Universitat Autònoma de Barcelona

Causes and consequences of brain size evolution: A global analysis on birds

Ferran Sayol Altarriba

Causes and consequences of brain size evolution: A global analysis on birds

Tesi doctoral

Ferran Sayol Altarriba

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Dirigida per:

Dr. Daniel Sol Rueda

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Dr. Daniel Sol Rueda, investigador científic del CSIC al Centre de Recerca Ecològica i Aplicacions Forestals,

Certifica que:

Aquesta tesi duta a terme per Ferran Sayol Altarriba al Centre de Recerca Ecològica i Aplicacions Forestals, i titulada **Causes and consequences of brain size evolution: A global analysis on birds** ha estat realitzada sota la seva direcció.

El director **El doctorand**

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La resta de figures contingudes en aquesta tesi han estat realitzades per l'autor.

Agraïments

L’elaboració d’una tesi doctoral suposa una tasca llarga i complexa que t’atrapa durant uns quants anys. Sens dubte, tot aquest camí no hauria estat possible sense el suport i entusiasme de moltes persones a qui vull agrair, molt sincerament, la seva ajuda.

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Resum

Per què alguns llinatges de vertebrats, incloent els humans, han evolucionat cervells grans malgrat els alts costos energètics i de desenvolupament que comporten és un dels grans trencaclosques de la biologia evolutiva. De les varies hipòtesis que s'han plantejat per intentar resoldre aquest misteri, la variació ambiental destaca com una de les principals causes dels canvis en la mida relativa del cervell. Més formalment, la hipòtesi del cervell protector (CBH, de *Cognitive buffer hypothesis*, en anglès) postula que els cervells relativament més grans han evolucionat per facilitar els ajustos de comportament, tot augmentant la supervivència en condicions canviants. La lògica de la hipòtesi és que una cognició avançada pot augmentar la *fitness* en ambients variables promovent la capacitat per recollir i emmagatzemar informació, facilitant així per exemple, les decisions de quan canviar de lloc o de tipus d'alimentació en períodes d'escassetat de recursos. Tot i que la CBH ha rebut suport empíric durant els darrers anys, alguns autors qüestionen la seva rellevància per explicar l'evolució del cervell.

Aquesta tesi doctoral explora les causes i conseqüències de l'evolució de la mida del cervell, amb especial atenció en la CBH, validant les seves assumpcions, assajant les seves prediccions i avaluant les seves implicacions. La tesi treu profit d'una base de dades de mesures del cervell per més de 1900 espècies d'ocells en combinació amb els mètodes filogenètics comparatius més recents per tal de descobrir els orígens de la variació de la mida del cervell en la classe de vertebrats més diversa.

Com a primer objectiu, aquesta tesi valida una de les assumpcions de la CBH, que és si la mida relativa del cervell és una bona aproximació dels canvis en estructures del cervell involucrades en la capacitat de construir respostes de comportament als nous reptes. Tot i que hi ha evidències amplies que les espècies amb cervell gran són millors en la resolució de problemes experimentals i tenen una major capacitat per les innovacions de comportament, encara existeix un intens debat en si el conjunt del cervell és una bona mesura o més aviat hauríem de focalitzar l'atenció en àrees específiques del cervell responsables d'aquests comportaments. El capítol 1 mostra que les àrees associatives del

cervell, tradicionalment relacionades amb la intel·ligència general, són desproporcionadament més grans en espècies de cervell gran i poden predir de forma acurada la variació en el conjunt del cervell, de manera que es valida la seva utilització en anàlisis comparatius globals. Com a segon objectiu, la tesi explora una de les prediccions de la CBH, que les espècies que viuen en regions amb alta variabilitat ambiental haurien de ser seleccionades per cervells grans, a menys que tinguin adaptacions especialitzades per evadir les caigudes en la disponibilitat de recursos. El Capítol 2 mostra com els ocells que viuen en ambients més estacionals i impredictibles, com les regions de latituds altes, posseeixen cervells relativament més grans que els residents d'altres regions, recolzant la CBH en ocells. En Capítol 3 es mostra com els ocells que colonitzen illes oceàniques han evolucionat cervells relativament més grans que els seus parents continentals. Aquests canvis sembla que en part s'expliquen per un augment de la incertesa en la disponibilitat de recursos que caracteritza les illes, donant un suport addicional a la CBH. En el capítol 4 explorem la possibilitat que el cervell també pugui tenir un rol actiu en l'evolució de les espècies. Tal com prediu la hipòtesi del *behavioural drive*, els animals que més freqüents fan canvis de comportament com a resposta als reptes ambientals hauria d'exposar els individus a nous conjunts de pressions selectives, tot afavorint la divergència evolutiva respecte els seus ancestres i finalment afavorint l'aparició de noves espècies. El Capítol 4 aporta evidències per aquesta hipòtesi, mostrant que els llinatges amb cervells relativament més grans han tingut majors taxes de diversificació taxonòmica que els de cervells més petits. Aquesta troballa recolza així la idea que els animals no són agents passius de la selecció, però que poden modificar activament la seva relació amb l'ambient i influenciar el seu propi camí evolutiu.

En resum, els resultats d'aquesta tesi aporten evidència empírica per la CBH, mostrant com els cervells relativament més grans funcionen, i per tant han evolucionat, per fer front als canvis ambientals, i que l'evolució de cervells grans pot a més influir en la diversificació evolutiva d'un llinatge. Aquests resultats poden ajudar a entendre perquè diferents llinatges animals han evolucionat els cervells grans de forma independent, que al seu temps pot ajudar a resoldre el misteri de com els nostres ancestres van evolucionar i donar claus de com els animals podrien respondre als canvis ambientals ràpids induïts pels humans característics de l'era de l'Antropocè.

Abstract

Why some vertebrate lineages, including humans, evolved large brains despite the associated energetic and developmental costs is one of the main puzzles in evolutionary biology. Of the many hypotheses that have been launched to try to resolve this puzzle, environmental variability stands out as a major cause of relative brain size variation. More formally, the cognitive buffer hypothesis (CBH) postulates that relatively large brains evolved to facilitate behavioural adjustments to enhance survival under changing conditions. The rationale of the CBH is that advanced cognition can increase fitness in varying environments by enhancing information gathering and learning, facilitating for instance shifts between different feeding sites or food types to alleviate periods of food scarcity. Increased survival would in turn facilitate a longer reproductive life, thereby compensating for the developmental and energetic costs of growing a large brain. While the CBH has received ample empirical support in recent years, some authors have questioned its relevance to account for the evolution of enlarged brains.

The present PhD thesis explores the causes and consequences of the CBH, validating its assumptions, testing its predictions and assessing its evolutionary implications. It takes advantage of a large database on brain size comprising more than 1900 extant bird species in combination with recently developed phylogenetic comparative methods to elucidate the origins of brain size variation in the most diverse vertebrate class.

As a first objective, the thesis validates a main assumption of the CBH, that is, the extent to which relative brain size is a good proxy of the brain structures involved in the capacity to construct behavioural responses to new challenges. Although there is ample evidence that big brained species are better problem-solvers and have higher capacity for behavioural innovation, the debate still exists on whether the whole brain is biologically meaningful or instead we should focus the attention to particular brain structures responsible for these cognitive abilities. Chapter 1 shows that the associative areas of the brain, classically related with general intelligence, are disproportionally larger in large brained species and accurately predict variation in the whole brain, therefore validating its use in broader comparative analyses. As a second objective, this thesis explores one of the predictions of the CBH, that species living in regions with higher environmental variation should be selected for larger brains, unless they have adaptive specialisations to avoid drops in resource availability. Chapter 2 shows that birds living in highly seasonal and unpredictable environments, like high-latitude regions, possess relatively large brains than residents from other regions, supporting the CBH in birds. Additional support for the hypothesis is found in Chapter 3, where birds colonizing oceanic islands seem to evolve relatively larger brains than their continental relatives. These changes seem to be in part caused by the increased uncertainty in resource availability that characterizes islands. In Chapter 4 we explore the intriguing possibility that it can also have an active role in evolution is less clear. As predicted by the behavioural drive hypothesis, frequent behavioural changes as a response to environmental challenges should expose individuals to new sets of selective pressures, thereby favouring evolutionary divergence from the ancestors, finally leading to speciation events. Chapter 4 provides evidence for the behavioural drive hypothesis, showing that avian lineages with relatively large brained have experienced higher diversification rates than those with smaller brains. This finding is in line with the view that animals are not passive agents of selection, but by actively modifying its relationship with their environment also influence their own pace of evolution.

Overall, the findings of the present thesis provide empirical support for the CBH, showing that a relatively large brain functions, and hence may have evolved, to cope with environmental changes, and that the evolution of enlarged brains may subsequently influence the evolutionary diversification of the lineage. These results help understand why big brains might have evolved independently in different animal groups, which can shade light on the mystery of how our ancestors evolved and also give clues on how animals might respond to the rapid human-induced environmental changes that characterize the Anthropocene era.

'The brain, the most important of all the organs, follows the same laws of natural selection'(Darwin 1871).

General introduction

The evolution of brain size is one of the most important puzzles in evolutionary biology. Why have some groups of vertebrates, like primates, dolphins, crows and parrots, evolved so disproportionally large brains despite important energetic and developmental costs? The answer is relevant to understand what makes us humans, as a relatively big brain also characterizes the evolution of early hominins and presumably allowed human expansion and the colonization of a wide array of environments. The analysis of how and why brain size varies in animals can also allow us to better predict how different species might respond to the challenges of a continuously changing world.

The brain of vertebrates controls the body basic functioning, but it is also the place where decisions are taken. Back to the 5th century, Alcmaeon of Croton was already convinced that inside our head was where cognitive deliveries where happening (Gross, 1995), but it was not until Darwin that scientists started to realize that the size of the brain had something to do with the cognitive capacity of animals (Darwin, 1872). Whereas some species rely on basic stimuli to guide their decisions, others can use their large brains to make a more sophisticated use of the information and even make predictions of the external world. This benefits of increasing the information processing capacity has long been thought to be associated with the increase of brain size beyond that expected from body size (Jerison & Barlow, 1985). For instance, while the New Caledonian crow (*Corvus moneduloides*) and the New Guinea Bronzewing (*Henicophaps albifrons*) have similar body sizes, the crow possesses a brain three times larger than the dove, presumably because it has to gather, process and store more information about the environment. However, having a big brain also entails costs. Producing and maintaining neural tissue is energetically expensive and takes time (Mink *et al.*, 1981), exposing offspring to predators and forcing to delay the onset of reproduction (Isler & van Schaik, 2006b; Sol, 2009a; Barton & Capellini, 2011). Despite the increasing interest in brain evolution in the last years, in which situations the benefits of affording a large brain outweigh the costs are still a matter of hot debate (**Fig. 1**).

