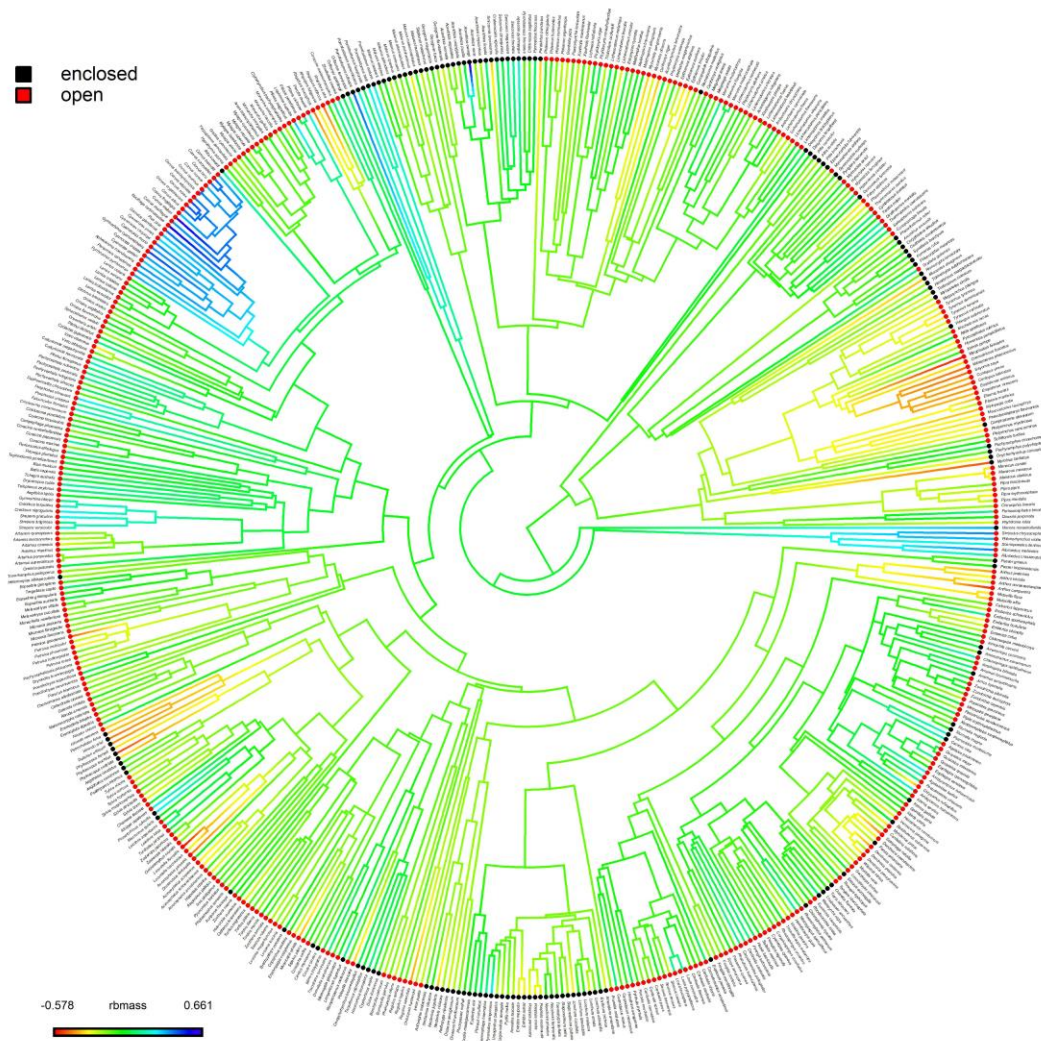


Figure 2. Phylogeny for 538 passerine species constructed with a consensus tree based on the 1,000 trees obtained from birdtree.org, showing the relationships between relative brain mass (Rbmass) and nest type. The color scale of the branches represents Rbmass variations, and the terminal nodes depict nest types (open/enclosed).