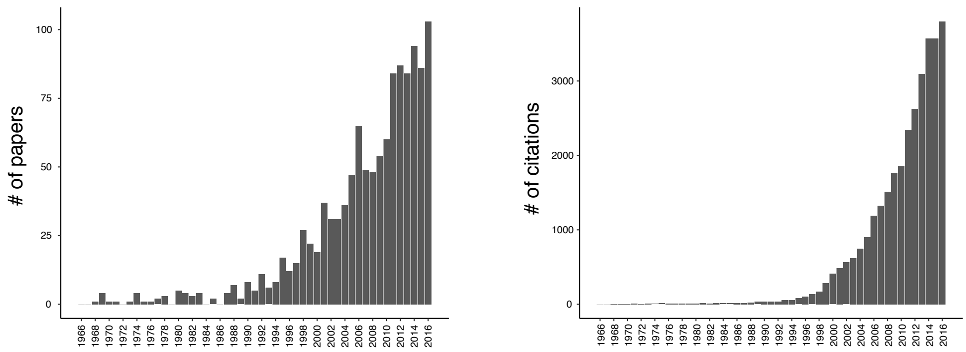

Figure 1. The interest on brain evolution in the last 50 years. Number of works (a) and citations (b) of papers containing the words "Brain evolution" from 1966 to 2016.

Several hypotheses have been proposed to explain the evolution of relatively larger brains (Dunbar, 1998; Isler & van Schaik, 2006b; Barton & Capellini, 2011; van Schaik *et al.*, 2012), but one of the main explanations that considers both the benefits and costs of large brains is the cognitive buffer hypothesis (CBH). This hypothesis posits that larger brains allow to buffer animals against environmental changes by facilitating the construction of behavioural responses (Allman *et al.*, 1993; Allman, 2000; Sol, 2009a). The hypothesis argues therefore that relatively larger brains have evolved as response to environmental variation. The CBH can theoretically explain in which circumstances large brains are more useful for survival, and how this can compensate for the energetic and developmental costs of producing and maintaining a large brain. In addition, the CBH has attracted attention for its implications in species conservation and evolution. According to the CBH, if a brain size allows to increase behavioural flexibility under changing conditions, it should help for instance invasive species to colonize novel environments (Sol *et al.*, 2005a, 2008; Amiel *et al.*, 2011) or the persistence of populations over time in fluctuating environments (Shultz *et al.*, 2005; Fristoe *et al.*, 2017).

This PhD thesis explores the causes and consequences of brain size evolution in birds, with a focus on the CBH (**Fig. 2**). The thesis has three specific objectives: (1) to explore the validity of relative brain size as a standard measure for comparing changes in brain structure among species; (2) to test the link between brain size and environmental variation, a major prediction of the CBH; and 3) to explore the consequences of relative brain size for the evolutionary diversification of the species. Below the state of the art of each of these sections is contextualized.

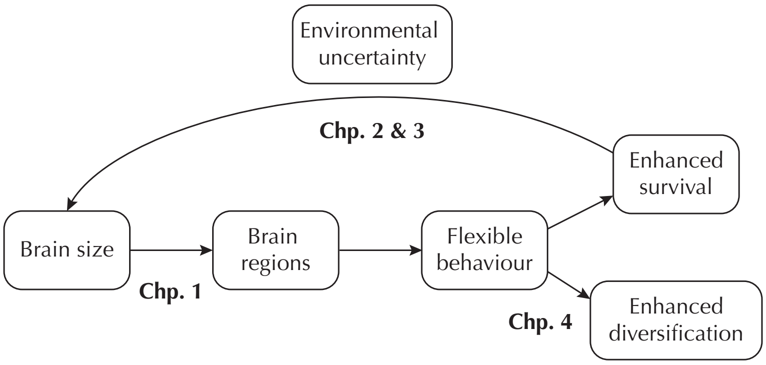

Figure 2. Schematic representation of the general framework of this PhD thesis

Objective 1: The assumptions of the CBH

The CBH is based on the assumption that the size of the brain is related to the capacity of animals to modify their behaviour plastically. Two lines of evidence provides support for this assumption. In experimental settings, big brained species are better problem solvers within carnivores (Benson-Amram *et al*., 2016), primates (Reader *et al*., 2011) and fish (Kotrschal *et al*., 2013). The second line of evidence is the existence of a relation between relative brain size and the propensity for behavioural innovations across species. An innovation is the appearance of a behaviour never observed before in a species. The incidence of cases of innovations reported in ornithology journals, once controlled for research effort, is positively related with relative brain size in both primates and birds (Lefebvre *et al*., 1997, 2004; Reader & Laland, 2002; Reader *et al*., 2011). Despite progress, whether the whole brain size is a biologically meaningful continues to be controversial. Some particular brain areas, like the mesopallium and nidopallium, are known to be responsible for the integration of stimuli and the subsequent construction of new or modified behaviours (Timmermans *et al*., 2000; Lefebvre *et al*., 2002). The question is nonetheless whether these areas have evolved independently of other brain structures (mosaic evolution) or in a coordinated way (concerted evolution). If larger brains have evolved by the independent increase of different brain regions in different species, comparisons of the whole brain might be biologically meaningless. Such an argument has been used to criticize comparative attempts to explain existing variation in whole brain size among species (Healy & Rowe, 2007). In **Chapter 1**, we test if the whole brain reflects consistent variation in associative areas of the brain responsible for behavioural innovations, and hence is a valid measure for broader comparative analyses.

Objective 2: The testable predictions of the CBH

If a big brain allows to buffer the individual against the effect of environmental changes, as suggested by the CBH, two main predictions are derived. First, big-brained species should better at coping with environmental changes than small-brained species. Direct evidence for this prediction comes from introductions of animals outside their native range (Sol et al. 2000). Big-brained species are more likely to persist after introduction in novel environments in reptiles and amphibians (Amiel *et al*., 2011), birds (Sol *et al*., 2005a) and mammals (Sol *et al*., 2008), although no relation has been found in fishes (Drake, 2007). Indirect evidence comes from studies in birds showing that populations of big-brained species are less likely to decrease in numbers (Shultz *et al*., 2005) and exhibit lower fluctuations (Fristoe *et al*., 2017) over time. The second prediction of the CBH is that species living in places where environmental changes are more frequent should be selected for enlarged brains. In contrast with the previous prediction, evidence that environmental variation has shaped brain size evolution are scanty. In birds, species that avoid the seasonal changes in the environment through migration have relatively smaller brains than the resident species (Sol *et al*., 2005b, 2010), providing indirect evidence for this prediction. However, studies on mammals suggest that the link between brain size and environmental variation could be more complex than often believed. For example, if growing and maintaining a large brain during periods of food scarcity is excessively costly, environmental variability could constrain rather than favour the evolution of large brains (van Woerden *et al*., 2010, 2011, 2014). Indeed, the existence of a trade-off between brain size and adipose depots in primates (Navarrete *et al*., 2011) suggest that enhanced cognition and fat storage could be alternative strategies to buffer against starvation. The goal of **Chapters 2 & 3** is to if test if environmental variation is related to relative brain size in birds. In the former, we will explore how living in seasonal environments affect brain size whereas in the latter we will explore the changes occurring after colonizing oceanic island characterized by higher environmental unpredictability.

Objective 3: The consequences of CBH for species diversification

When there are changes in the environment, a mismatch can occur between the current phenotype and that that would be optimal under the new circumstances. As we have seen, a relatively bigger brain can help to reduce this mismatch by favouring plastic behavioural responses to cope with the new situation. The woodpecker finch (*Cactospiza pallida*), for instance, can build tools to consume caterpillars from wood crevices, increasing survival during seasonal droughts causing food shortage (Tebbich *et al*., 2002). Behavioural changes may buffer individuals against environmental changes, but they may also favour evolutionary divergence if the behavioural changes are insufficient to reduce the mismatch between the phenotype and the environment. While this theory, called the "behavioural drive hypothesis" (Wyles *et al*., 1983), is supported by some evidence (Nicolakakis *et al*., 2003; Sol *et al*., 2005c; Sol & Price, 2008), current evidence is based on higher taxonomic orders (e.g. families or parvorders) or indirect measures of diversification rates (e.g. subspecies or species richness). The availability of new phylogenetic metrics to describe evolutionary rates, together with fully resolved phylogenies, provide an unprecedented opportunity to investigate how brain size affects diversification rates using species-level traits. Filling this gap is the goal of **Chapter 4**.

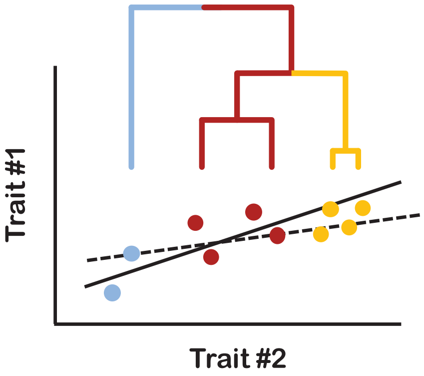

Figure 3. Correlation of two traits, where each point represents a species. An ordinary linear model (solid line) would be incorrect as it assumes that all points are independent, whereas a phylogenetic informed model (dashed line), takes into account the non-independence of data point by accounting for their phylogenetic relations.

How the above questions will be addressed?

All the above objectives are addressed using the phylogenetic comparative method (hereafter "PCM"), a collection of statistical methods developed to address evolutionary questions (Felsenstein, 1985; Freckleton *et al*., 2002). PCM combines two types of data: an estimate of species relatedness (the phylogeny) and the trait values of extant organisms (species traits). With this information, we can investigate associations between species traits, and test evolutionary hypotheses. One reason for the need to use PCM is that much of the phenotypic resemblance between closely-related species comes from their common ancestor rather than from independent evolution (Adams, 2008). If species cannot be treated as independent observations, the basic assumption of data independence of statistical methods is not fulfilled. PCM deals with this problem by estimating how well the phylogeny predicts the values of a focal trait. By estimating the degree of phylogenetic autocorrelation of the data, we can use this to give a proportional weight to each unit data ("each species") as an independent evidence of the hypothesis (**Fig. 3**). There are several available methods that can correct for phylogenetic non-independence between species. The phylogenetic least square approach was used in **Chapters 1 & 2**, whereas the phylogenetic Bayesian mixed model approach was used in **Chapters 3 & 4**.

PCM does not only allow to control for the non-independence of species, but also enables to investigate the "tempo and mode of evolution" (sensu Simpson, 1944). Methods like the Character Stochastic Mapping (Huelsenbeck *et al*., 2003) allow to reconstruct discrete traits and study the occurrence and distribution of different evolutionary transitions along the phylogeny. The reconstructed phylogenies can then be used to explore the "mode" of evolution by asking whether these evolutionary transitions influence selection on other phenotypic traits (**Fig. 4**). In **Chapter 2** these models were used to investigate whether random evolution or optimal selection better explain the brain size variation we observe today. Other PCMs allow to estimate the trait values at ancestral nodes, which can help disentangling whether changes in a trait occurred before or after changes in another trait. This provides important insight into the direction of evolutionary events and informs about causality. This method was used in **Chapter 3**. Finally, phylogenies can be used to quantify the rate of lineage diversification. There is plenty of evidence of shifts in speciation and extinction rates in different lineages and evolutionary biologists are intrigued by the origin of such shifts. PCMs also contain a vast number of statistical methods aiming to find how species traits affect diversification rates. Some of these models were used in **Chapter 4**.

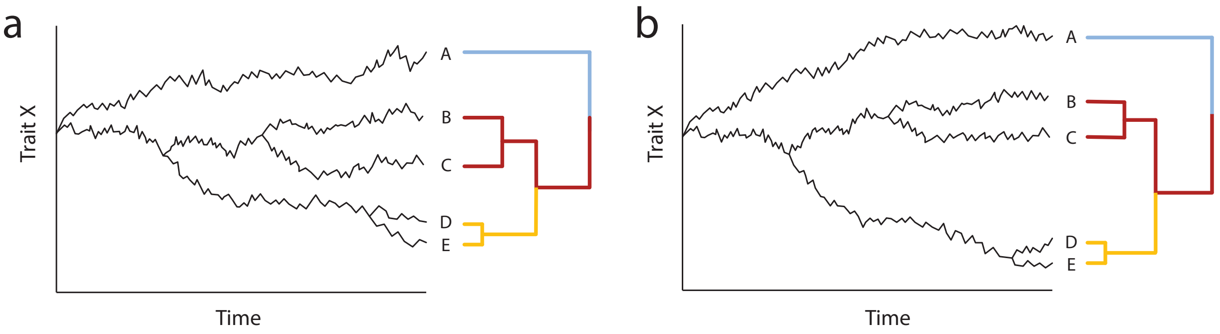

Figure 4. How the phenotype evolves might differ depending on another trait (A categorical trait represented by different colors). The focal trait X might just evolve through time at random (e.g. Brownian motion model,), where the amount of change depends on the time since speciation and the evolutionary rate of change of the trait under study (**a**). Another model of evolution can be described as a pull towards and optimal value (e.g. Ornstein-Uhlenbeck model), where there are distinct optimal values for trait X (**b**).

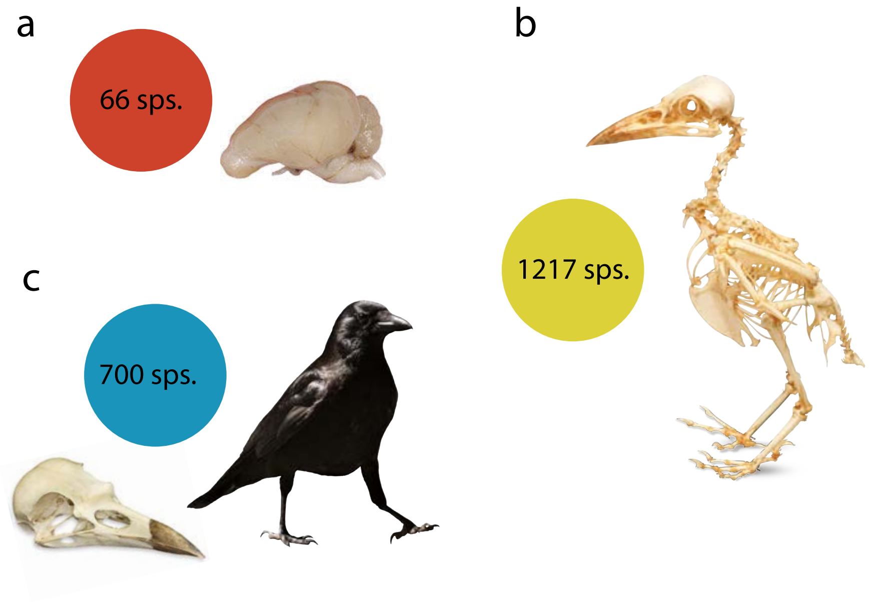

Figure 5. Summary of different sets of brain and body size data used in this PhD thesis. We used the volumes of several brain regions (a) in Chapter 1, the volume of the skull and their associated body size (b) in Chapter 2 and an additional 700 species in Chapters 3&4, with data on skull volume together with body data from the literature (c).

The study model: Birds

In this thesis, we used the whole radiation of extant birds as our study model. One of the main reasons is the huge availability of data for birds, compared to other animal groups. Because birds are relatively abundant and easy to observe, they are the best-known vertebrate group in terms of ecology, reproduction and behaviour, with highly detailed information available in the literature. The Handbook of birds of the World (Del Hoyo *et al*., 2016) represents a titanic initiative that gathers a large portion of this information in a single platform, which undoubtedly helped the acquisition of species trait information for this thesis. Another advantage of using birds is the existence of a complete phylogeny (Jetz *et al*., 2012), which provides an unprecedented opportunity to test many evolutionary questions.

Finally, birds also have the most extended databases of vertebrate brain size. In our case, we used three datasets gathered by Dr. Andrew Iwaniuk that allowed to answer the questions of each chapter (**Fig. 5**). Birds are also a good study system for brain evolution because several large brained lineages have evolved independently (**Fig. 6**), acquiring equivalent cognition capacities to that of primates (Emery & Clayton, 2004). Studying birds thus allows to broaden the focus from an anthropocentric view on the evolution of intelligence and helps to understand how higher cognitive capacities can evolve outside of the human lineage.

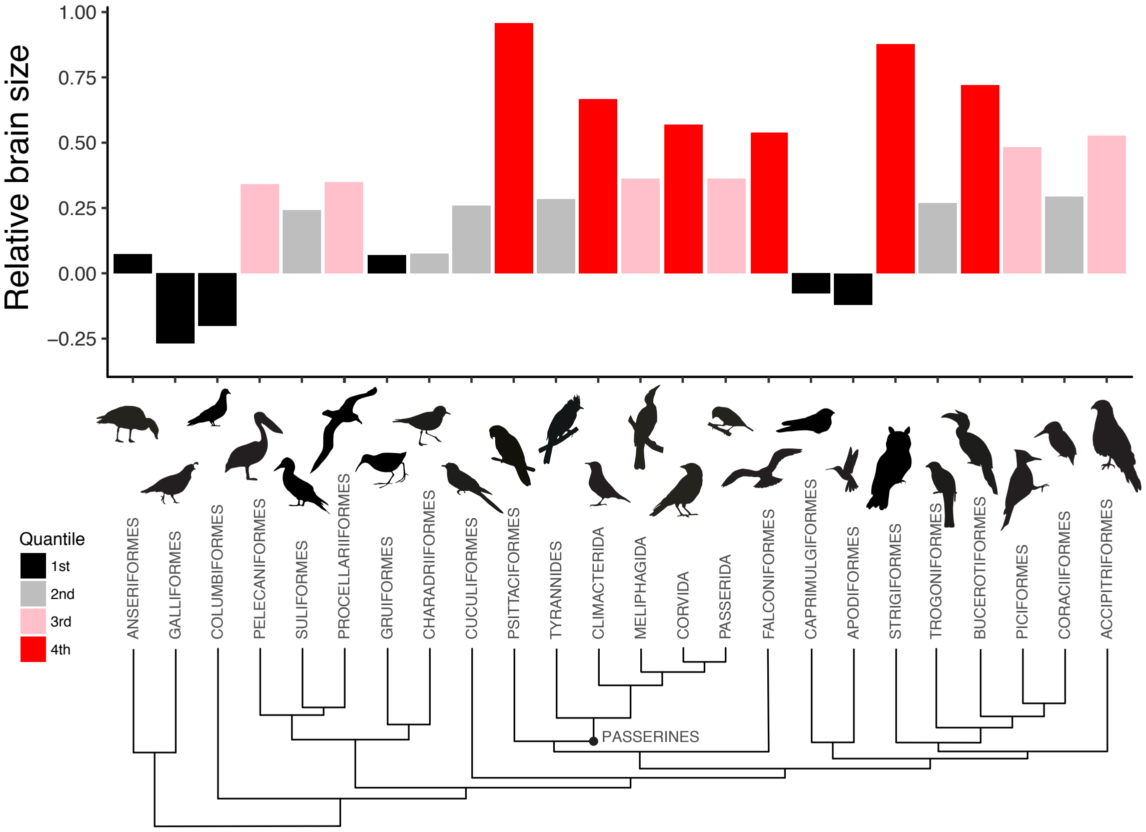

Figure 6. Independent brain size evolution in several bird lineages. The diagram represents the residual of a phylogenetically corrected log-log regression between brain size and body size across bird orders/ infraorders. The mean residual is shown for clades containing at least 15 species with brain information and coloured according to the degree of encephalization. When looking at the phylogenetic relations among clades, it becomes evident that relatively enlarged brains have evolved several independent times in the history of birds both within passerines (e.g. infraorders Climacterida and Corvida) and in other bird orders (e.g. Psittaciformes and Strigiformes). Although clades at the base of birds tend to have relatively smaller brains, other clades such as the orders Caprimulgiformes and Apodiformes have evolved relatively smaller brains secondarily.

Chapter 1

Relative brain size and its relation with the associative pallium in birds

SAYOL, F., LEFEBVRE, L., SOL, D.

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Abstract

Despite growing interest in the evolution of enlarged brains, the biological significance of brain size variation remains controversial. Much of the controversy is over the extent to which brain structures have evolved independently of each other (mosaic evolution) or in a coordinated way (concerted evolution). If larger brains have evolved by the increase of different brain regions in different species, it follows that comparisons of the whole brain might be biologically meaningless. Such an argument has been used to criticize comparative attempts to explain existing variation in whole brain size among species. Here, we show that pallium areas associated with domain-general cognition represent a large fraction of the entire brain, are disproportionally larger in large-brained birds and accurately predict variation in the whole brain when allometric effects are appropriately accounted for. While this does not question the importance of mosaic evolution, it suggests that examining specialized, small areas of the brain is not very helpful for understanding why some birds have evolved such large brains. Instead, the size of the whole brain reflects consistent variation in associative pallium areas and hence is functionally meaningful for comparative analyses.

1.1 Introduction

The phylogenetic-based comparative approach has become a major tool in investigating the evolution of the vertebrate neural architecture. Much of past effort has been devoted to assess whether existing variation in brain size among species predicts differences in cognitively-demanding behaviours. This has yielded ample evidence that larger brains are associated with enhanced domain-general cognition (Lefebvre *et al.*, 1997; Reader & Laland, 2002; Reader *et al.*, 2011; Benson-Amram *et al.*, 2016) and function to facilitate behavioural adjustments to socio-environmental changes (Reader & Laland, 2002; Sol *et al.*, 2005a, 2007; Schuck-Paim *et al.*, 2008; Sol, 2009a). Despite the progress, the biological significance of brain size variation across species is not exempt of criticisms (Healy & Rowe, 2007). A main argument has been that because brains are divided into functionally distinct areas, the analyses should focus on the areas to which a particular function could be ascribed (Healy & Rowe, 2007).