3.5 DISCUSSION

Our prediction of increased brain sizes in closed-nester species was corroborated only by conventional statistics, while the use of the Bayesian modeling procedures with phylogenetic control permitted to recuperate only the effects of body size and migration to explain brain size, independently of the type of data partitioning and of the used response variables (log-brain mass and Rbmass). In comparative analyses using multiple species, correlations cannot be inferred based solely on conventional modeling

because phenotypes from different species can be similar due to shared ancestry (HARVEY; PAGEL, 1991). Comparing the different analytical approaches, however, was useful to evidence that the larger relative brain sizes we found for closed-nester species resulted from phylogenetic effect, rather than by independent evolution. This can be evidenced by the fact that almost half of the closed-nester species were concentrated within only four main clades: the clade formed by the Australasian families Acanthizidae and Maluridae; the clade formed by the African Estrildidae and Ploceidae; the clade of the mostly African Nectariniidae, and the clade of the Neotropical Furnariidae. Although our phylogeny reconstruction revealed a tendency for increased Rbmass within these clades, in many other clades of predominantly open-nester species, enclosed nests merged without noticeable increases in residual brain size (*Heteromyias albispecularis*, *Plocepasser mahali*, *Dasyornis broadbenti*, *Orthonix spaldingii*), suggesting that even passerine birds with relatively small brains can construct enclosed nests. This is also consistent with a model of evolution in which nest construction abilities are governed by specific brain regions for which increases in complexity has no reflects on overall brain sizes (IWANIUK; ARNOLD, 2004; HALL; STREET; HEALY, 2013). Exploiting this possibility, however, is intractable due to the lack of information on specific brain areas for most bird species.

Other potential explanations to the lack of significance of our results include the existence of variations in nest complexity within both open and enclosed nests categories, as well as the effects of the negative allometry. Although enclosed nests have long been thought to be more complex than open nests, and its construction more cognitively demanding (COLLIAS, 1986; HANSELL, 2000; PRICE; GRIFFITH, 2017), it is not so obvious because open nests also can have high levels of complexity. While many open nests can present various layers of different materials, many enclosed nests can be relatively simple. Examples include certain domed nests supported from below, for which layers are poorly detectable and nest material is only loosely woven (i.e. *Pitangus sulphuratus*). Testing the premise that enclosed nests are more complex is not straightforward, but the non-significant correlation between enclosed nest construction and brain size we found can be an empirical evidence that, on average, the construction of enclosed nests do not require more complex behavioral skills. On the other hand, future comparative studies might address whether other dimensions of nest complexity, i.e. the diversity of materials or layers used; types of attachment to supporting structures, and woven techniques, could correlate with relative brain size or with the performance in cognitive demanding skills.

A recent work evidenced that during the Neoaves radiation, groups that were selected for miniaturization tended to show disproportionately larger brains because body size reduction outpaced brain size reduction (negative allometry) (KSEPKA et al., 2020). This is relevant because it is known that enclosed nests are more common among the smaller passerines (COLLIAS, 1997; MARTIN et al., 2016), and potential explanations are that: the smaller taxa are more capable to woven finer and flexible materials needed for enclosed nests construction (COLLIAS, 1997; HANSELL, 2000); or that eggs and young of smaller passerines may lose heat faster, being the thermal benefits of the enclosed nests more important for these species (MARTIN et al., 2016). Then, it is possible that for the smaller passerines, which concentrates the higher proportion of the enclosed nests, the negative allometry could have led both open, and closed-nester species to present relatively larger brains, overriding the effects of nest types.

In summary, we reveal that disproportionately enlarged brains are not a prerequisite for enclosed nest construction by passerine birds. However, our study do not precludes the need for further investigations involving a larger number of clades with complete brain size information. Our analyses involved only about 8% of the passerine species and the highly uneven distribution of enclosed and open nests within the clades likely contributed to the phylogenetic effect that reduced the significance of the nest type parameter in the Bayesian models. It suggests that despite our results, the idea that, on average, enclosed nests could be associated to larger brains may not be promptly discarded. As a tractable amount of brain size data becomes available, analyses should focus, for instance, on specific families presenting as many independent nest type transitions as possible.

3.6 DATA ACCESSIBILITY

All the data and scripts are available in the electronic supplementary material.

3.7 AUTHOR'S CONTRIBUTION

A.B.L., M.R.F., and A.C.G. conceived the study design; A.B.L. carried out data survey; A.B.L. and A.C.G. analyzed the data; A.B.L. and M.R.F. wrote the first version of the paper, and A.B.L., M.R.F., and A.C.G. contributed with the elaboration of the final version of the manuscript.