In fact, the validity of the above criticism depends on the classic, unresolved debate over the extent to which brain areas evolve independently of each other in a mosaic fashion (Barton & Harvey, 2000; Iwaniuk & Hurd, 2005; Barrett & Kurzban, 2006) or in a concerted way as a result of conserved developmental programs (Charvet *et al.*, 2011; Anderson & Finlay, 2013). If information processing in the brain is massively modular (Barrett & Kurzban, 2006), then larger brains can evolve by the increase of different brain regions in different species, making comparisons of whole brain size biologically meaningless (Harvey & Krebs, 1990; Healy & Rowe, 2007). However, if only some areas evolve in a concerted way, but together occupy a large part of the brain, then a disproportionate increase in these brain areas would be reflected in a larger brain regardless of the fact that smaller, more specialized, brain regions might evolve independently. This could be the case of brain areas like the avian mesopallium and nidopallium (which together form the associative pallium, hereafter AP) and the mammalian isocortex (Rehkämper *et al.*, 1991). If the most important part of whole brain size variation is driven by these large, concertedly evolving areas, then focusing on the whole brain in comparative studies would be a good proxy for variation in these areas. Comparative evidence suggests that taxonomic variation in the size of the primate isocortex and avian AP is associated with variation in a suite of correlated, domain-general cognitive abilities (Lefebvre *et al.*, 2004; Reader *et al.*, 2011) that include feeding innovation and tool use (Timmermans *et al.*, 2000; Lefebvre *et al.*, 2002; Reader & Laland, 2002; Mehlhorn *et al.*, 2010). Enhanced demands on domain-general cognition could thus be reflected in an enlarged cortex and AP, as well as an enlarged brain.

The debate over models of brain size evolution has not yet been settled in part due to disagreements on how brain size should be best quantified. In primates, as many as 26 different metrics have been used in large scale studies exploring ecological, life history and cognitive correlates of encephalization (reviewed in Lefebvre 2012). The comparative literature on birds is similarly based on a variety of metrics, which go from residuals to fractions and proportions of the whole or of parts of the brain (see table 1.1). The different ways in which the data are combined in the analyses adds additional uncertainties about what the size of the whole brain really means (Healy & Rowe, 2007).

In this paper, we use the most complete dataset on avian brain regions currently available (Iwaniuk & Hurd, 2005) to ask what really means the variation in brain size in terms of underlying structures. We use phylogenetically controlled analyses based on the current Bird Tree project (Jetz *et al.*, 2012) to examine inter-relationships between brain size, body size and the volume of six major brain parts, and assess the validity of several data transformation metrics used to control for allometry. We predict that a bigger brain should mainly correspond to an increase in AP, and hence that variation in these areas would strongly predict variation in the whole brain when using appropriate methods to remove allometric effects.

1.2 Methods

1.2.1 Data sources and phylogenetic hypotheses

Data on the whole brain and on volume of six brain parts were taken from Iwaniuk and Hurd (2005). Three regions part of the telencephalon which are the nidopallium - which includes also all of the nidopallial subregions (but see Iwaniuk and Hurd (2005) for more details)-, the mesopallium and the hyperpallium. Three other non-telencephalic regions include the cerebellum, the diencephalon and the brainstem – which is the sum of the mesencephalon and the myelencephalon. The six areas together form between 70 and 87 % of avian brain volume. Body mass data (g) were obtained from Dunning (2008). The phylogenetic hypotheses we used were taken from the Bird Tree project (Jetz *et al.*, 2012), where randomly sampled trees were taken from 2 different backbone coming from two independent studies (Hackett *et al.*, 2008; Ericson, 2012). We removed one species (*Pavo meleagris*) from the Iwaniuk and Hurd database, as in this set of phylogenetic trees it is considered the same species as *Meleagris gallopavo*, already present in the database (See Appendix Figure A.1 for an example of one of the phylogenetic hypothesis used).

1.2.2 Statistical analyses

We first calculated a correlation matrix between the six brain areas. We used the *phyl.vcv* function from 'phytools' R-package (Revell, 2012) with optimization of the parameter Lambda using maximum likelihood criteria to account for phylogenetic non-independence of the data. We then compared different ways of removing allometric effects for each brain part, using either body mass, volume of the entire brain or of a basal part, the brainstem. For a given brain part, for example the nidopallium, we tested the following measures: (1) absolute nidopallium volume; (2) residuals of nidopallium volume from a log-log regression against body mass or (3) brainstem volume; (4) nidopallium volume divided by brainstem volume, similar to the executive brain ratio used for primates; (5) nidopallium volume divided by the volume of the rest of the brain (fraction); or (6) by the volume of the entire brain (proportion). Measures 2 and 3 are thus residuals of log-log regressions and measures 4, 5 and 6 can be calculated using untransformed or log transformed volumes. We thus had nine different measures that we compared and tested for potential remaining effects of body size using phylogenetically corrected least-squares regressions (PGLS) using the R-package 'caper' (Orme *et al.*, 2013). This method, compared to a non-corrected regression, controls for the non-independence of data due to shared ancestry. Contrary to independent contrasts, however, it first determines the strength of the phylogenetic signal in the data (parameter lambda, which varies between 0 and 1 and is calculated using Maximum Likelihood; Pagel, 1999) and controls it accordingly, without assuming, as do contrasts, that lambda is 1. To this purpose, we used a set of 20 phylogenetic trees and calculated means over the 20 models.

For all further analyses, we used residuals only, as other metrics do not eliminate the effect of body mass (see Results). We next analysed the extent to which each brain region is associated with body size using PGLS models with log-transformed variables. To see which brain part best predicts whole brain variation, we took the residuals of whole brain volume against body mass and examined their relationship with the residuals of each brain part regressed against body mass. To illustrate these relationships, we plotted positive and negative whole brain residuals in different shades (black for positive and white for negative) and graphed them against brain part residuals. A brain part that predicts whole brain size well will yield clearly separated clouds of white and black points; in contrast, a brain part that does not predict whole brain size well will yield overlapping black and white data points. The extent to which positive and negative whole brain residuals are well separated in each graph can then be expressed by a histogram illustrating overlaps. We also used a set of PGLS models to determine which allometrically corrected brain part best explains variation in allometrically corrected whole brain size. A possible problem in the last two analyses is that we are correlating two variables that are residuals from the same predictor (body size), which might lead to some circularity. However, when using brainstem to remove allometry in the brain regions and body size to remove allometry in the whole brain, we obtained exactly the same results in terms of which parts explain most variation in the whole brain.

Finally, we conducted a phylogenetic reconstruction of whole brain residuals and associative pallium residuals - all corrected for body mass by taking phylogenetic residuals- on a sample tree using the *contMap* function of the ‘phytools’ R-package (Revell, 2012). This technique combines data on phylogeny and trait variation between clades to estimate evolutionary increases or decreases in different lineages.

1.3 Results

In terms of absolute size, all brain areas are positively associated with each other in phylogenetically corrected analyses (fig. 1.1a, Appendix Table A.1). Much of this trend is due to body size allometry, however, so we next examined the way different transformations of the original data affect the body size confound. Of all the metrics we tested, only those based on residuals and executive brain ratio calculated on log-transformed data completely removed the effects of body size (Appendix Table A.2). Analyses based on metrics such as fractions and proportions therefore do not deal exclusively with brain part variation, but also include body size.

When allometric effects are taken into account by estimating residuals, some areas show stronger inter-relationships than others, suggesting a combination of concerted and mosaic evolution (fig.1.1b, Appendix Table A.3). Concerted evolution is particularly evident for the areas forming the associative part of the telencephalon, notably the nidopallium and mesopallium ($r = 0.94$). These two areas show much larger amounts of variation independent of body size than do basal brain areas such as the brainstem (fig. 1.2, Appendix Table A.4). Phylogenetically corrected variation in nidopallium and mesopallium size correctly classifies 95 and 92% respectively of the positive and negative residuals of whole brain size regressed against body size (fig. 1.2a-b). In contrast, brainstem volume is strongly related to body size and does not discriminate between species with large versus small brain residuals (fig. 1.2e). As a consequence, brain to body size residuals are better predicted by variation in associative pallium residuals (mesopallium + nidopallium) than by other brain parts (fig. 1.3), regardless of whether allometry is corrected by body mass or brainstem volume (Appendix Table A.5). In fact, brain size and associative pallium (after corrections for allometric effects) are almost indistinguishable measures of encephalization (fig. 1.4; PGLS: $R^2 = 0.91$, $p < 0.001$). Inferring the evolution of avian brains with phylogenetic reconstructions yields virtually identical results with the two metrics (fig. 1.5), where we can see independent shifts in the increase of both relative brain and associative pallium sizes in crows and parrots and the reduction of these two measures in three practically independent clades (rheids, galliforms and swifts).

1.4 Discussion

Our analyses lead to three main conclusions regarding the evolution of the avian brain. First, all six brain parts analysed here tended to increase in a concerted way, a trend that was not simply a consequence of allometry or phylogeny. Second, some areas, notably those belonging to the associative pallium, evolved in a more concerted way than others. Finally, large brains primarily resulted from a disproportionate increase in these pallial areas. These areas are not only anatomically well delineated (thus minimizing measurement error), but also comprise a large fraction of the brain, in particular the nidopallium. Thus, the same proportional increase of these areas is likely to have a stronger effect on the size of the whole brain than that of smaller areas, an idea previously proposed by Rehkämper et al's (1991).

The associative pallium areas are known to have key roles in avian cognition. The nidopallium, in particular its caudolateral part, the NCL, is the closest avian equivalent of the mammalian pre-frontal cortex. Several lines of evidence, using different approaches and techniques connectome: (Shanahan *et al.*, 2013); single unit recording: (Rose & Colombo, 2005; Veit & Nieder, 2013; Lengersdorf *et al.*, 2015); receptor architecture: (Rose *et al.*, 2010; Herold *et al.*, 2011); temporary inactivation: (Helduser & Güntürkün, 2012); lesions: (Mogensen & Divac, 1993) point to the importance of NCL in avian executive control. Comparative work also suggests that the nidopallium is the brain area most closely correlated with avian tool use (Lefebvre *et al.*, 2002), while the other part of the associative pallium, the mesopallium, is most closely correlated with innovation rate (Timmermans *et al.*, 2000). The mesopallium is significantly enlarged in the bird with the most sophisticated form of tool use, the New Caledonian crow (*Corvus moneduloides*) (Mehlhorn *et al.*, 2010). The very tight relationship between nidopallium and mesopallium size, once phylogeny and allometry have been removed, further suggests that evolutionary changes in the two structures are strongly linked. Together, the two structures are the closest avian equivalent of the mammalian non-visual cortex. These areas appear to be a crucial to domain-general cognitive abilities.

Our results suggest caution in the use of absolute brain size to study the neural basis of cognitive skills, at least in birds. Given that this measure is confounded with body size, traits associated with body size (e.g. range, energetics, prey size) will confound any comparative test of brain size correlates. Using relative measures could be a solution to remove allometric effects, but we found here that dividing brain part volume by the volume of the whole (proportions) or the rest of the brain (fractions), with or without prior log transforms of the volumes, leaves significant body size confounds (Appendix Table A.1). Studies using these metrics (e.g. (Clark *et al.*, 2001; Burish *et al.*, 2004)) thus contain a hidden confound that might affect conclusions about evolutionary trends.