3.8 COMPETING INTERESTS

The authors declare no competing interests

3.9 FUNDING

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4 CONSIDERAÇÕES FINAIS

Nossos resultados mostraram que o tipo de ninho construído pelos Passeriformes é um fator determinado filogeneticamente, o qual não tem efeito sobre a massa cerebral relativa das espécies construtoras. Desta forma, pode-se considerar que a complexidade no *design* do ninho não evoluiu de forma direcionada para um tipo estrutural específico. Assim, tanto ninhos fechados quanto os ninhos abertos podem ser complexos, e consequentemente exigirem um alto valor de massa cerebral relativa e também complexas habilidades para serem construídos.

Além disso, a alometria negativa pode ter afetado a evolução da massa cerebral dos Passeriformes, sendo este efeito evidenciado através das espécies com uma maior massa cerebral relativa que ao invés de ser resultante das altas exigências comportamentais para se construir os ninhos, esta massa cerebral foi determinada devido as alterações morfológicas que ocorreram ao longo da radiação dos Neoaves.

Também recuperamos o efeito da migração sobre o tamanho do cérebro, evidenciando assim a força das pressões evolutivas exercidas sobre as características morfológicas das aves para que estes animais se tornassem migratórios.

Diante do exposto, este estudo suporta as seguintes ideias; a alta complexidade estrutural do ninho sempre deverá ser considerada, independentemente do tipo de ninho, e também que tanto as transições do tipo de ninhos quanto as exigências cognitivas para serem construídos, não levaram a uma maior massa cerebral relativa. No entanto, nossos resultados não excluem a necessidade de novas investigações que considerem uma

maior amostragem de clados com informações mais completas a respeito do tamanho cerebral na ordem dos Passeriformes.

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6 ANEXOS - SCRIPT DO SOFTWARE R

6.1.1 Pacotes exigidos

library(lme4)

library(sensiPhy)

library(phangorn)

library(MCMCglmm)

library(geiger)

library(phytools)

library(plotrix)

```

library(ape)
library(versitree)
library(nlme)
library(ggtree)
library(ggplot2)
library(plotly)
library(MuMIn)
library(mosaic)
library(cowplot)
library(ggpubr)
library(Hmisc)
library(nortest)
library(dplyr)
library(plyr)
library(lattice)
library(corrplot)
library(car)
library(PerformanceAnalytics)
library(rgl)
library(png)
library(rphylopic) library(ggmap) library(maps) library(rgdal) library(maptools)
library(rgdal) library(raster) library(mapdata) library(lattice)

```

6.1.2 Análise Bayesiana

```

databir<-read.csv2("birddata.csv",sep = ";",dec=".",header=T,fileEncoding="UTF-8-
BOM")
tree<-read.tree(file = "birdtree.phy")
no_branch <- function(multiphylo){ res <- character()
for (i in 1:1000) {
res[i] <- class(multiphylo[[i]]$edge.length)
}
which(res != "numeric")
}
no_branch(multiphylo =tree)
tree <-tree[-c(25)]
contree<-maxCladeCred(tree, tree = TRUE, part = NULL, rooted = TRUE)

```



```

databir$species <- gsub(pattern = " ", replacement = "_", x = databir$species)
rownames(databir) <- databir$species
databir <- databir[match(contree$tip.label,databir$species),]
databir$brain.res <-
phyl.resid(contree,x=log(databir$body),Y=log(databir$brain))$resid
names(databir)[4] <- "latinFamily"
databir$animal<-databir$species
prior3.1 <- list(G = list(G1 = list(nu=0.02, V=1)), R = list(nu=0.02, V=1))
mod3.1<-MCMCglmm(log(brain)~log(body)*nest+nest+move+log(body),data=databir,
pedigree=contree,random=~animal,prior = prior3.1,verbose=F,nitt = 1010000,
thin=1000, burnin = 10000)
summary(mod3.1)
lambda<-mod3.1$VCV['animal']/
(mod3.1$VCV['animal']+mod3.1$VCV['units'])
mean(lambda)
posterior.mode(lambda)
HPDinterval(lambda)

```

6.1.3 Análise de Modelos Mistos Generalizados (GLM)

```

databir<-read.csv2("birddata.csv",sep = ";",dec="," ,header=T,fileEncoding="UTF-8-
BOM")
res<-lm(log(brain)~log(body),data=databir)
databir$bird.res<-residuals(res)
modglm<- glm(formula =log(brain) ~log(body)+nest+move+log(body)*nest,family =
gaussian,data =databir)
modglm<-glmer(bird.res~+nest+log(body)*nest, data=databir, family = "gaussian")
summary(modglm)
confint(modglm)

```

6.1.4. Construção da filogenia geral

```

databir<-read.csv("birddata.csv",sep = ";",dec="," ,header=T,fileEncoding="UTF-8-
BOM")
tree<-read.tree(file = "birdtree.phy")
no_branch <- function(multiplylo){
res <- character()
for (i in 1:1000) {
res[i] <- class(multiplylo[[i]]$edge.length)

```

```

}
which(res != "numeric")
}
no_branch(multiphylo =tree)
tree <-tree[-c(25)]
contree<-maxCladeCred(tree, tree = TRUE, part = NULL, rooted = TRUE)
databir$species <- gsub(pattern = " ", replacement = "_", x = databir$species)
rownames(databir) <- databir$species
databir <- databir[match(contree$tip.label,databir$species),]
databir$brain.res <-
phyl.resid(contree,x=log(databir$body),Y=log(databir$brain))$resid
plotTree(contree,fsize=0.3,lwd=0.5)
nodelabels(frame="none",font=1)
fmode<-as.factor(setNames(databir[,9],rownames(databir)))
trees<-make.simmap(contree,fmode,model="ER")
x<-getStates(trees,"tips")
tree<-trees
rm(trees)
tree
x
fit4<-rerootingMethod(tree,x,model="ER")
relbmass<-setNames(databir[,13],rownames(databir))
cols<-setNames(palette()[1:length(unique(fmode))],sort(unique(fmode)))
obj<-contMap(tree,relbmass,outline=FALSE,plot=FALSE)
jpeg("General Phylogenie.jpeg", units="in", width=5, height=5, res=1000)
plot(obj,type="fan",ftype="i",fsize=0.1,legend=FALSE,outline =
FALSE,add=TRUE,lwd=0.9,colors=obj$cols,offset=5)
par(fg="transparent")
#nodelabels(text=1:tree$Nnode,cex=0.2,node=1:tree$Nnode+Ntip(tree),frame="circle")
tiplabels(pie=to.matrix(fmode[tree$tip.label],
levels(fmode)),bg=cols,piecol=cols,cex=0.1)
par(fg="black")
add.color.bar(0.3*max(nodeHeights(tree)),obj$cols,lims=obj$lims,digits=3,prompt=FA
LSE,x=-1*max(nodeHeights(tree)),
y=0.9*(1+par()$usr[3]),lwd=2,fsize=0.3,title="rbmass",length=60,subtitle="")

```

```
add.simmap.legend(colors = cols,prompt=FALSE,x=0.9*par()$usr[1],
y=-0.8*par()$usr[3],fsize=0.5)
dev.off()
```