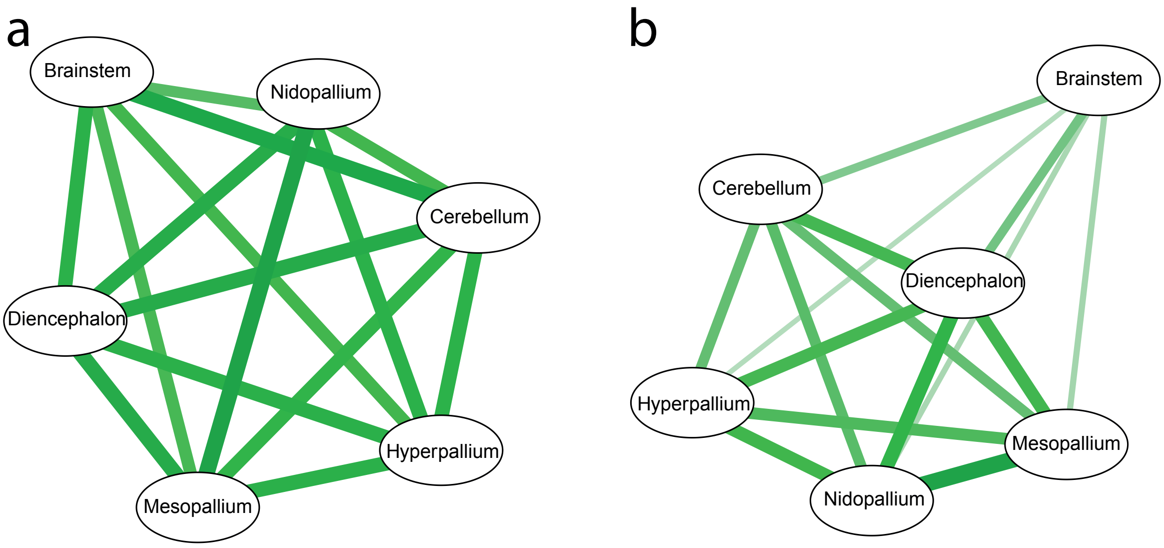
In contrast, residual brain size seems to better describe how brains increase due to a disproportionate enlargement of specific, large brain areas. Using residuals completely removes allometric effects on the brain but might face a problem of interpretation, as it is unclear what a disproportionately large area means in functional terms. The underlying assumption for existing variation in brain size among species is that any increase in size provides some increase in function. Although this is supported by growing evidence linking residual brain to enhanced cognition (Sol *et al.*, 2005a; Benson-Amram *et al.*, 2016) (but see a revision by Lefebvre & Sol, 2008), why should a disproportionate increase matter at all? Because the brain processes information, and this is done by discrete neurons acting together via neurotransmitters and receptors, the functional significance of volume differences might not be clear. In mammals, different orders have different scaling relationships of neuron numbers to brain area volume (Herculano-Houzel, 2011, 2012). Similar differences might well characterize bird brains. One can imagine, for example, that a corvid or a parrot mesopallium might have more neurons per mm^3 than a quail brainstem. Knowing this would obviously be important, but it would not change correlational trends of the type we report here, or the associations with cognition reported in the literature. We might in fact be underestimating selection on brain areas associated with cognition by focusing on mass or volume rather than neuron numbers if differences in density go in the same direction as differences in classical metrics of encephalization. This also assumes that neuron numbers is the main determinant of information processing capacity, not their connectedness or the density and type of neurotransmitters and receptors. Comparative studies of receptor density and gene expression in brain areas will shed new light on the functional significance enlarged brains (Goodson *et al.*, 2012).

The finding that enlarged brains have primarily evolved by the concerted increase of certain brain regions does not deny the importance of mosaic evolution. Indeed, the fact that some areas evolve more concertedly than others can be interpreted as a combination of mosaic and concerted evolution. Theoretical work on other biological systems (e.g. metabolic networks, (Ravasz *et al.*, 2002)) suggests that modular units are organized into hierarchical clusters, a principle that might reconcile modular and concerted views on the way in which the neural substrate of cognitive abilities operate and evolve. Moreover, mosaic evolution could be more important for small areas specialized in particular behaviours, which have not been evaluated here. A case in point is the network of song nuclei that has been extensively studied in oscines. Nuclei of this type are absent in non-oscines, with the exception of parrots and hummingbirds (Jarvis, 2007), and at least one of them, HVC, varies strongly as a result of sexual selection on repertoire size (Devoogd *et al.*, 1993; Moore *et al.*, 2011). If there is one clear case of adaptive specialization of brain areas in birds, it is the case of oscine song nuclei, which could evolve independently from other brain regions. However, these findings do not deny that, as our study suggests, the main variation in whole brain size is due to concerted changes in pallial areas, allowing the use of relative brain size as a proxy for relative pallium size in comparative studies.

Table 1. Encephalization metrics used in the comparative literature on birds. Res = residual; tel = telencephalon; region = varies according to study (e.g. mesopallium, nidopallium, hyperpallium, visual areas); rest of brain or tel = volume of the brain or telencephalon minus volume of the region studied.

Metric	Reference
Frequently used metrics	
Log brain mass	(Lefebvre & Sol, 2008); (Shultz & Dunbar, 2010b)
Res log (brain) log (body)	(Isler & van Schaik, 2006a); (Franklin *et al.*, 2014)
Res log (tel) log (body)	(Nicolakakis & Lefebvre, 2000); (Lefebvre & Sol, 2008); (Iwaniuk & Wylie, 2006)
Res log (tel) log (rest of brain)	(Iwaniuk & Wylie, 2006)
Volume tel/brainstem	(Lefebvre *et al.*, 1997)
Volume tel/brain	(Burish *et al.*, 2004)
Volume tel/rest of brain	(Shultz & Dunbar, 2010b)
Log region	(Lefebvre & Sol, 2008)
Res log (region) log (body)	(Timmermans *et al.*, 2000; Mehlhorn *et al.*, 2010)
Res log (region) log (body) log (other regions)	(Iwaniuk *et al.*, 2004)
Res log (region) log (tel)	(Fuchs & Winkler, 2014)
Res log (region) log rest of brain)	(Iwaniuk & Wylie, 2006; Gutiérrez-Ibáñez *et al.*, 2014)
Res log (region) log (rest of tel)	(Iwaniuk & Wylie, 2006);(Iwaniuk *et al.*, 2008)
Volume region/brainstem	(Lefebvre & Sol, 2008)
Volume region/ brain	(Iwaniuk & Hurd, 2005; Fuchs & Winkler, 2014)
Rarely used metrics	
Martin EQ	(Lefebvre & Sol, 2008)
Head volume	(Møller, 2010)
Shape based on absolute values	(Kawabe *et al.*, 2013)
Shape based on regressions against body size	(Kawabe *et al.*, 2013)
Telencephalon/brainstem of galliforme	(Lefebvre *et al.*, 1997; Zorina & Obozova, 2012)
Log tel/brainstem of galliforme	(Lefebvre *et al.*, 1998)
Skull height	(Winkler *et al.*, 2004)

Figure 1.1. Phylogenetic correlations between different brain regions, using (a) absolute values or (b) residuals from log-log regressions against body size.



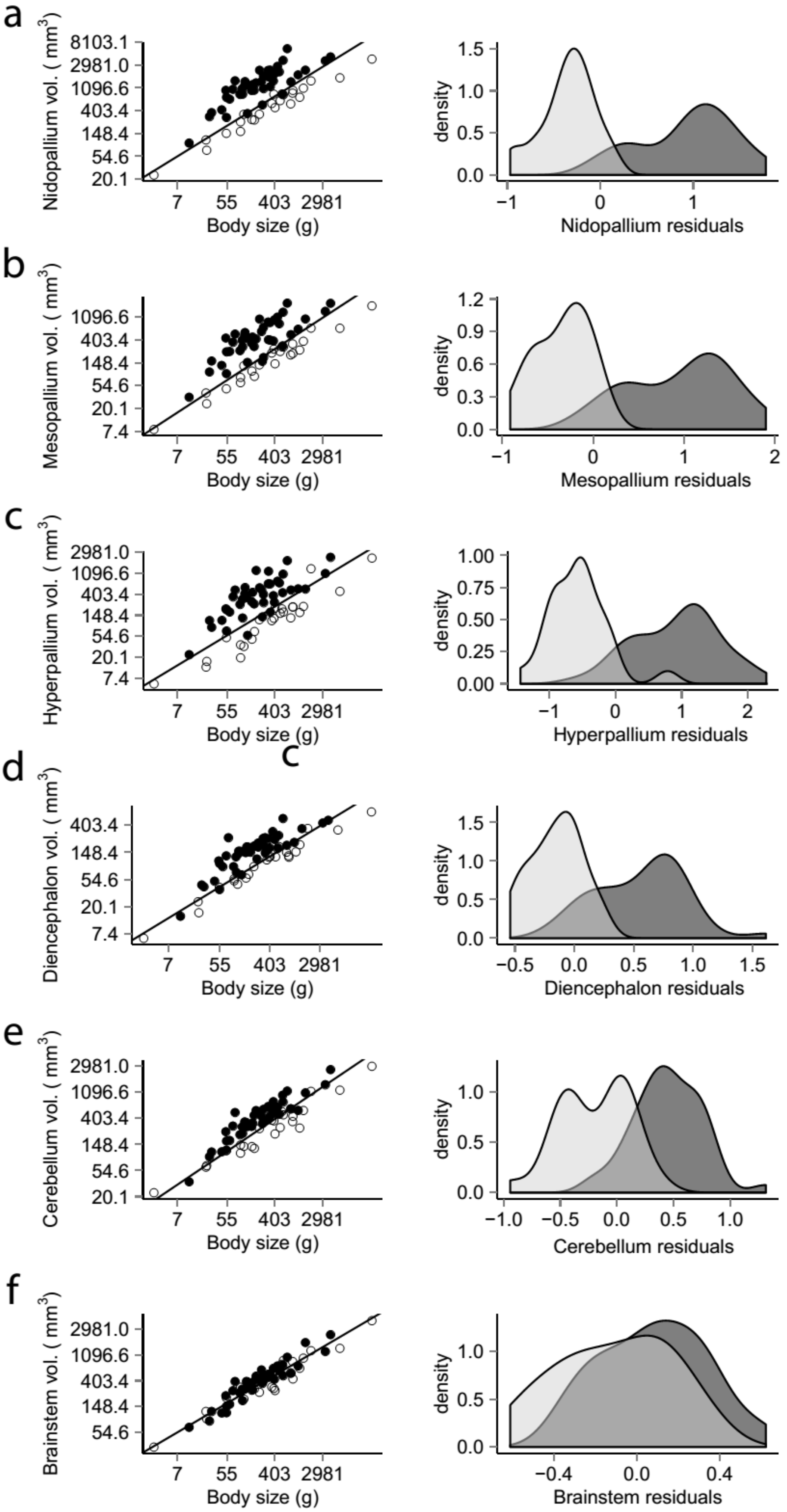


Figure 1.2. Log size of the six brain parts against log body mass, distinguishing species with positive brain residuals (black data points) and species with negative brain residuals (open data points). In the right of each plot, we present two histograms, one for each set of dots from the plots (black and open), corresponding to positive and negative brain residuals.

Figure 1.3. Relationship between residuals of different brain parts and whole brain residuals, all regressed against log body mass, with the R^2 for PGLS models represented on a schematic avian brain (redrawn based on Nottebohm, 2005).

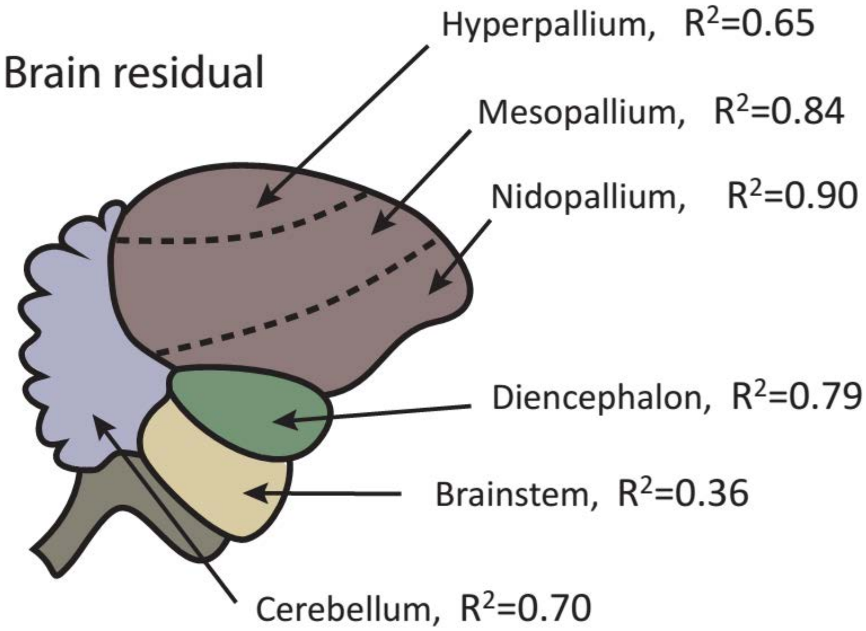


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Figure 1.4. Residual of whole brain size against body size plotted against residual of associative pallium size against brainstem size. The data points represent actual species, while the line represents the PGLS model. The slightly lower slope of the regression with respect to the cloud of data points is due to the phylogenetic corrections.

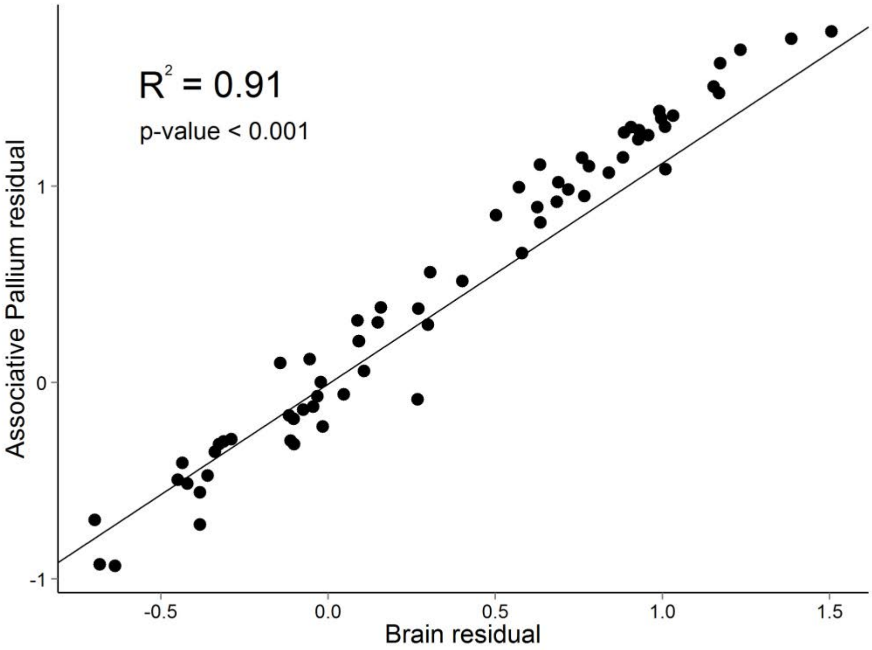

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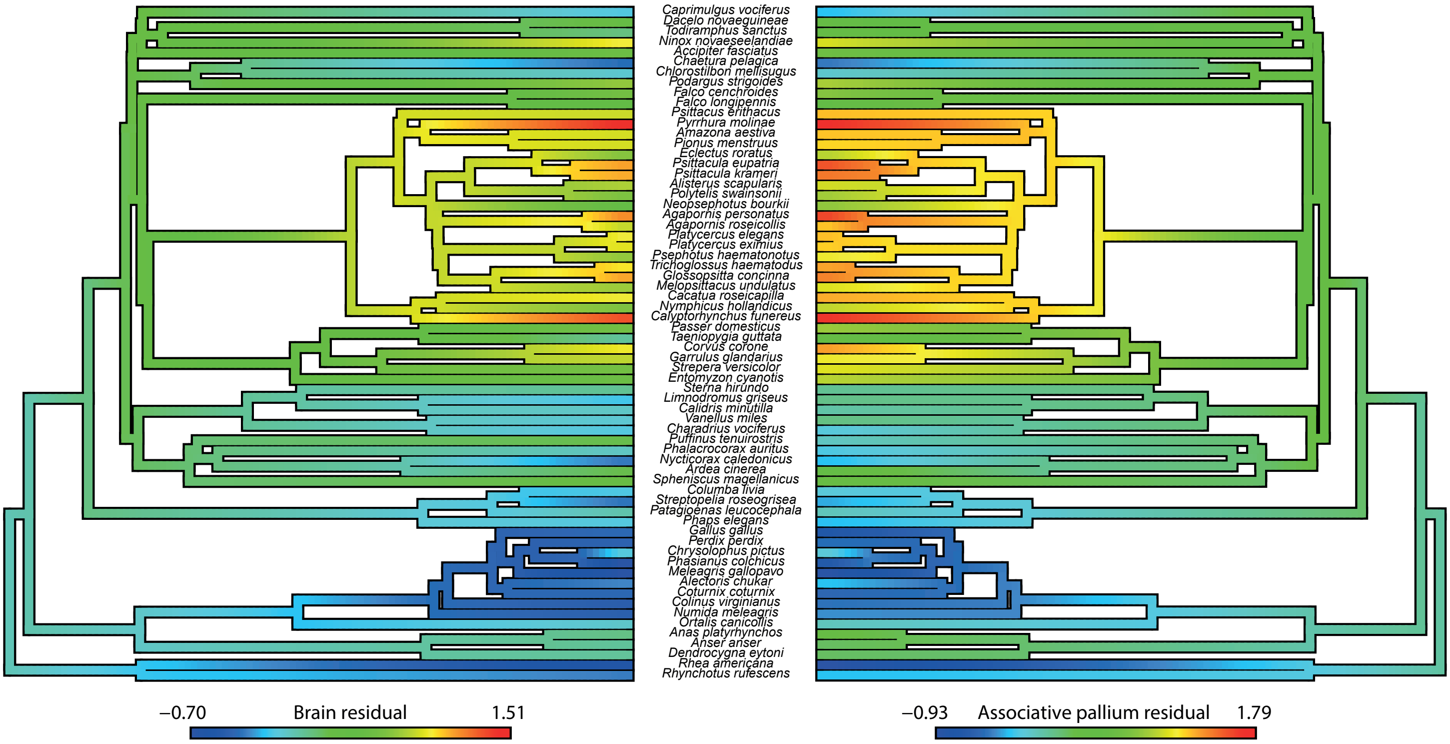
Figure. 1.5. Phylogenetic reconstruction in a sample phylogenetic hypothesis of birds in our dataset, representing residual brain size evolution and residual associative pallium size evolution.



Chapter 2

Environmental variation and the evolution of enlarged brains in birds

SAYOL, F., MASPONS, J., LAPIEDRA, O., IWANIUK, A.N., SZÉKELY, T., SOL, D.

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Abstract

Environmental variability has long been postulated as a major selective force in the evolution of large brains. However, assembling evidence for this hypothesis has proved difficult. Here, by combining brain size information for over 1,200 bird species with remote-sensing analyses to estimate temporal variation in ecosystem productivity, we show that larger brains (relative to body size) are more likely to occur in species exposed to larger environmental variation throughout their geographic range. Our reconstructions of evolutionary trajectories are consistent with the hypothesis that larger brains (relative to body size) evolved when the species invaded more seasonal regions. However, the alternative - that the species already possessed larger brains when they invaded more seasonal regions - cannot be ruled out. Regardless of the exact evolutionary route, our findings provide strong empirical support for the association between large brains and environmental variability.

2.1 Introduction

Despite wide interest in the evolution of the vertebrate brain, the reasons why some animal lineages—including humans—have evolved disproportionally large brains despite substantial energetic and developmental costs remain contentious. While a variety of selective pressures may have favoured the evolution of enlarged brains (Dunbar & Shultz, 2007; Isler & van Schaik, 2009; Barton & Capellini, 2011), one that has repeatedly been invoked in the literature is environmental variation. This idea is formally developed in the 'cognitive buffer' hypothesis (CBH, hereafter), which postulates that large brains evolved to facilitate behavioural adjustments to enhance survival under changing conditions (Allman *et al.*, 1993; Deaner *et al.*, 2003; Sol, 2009a). Cognition can increase fitness in varying environments by enhancing information gathering and learning, facilitating for instance shifts between different feeding sites or food types to alleviate periods of food scarcity (Sol *et al.*, 2005b; Roth *et al.*, 2010; van Woerden *et al.*, 2011).

Although the CBH was proposed more than 20 years ago (Allman *et al.*, 1993), the possibility that environmental variation has shaped brain evolution has garnered only modest empirical support (Reader & MacDonald, 2003; Schuck-Paim *et al.*, 2008; Sol, 2009a; van Woerden *et al.*, 2011). The absence of strong evidence is striking given the ample support for its main assumption that larger brains (relative to body size) facilitate coping with environmental changes by constructing behavioural responses (van der Bijl *et al.*, 2015; Benson-Amram *et al.*, 2016). The current modest support for the CBH hypothesis has led some authors to suggest that the link between brain size and environmental variation could be more complex than often believed (van Woerden *et al.*, 2010, 2011, 2014). For example, if growing and maintaining the brain during periods of food scarcity is excessively costly, environmental variability could constrain rather than favour the evolution of large brains (van Woerden *et al.*, 2010, 2011, 2014). The complexity of mechanisms linking brain size and environmental variation would explain why attempts to address the CBH in primates have generally been inconclusive (Reader & MacDonald, 2003; van Woerden *et al.*, 2010, 2011, 2014), despite its relevance to the evolution of large brains and enhanced cognition in humans (Vrba, 1985; Potts, 1998; Richerson & Boyd, 2000; Lefebvre, 2013). However, the absence of clear patterns in primates may also reflect that they live mostly in relatively benign tropical environments, where the realized net energy intake experienced by individuals does not necessarily match environmental variability (van Woerden *et al.*, 2011).