6.1.5 Construção do gráfico de barras

```
nest<-c("enclosed","open")
total<-c(144,394)
percentage<-c(26.76,73.23)
nest<- data.frame(nest,total,percentage)
ggplot(data=nest, aes(x=nest, y=percentage,fill=nest)) + geom_bar(stat = "identity")+
scale_fill_manual(legend, values = c("enclosed" = "black", "open" =
"darkgray"))+ ylab("% of species")+ theme_bw()+theme(axis.text=element_text(size
=10,face="bold"),axis.title.y=element_text(size=10),axis.title.x=element_blank(),
legend.text=element_blank(),legend.position="none",panel.border=
element_blank(),panel.grid.major=element_blank(),panel.grid.minor= element_blank(),
axis.line = element_line(colour = "black"))+
geom_text(aes(label=total), position = position_dodge(0.9),vjust=1.5, color="white",
size=2.5)
nest<-c("enclosed","open","enclosed","open")
movement<-c("migratory","migratory","resident","resident")
total<-c(20,160,124,134)
percentage<-c(11.11,88.88,34.63,65.39)
nestmove<- data.frame(nest,movement,total,percentage)
ggplot(data=nestmove, aes(x=movement, y=percentage,fill=nest)) +
geom_bar(stat="identity", position=position_dodge())+ scale_fill_manual("legend",
values = c("enclosed" = "black", "open" = "darkgray"))+
lab("% of species")+theme_bw()+theme(axis.text=element_text(size=10,face="bold"),
axis.title.y=element_text(size=10),axis.title.x=element_blank(),legend.text=element_
blank(),legend.position="none",panel.border=element_blank(),panel.grid.major =
element_blank(),panel.grid.minor
=element_blank(),axis.line=element_line(colour="black"))+geom_text(aes(label=total),
position= position_dodge(0.9), vjust = 1.5,color="white", size=2.5)
6.1.6 Construção do mapa de distribuição das espécies
data(wrld_simpl)
colorForCountries<setNames(rep(gray(0.8),nrow(wrld_simpl@data)),wrld_simpl@data
$NAME)
```

```

colorForCountries[wrlld_simpl@data$NAME%in%c('French Guiana','Belize','Costa
Rica','El Salvador',
'Guatemala','Honduras','Nicaragua','Argentina','Peru','Chile','Uruguay','Brazil','Panama',
Bolivia','Colombia','Ecuador','Guyana','Paraguay','Suriname','Panama','Uruguay','Venez
uela','Suriname','Cayenne','Cuba','Dominica','Dominican Republic','El
Salvador','Grenada','Guatemala','Antigua and
Barbuda','Bahamas','Barbados','Bermuda','Haiti','Jamaica','Cayman Island')] = 'blue'
colorForCountries[wrlld_simpl@data$NAME%in%c('Canada','Mexico','United
States','Greenland','Iceland')]='yellow'
colorForCountries[wrlld_simpl@data$NAME%in%c('Angola','Cameroon',
'Central African','Chad','Guinea','Kenya','Nigeria','Rwanda','São Tomé and
Principe','Uganda','South Africa',
'Sudan','Djibouti','Eritrea','Ethiopia','Somalia','Botswana','Comoros','Lesotho','Madagasc
ar','Seychelles','Mali','Burkina Faso','Cape Verde','Gambia','Guinea-
Bissau','Liberia','Mauritania','Niger','Senegal','Central African
Republic','Malawi','Namibia','Zambia','Burundi','Eswatini','Zimbabwe','Mozambique','G
hana','Togo','Equatorial Guinea','Sierra Leone','Benin','Congo','Gabon','Democratic
Republic of the Congo','United Republic of Tanzania','Lesotho','Eswatini','Equatorial
Guinea','Ivory Coast','Cote d'Ivoire')] = 'red'
colorForCountries[wrlld_simpl@data$NAME%in%c("Germany","Belgium","Spain','Mo
ldova","United Kingdom","United Arab
Emirates","Portugal','French','Finland','Greece','Italy')] = 'gray'
colorForCountries[wrlld_simpl@data$NAME%in%c('New
Caledonia','Indonesia',"Australia","Papua New Guinea','New Guinea',
'Polinesia','Federated States of Micronesia','Vanadu','Borneu','New Zealand')]='green'
colorForCountries[wrlld_simpl@data$NAME%in%c('Philippines','Cambodia','India',"L
ao People's Democratic
Republic","Vietnam","Malaysia","Thailand","Pakistan","Burma","Bangladesh","Nepal","Bh
utan","Sri Lanka','Viet Nam')]='magenta'
par(mar=rep(0,4))
plot(wrlld_simpl,col = colorForCountries)
legend(-165.5046,150.8739,legend=c("38","120","83","76","205","16"),title="species
number",pch=16,bty="n",col=c("red","blue","yellow","gray","green","magenta"),
lty=1:2,horiz=TRUE, cex=1)
text(35.5046,-31.8739, cex=0.6,font=2,pos = 1, label = bquote(paste("Afrotropical")))

```

```
text(-30.5046,-35.8739, cex=0.6,font=2,pos = 1, label = bquote(paste("Neotropical")))
text(-150.5046,90.8739,cex=0.6,font=2, pos = 1, label = bquote(paste("Nearctic")))
text(120.5046,97.8739, cex=0.6,font=2,pos = 1, label = bquote(paste("Palearctic")))
text(105.5046,-32.8739, cex=0.6,font=2,pos = 1, label = bquote(paste("Australasian")))
text(75.5046,6.8739,cex=0.6,font=2,pos = 1, label = bquote(paste("Indomalayan")))
```