An excellent group in which to test for a link between brain size and environmental variability is birds, a clade containing species with some of the largest brains, relative to their body size, of any animal (Iwaniuk *et al.*, 2005). Being among the most widespread land animals, birds experience strikingly different degrees of environmental variation. Moreover, they have been at the forefront of the research into the functional role of enlarged brains in devising behavioural solutions to new challenges (Lefebvre *et al.*, 2004; Sol *et al.*, 2005a; Overington *et al.*, 2009). Surprisingly, however, only a few studies have addressed the CBH in birds, and the results do not always support it. In parrots, larger brains are associated with higher seasonality in temperature and precipitation (Schuck-Paim *et al.*, 2008). In passerine birds, species that reside the entire year in highly seasonal regions have brains that are substantially larger than those that experience lower environmental variation by migrating to benign areas during the winter (Sol *et al.*, 2005b). However, phylogenetic reconstructions have revealed that rather than selection for enlarged brains in resident species, the pattern could reflect costs associated with cognitive functions that have become less necessary in migratory species (Sol *et al.*, 2010).

Here, we test whether larger brains are related to environmental variability by means of a phylogenetic-based comparative analysis in birds. We assembled a large database of brain and body size measures of 4,744 individuals of 1,217 species from five continents. We then estimated annual variation in plant productivity (a more direct surrogate of resource variation than temperature and precipitation) throughout their geographic ranges and tested whether species exposed to larger environmental fluctuations within and among years also have relatively larger brains. Having shown this to be the case, we then conducted phylogenetic reconstructions of ancestral traits to ask whether the observed differences are consistent with past selection for enlarged brains in lineages invading regions with high temporal environmental fluctuations. This is achieved by testing whether the evolution of brain size fits better to an adaptive model of phenotypic evolution than a Brownian motion model (Beaulieu *et al.*, 2012). Although our main focus was on species residing the entire year in the same region, whose exposure to environmental variation is easier to characterize, we also investigated how species that migrate are affected by environmental variation. In this way, we could reconcile our findings with previous evidence suggesting selection for smaller brains in birds that experience lower degrees of environmental variation by moving to more benign regions during the winter (Sol *et al.*, 2010).

2.2 Results

2.2.1 The effect of seasonality on brain size

Previous work suggests that selection for larger brains and enhanced learning abilities should be particularly strong in animals inhabiting highly seasonal environments, which demand improved capacity of individuals to track resources that change during the year (Roth *et al.*, 2010; Gonzalez-Gomez *et al.*, 2015). Consequently, we first asked whether birds exposed to more pronounce seasonal fluctuations in resources are also characterized by disproportionally larger brains. In agreement with the CBH, birds residing the whole year in places with higher seasonal variation in EVI have significantly larger brains once accounting for phylogenetic and allometric effects (Table 1). Much of this seasonal variation is associated with latitude. Seasonal changes in EVI are more intense at higher latitudes than at lower latitudes (Appendix Figure B.1a), reflecting the drop on plant productivity during the cold winters. Supporting the importance of latitude on brain evolution, birds inhabiting regions at higher latitudes tend to have relatively larger brains compared to birds living at lower latitudes (Appendix Figure B.2, Appendix Table B.1).

2.2.2 Among-year variation, snow cover and brain size

At higher latitudes, the period of snow cover is longer than at lower latitudes (Appendix Figure B.1b). In places with frequent snow, selection for enlarged brains should be particularly strong as food must be obtained under difficult conditions and in a shorter daylight period (Roth *et al.*, 2010). Indeed, relative brain size significantly increases with the period of snow cover in resident species (Table 1). High latitude regions do not only experience more snow and higher seasonal variation in plant productivity, but variation in EVI among years is also more pronounced (Appendix Figure B.1c). This suggests that resources might not only be difficult to track during periods of food scarcity, but they could be unpredictable from year to year

(Stephens, 1991; Ancel, 2000). Again consistent with theoretical expectations (Stephens, 1991; Ancel, 2000), brain size (adjusted by body size) is positively associated with variation in EVI among years (Table 1).

2.2.3 The principal components of environmental variation

As the above environmental factors are not entirely independent of each other (see Appendix Table B.2), we used a Phylogenetic Principal Component Analysis (PPCA) (Revell, 2009) to produce orthogonal axes describing environmental variation. The first component explains 79% of the variance and has positive loadings on seasonal variation, duration of snow cover and among-year variation (0.97, 0.89 and 0.94 respectively, Appendix Figure B.1d). This axis therefore represents general environmental variation, with higher values at higher latitudes (Appendix Figure B.1e). The second axis explains 16% of environmental variation and loads positively on variation of EVI among years and negatively on snow cover (component loadings = 0.46, and -0.52, respectively). In contrast with the first axis, this second axis does not describe seasonal variation in EVI (component loading = 0.04) and has higher values at lower latitudes (Appendix Figure B.1f). Therefore, the second axis primarily reflects variation in EVI among years at lower latitudes (e.g. sporadic drought events).

2.2.4 Consistent evidence for the cognitive buffer-hypothesis

As predicted by the CBH, the two axes describing environmental variation are positively associated with brain size, relative to body size (Table 1), meaning that species that live in more variable environments also tend to have larger brains regardless of the type of variation (Ancel, 2000). This finding is consistent with the view that a relatively larger brain is useful not only in harsh regions (e.g. high latitudes with cold winters) (Roth & Pravosudov, 2009; Vincze, 2016) , but also in more benign regions that exhibit substantial year-to-year variation in environmental conditions (Schuck-Paim *et al.*, 2008).

2.2.5 Examining possible confound factors

The link between relative brain size and the axes of environmental variation (PPC1 and PPC2) in resident birds is not sensitive to phylogenetic uncertainties or potentially confounding variables. First, the results are highly consistent when using 100 randomly selected trees

(Appendix Figure B.3) from the posterior distribution of trees from BirdTree project (Jetz *et al.*, 2012). Second, the observed patterns cannot be attributed to changes in body size as being larger or smaller does not co-vary with PPC1 or PPC2 (PGLS: $P > 0.12$ in all cases; see also refs (Mayr, 1956; James, 1970)). Third, although previous work has suggested that species may be more or less vulnerable to seasonal changes depending on their diet type (e.g. frugivoury or insectivoury) and preference for buffered habitats (e.g. forests) (Sol *et al.*, 2010), including these factors in the models does not alter the conclusions (Appendix Table B.3). Fourth, the association between environmental variation and relative brain size is not indirectly caused by differences in diet generalism (Appendix Table B.4), despite generalists tending to have relatively larger brains and a higher propensity for behavioural innovation (Ducatez *et al.*, 2014; Sol *et al.*, 2016). Fifth, the effect of environmental variation on relative brain size remains significant even when considering life history traits (particularly developmental periods (Iwaniuk & Nelson, 2003; Isler & van Schaik, 2009; Barton & Capellini, 2011)) that may constrain brain size evolution (Appendix Table B.5). Sixth, although according to the social intelligence hypothesis the demands of social living might have selected for enlarged brains (Dunbar & Shultz, 2007; Shultz & Dunbar, 2010b), including factors that represent social behaviour (i.e. social mating system (Dunbar & Shultz, 2007), coloniality (Evans *et al.*, 2016) and social foraging (Shultz & Dunbar, 2010b)) does not alter the patterns we report in the present study (Appendix Table B.6) . Finally, the axes defining environmental variation are not only significantly associated with brain size even when simultaneously accounting for all the suggested confounds (Appendix Table B.7), but both also consistently appear in all the best models resulting from a model selection procedure (See Appendix Table B.8 for the best models and Fig. 2.1 for the weight importance of each factor). Although the paucity of information for some traits notably reduced sample size, the model selection and the full model confirmed some previous findings. Thus, larger brains, relative to body size, are also associated with longer incubation periods (see also Appendix Table B.5) and broad diet requirements (see Appendix Table B.4).

2.2.6 The brain-environment association inside avian orders

While the positive association between environmental variation and brain size holds for the majority of avian orders with representatives in regions with highest environmental variation, a notable exception is Galliformes (Fig. 2.2). The reasons of such discrepancy are unclear, but could reflect that these species thrive in seasonal regions by means of specialized adaptations rather than plastic behavioural responses. Possible adaptations include a reduced metabolism, specialization on low-quality foods (e.g. coniferous needles) that are available the whole year (Stokkan, 1992) and the investment in other organs at the expense of the brain (Navarrete *et al.*, 2011). These specializations would not only constrain the evolution of larger brains, which are energetically costly (Navarrete *et al.*, 2011), but also would make exploration and learning less critical for survival (Overington *et al.*, 2011; Ducatez *et al.*, 2014).

2.2.7 The effect of the environment on migratory birds

Unlike species that reside the entire year in the same region, migratory birds avoid the drop in resources during the winter by moving to more benign regions (Fig. 2.3, Appendix Table B.9). Moving also allows them to mitigate variation in productivity across years, as at the wintering areas fluctuations in EVI among years are highly reduced compared to those observed at higher latitudes (Appendix Figure B.4). Consistent with the lower exposure to environmental variation, in migratory birds the relative size of the brain does not covary with seasonal or among year variation in EVI (Appendix Table B.10). However, the strategy of avoiding the harshest season by moving away is costly, requiring substantial amount of energy to travel between breeding and wintering areas (Klaassen, 1996). Interestingly, relative brain size is not only smaller in migrants compared to tropical and temperate residents, in agreement with previous studies(Sol *et al.*, 2010), but brain size also decreases with travelling distance (Appendix Table B.11). This effect remains robust to the influence of confounding variables (Appendix Tables B.12-13, see also Appendix Figure B.5 for differences within orders). The relationship between migratory distance and relative brain size thus agrees with the energy trade-off hypothesis, which predicts that the brain should be smaller if more energy needs to be allocated to other tissues (e.g. pectoral muscle to fly longer distances (Isler & van Schaik, 2006a)).

2.2.8 Evolutionary reconstructions of the evolution of brain size

To more formally investigate the adaptive nature of the links between brain size and environmental variation, we used a character stochastic mapping approach to reconstruct in a phylogeny transitions among tropical and temperate regions and, within the latter, between resident and migratory strategies (Fig. 2.4). These reconstructions were then used to test whether the subsequent evolutionary trajectories in relative brain size better fit either adaptive

(Ornstein–Uhlenbeck - OU) or random (Brownian motion - BM) models of evolution (O'Meara *et al.*, 2006; Thomas *et al.*, 2006; Beaulieu *et al.*, 2012). Evolutionary reconstructions based on stochastic character mapping (Nielsen, 2002; Huelsenbeck *et al.*, 2003) reveal several independent transitions between tropical and temperate regions and between resident and migratory strategies (Fig. 2.5a). The best supported evolutionary model is an adaptive model, called OUMV model (Arnold, 1992), that assumes the existence of different optima for each selective regime and differences in the amount of phenotypic variation (σ^2) around each optimum (Appendix Table B.14). The estimates of brain size optima from this model are consistent with the hypothesis that species evolved towards larger brains (relative to body size) when moving from tropical to temperate regions (Fig. 2.5b, Appendix Table B.15). In addition, long distance migrants have a smaller brain optimum compared with residents, further confirming previous evidence (Sol *et al.*, 2010; Vincze, 2016), and exhibit lower variation around this optimum perhaps reflecting a trade-off between brain size and the costs of locomotion (Navarrete *et al.*, 2011).

2.3 Discussion

Our results are consistent with the long-held hypothesis that environmental variation may have been an important selective force in the evolution of enlarged brains (Allman *et al.*, 1993; Deaner *et al.*, 2003; Sol, 2009a). However, encephalization is a multifaceted process and other selective pressures are likely to have played a role in brain size evolution (Dunbar & Shultz, 2007; Barton & Capellini, 2011; van Schaik & Burkart, 2011). Although the some of our models have limited explanatory power, this is nonetheless unsurprising considering that body size accounts for the major part of variation and other environmental factors and constraints may also influence brain size evolution (Iwaniuk & Nelson, 2003; Isler & van Schaik, 2006a; Dunbar & Shultz, 2007; Shultz & Dunbar, 2010b). Yet, it is worth noting that when accounting for several confound factors or within particular clades the variation in brain size explained by environmental variability is substantial (e.g. 43% with all confound factors; 19% in Piciformes and 44% in Strigiformes). Thus, although the external environment might exert strong selection on cognition and brain size, the evolutionary response is likely to also depend on how the animal interacts with the environment and the extent to which its phenotype constraints certain evolutionary trajectories (Ancel, 2000). The fact that the explanatory power of environmental variation is low for some avian lineages is indeed consistent with the existence of alternative factors influencing brain size evolution. One factor particularly important according to our analyses is a generalist ecology, which may favour larger brains by frequently exposing individuals to novel or unusual conditions that require behavioural adjustments (Overington *et al.*, 2011; Ducatez *et al.*, 2014; Sol *et al.*, 2016). Other factors may also be important despite not being identified in our analyses. For instance, although none of our three measures of sociality was associated with relative brain size, in clear contrast with previous analyses (Shultz & Dunbar, 2010b; van Schaik *et al.*, 2012), this may simply reflect that our metrics do not fully capture key aspects of bird sociality. Finally, our analyses highlight that brain size evolution may also be influenced by constrains (Iwaniuk & Nelson, 2003; Isler & van Schaik, 2009; Barton & Capellini, 2011), like the need of a long developmental period to grow a disproportionally larger brain, and selective pressures favouring smaller brains, like those associated with long-distance movements in migratory birds.

Our approach, however, does not reveal whether species evolved larger brains when they invaded more seasonal regions or instead their ancestors already possessed larger brains when those regions were colonized. Yet given the high metabolic and developmental costs of a large brain (Isler & van Schaik, 2006a; b), in highly variable environments the maintenance of a large brain through stabilizing selection seems unlikely unless it provides some sort of benefit that compensates for the costs. If so, the alternative that the ancestors already possessed larger brains when colonized highly variable environments would still be consistent with the CBH. In fact, the two explanations are not mutually exclusive. If a large brain is an important adaptation to cope with environmental variation, highly variable environments should both prevent the establishment of species with small brains and select for larger brains in those that are able to persist there by means of plastic behaviours.

The possibility that a large brain functions, and hence may have evolved, to cope with environmental variation is relevant to understand how animals will be threatened by human-induced rapid environmental changes, notably climate change (Sih, 2013). If large brains have evolved in slow-lived species to cope with environmental changes, the same species should also be better prepared to cope with climate change and habitat loss. While evidence is accumulating in support of this possibility (Shultz *et al.*, 2005; Sol *et al.*, 2005a; Maklakov *et al.*, 2011), it still remains an open question whether adaptive strategies that have been selected in past environments are necessarily appropriate to cope with current environmental challenges

(Sih, 2013). Given the increased concern over how climate change and habitat loss will impact on biodiversity, we anticipate that addressing this issue will be an important avenue for future research.

2.4 Methods

2.4.1 Brain measurements

We estimated brain volumes for 4,744 museum specimens from 1,217 species using the endocranial volume technique. This method consists in filling each skull via the foramen magnum with a 50:50 mixture of sizes 10 and 11 lead shot. Once the endocranial cavity was filled, the lead shot was decanted into modified syringes to determine brain volume. This method is highly repeatable and yields a reliable estimate of true brain size (Iwaniuk & Nelson, 2002). As a way to improve the precision of the measures, we only measured museum specimens of known body size and sex. When more than one specimen per species was examined, we first estimated the average brain volume for each sex and then we estimated the species value as the mean brain volume of the two sexes. Despite the heterogeneous functional organization of the brain, the pallial areas associated with general-domain cognition represent a large fraction of the entire brain, are disproportionally larger in large brained birds and accurately predict variation in the whole brain when allometric effects are appropriately accounted for (Lefebvre & Sol, 2008; Sayol *et al.*, 2016a).

2.4.2 Species geographical range and migratory behaviour

For each species, we extracted the information of the geographical range from BirdLife International Maps (BirdLife International & NatureServe, 2012). In our analysis, only distribution areas (e.g. polygons) coded as extant or probably extant were included. Non-native distribution areas (i.e. places where species have been introduced species) were excluded. Based on geographic information, we distinguished migratory from resident species on the basis of the existence of distinct breeding and non-breeding regions (Newton, 2010). Therefore we use migratory category in a broader sense, partial migrants being included in this category as well(Somveille *et al.*, 2013). However, we further refined it by estimating migratory distance, measured as the distance on the Earth surface from the breeding centroid to the non-breeding centroid. This two points (P1 and P2) on the earth surface are determined by a latitude and longitude in radiant measures: P1(*Lat1,Lon1*), P2(*Lat2,Lon2*). In Cartesian coordinates we have P1(*x1,y1,z1*) and P2(*x2,y2,z2*), where x, y and z are determined by the spherical coordinates (where R is the earth radius; R=6378 Km). Accordingly, $x= R * \cos(Lat) * \cos(Lon)$; $y = R * \cos(Lat) * \sin(Lon)$; $z = R * \sin(Lat)$ and we can calculate then the Euclidean distance d between P1 and P2 by the three-dimensional Pythagorean theorem: $d = \sqrt{(x1-x2)^2+(y1-y2)^2+(z1-z2)^2}$. This Euclidean distance was used as a proxy of the migratory distance travelled in kilometres. For partial migrants, if both breeding and wintering areas were available, the distance was calculated between these two areas. If not, the distance was calculated as the distance between resident centroid and non-breeding centroid or resident centroid and breeding centroid. We then plotted the migratory distance frequencies and we identified two clearly defined groups: birds migrating less than 5000 km and birds migrating more than 5000 km (Appendix Figure B.6). This threshold was used to classify short and long-distance migrants. Finally, we also divided resident species into low latitudes (between 0° and 20° of latitude centroid of breeding regions), medium latitudes (between 20° and 40°) and high latitudes (above 40° of latitude). Therefore, we ended up with five categories (short-distance migrants, long-distance migrants, high latitude residents, medium latitude residents and low latitude residents) representing different selective regimes for environmental variation (either characterized by degree of seasonality due to latitude differences or by mobility among regions). We then classified each of the 1,217 species for which we had information for brain size in one of these categories (See Appendix Figure B.7, drawn using 'mapdata' (Becker *et al.*, 2016a) and 'maps' (Becker *et al.*, 2016b) R-packages). Altitudinal movements and nomadic movements were not considered, so species following these movement patterns were pooled together within the category of resident species. Finally, birds that spent an important part of their life in open sea (e.g. pelagic birds) were neither considered because their migratory routes are largely unknown and the seasonality in their resources cannot be estimated using EVI information, as is the case for land species.

2.4.3 Environmental data. To characterise environmental variability, we used data from MODIS sensor, which was processed to generate the enhanced vegetation index (EVI)(Land Processes Distributed Active Archive Center (LP DAAC), 2001), which measures the degree of greenness and provides a proxy to quantify plant productivity at large scales (Boyd *et al.*, 2011; Fernández-Martínez *et al.*, 2015). EVI is a measure derived from the normalized difference vegetation index (NDVI). Both indices use chlorophyll radiation to estimate active leave density, which is a good proxy of primary production(Phillips *et al.*, 2008). However, EVI has improved sensitivity in high biomass regions and improved vegetation monitoring through a decoupling of the canopy background signal and a reduction in atmosphere influences. EVI index is therefore a good proxy for primary productivity over time (Boyd *et al.*, 2011; Fernández-Martínez *et al.*, 2015). We used EVI time series from the available years (2000 to 2014) at 16 days of temporal resolution and 0.05° of spatial resolution(Land Processes Distributed Active Archive Center (LP DAAC), 2001). We estimated EVI of each breeding and non-breeding area using 'sp' (Pebesma & Bivand, 2005; Roger S. Bivand, Edzer Pebesma, 2013), 'raster' (Hijmans *et al.*, 2015) and 'rgdal' (Bivand *et al.*, 2016), 'rgeos' (Bivand & Rundel, 2016) R-packages (R, 2013). This was done by intersecting the raster of environmental data with the polygons of the corresponding distribution areas of species in each period of the year. Using the 16 day product, we calculated inter-year Mean and SD for each of the 23 Julian days provided for the product along the 15 year of the temporal series. With this data, we obtained EVI annual mean, the EVI mean for breeding and non-breeding periods and the coefficient of variation (CV) of EVI among years and within years. For CV of EVI among years, we first calculated the CV for each day of the year and then computed the mean of the values. For the CV of EVI within the year, we used the mean values of EVI for each day of the year to calculate the CV. For migratory birds, we only used information from the breeding areas in the breeding season and the wintering areas in the non-breeding season, thus avoiding the period for which migratory birds are moving. For the northern hemisphere, December-February is considered the non-breeding season and May-July is the breeding season. In the southern hemisphere we considered December-February (Julian days 337, 353, 1, 17, 33 & 49) to be the breeding period and May-July is the non-breeding season (Julian days 129, 145, 161, 177, 193 & 209). To measure the variation we used the coefficient of variation (CV hereafter) instead of the standard deviation (SD) to avoid the higher influence of the mean on the SD. When calculating the CV, we added to all values of the mean EVI the minimum value plus 1 to make sure the minimum value of the data did not included 0 or any negative value. For resident species, it was also possible to quantify the average weeks of snow cover per year over their distribution areas. For this purpose, we used MODIS snow cover series (Hall *et al.*, n.d.) from 2000 to 2014 at 1 week of temporal resolution and 0.05° of spatial resolution. With the snow cover data, CV of EVI among years and along the year, we calculated the First and Second Component of a PCA using the *phyl.pca* function from 'phytools' R-package (Revell, 2012).

2.4.4 Diet breadth and other ecological factors. Birds could be affected differently by the seasonality of the environment depending on a number of factors, and these were taken into account in the analyses. First, we estimated diet breadth of each species. Each species was scored along a scale for every one of the seven different food categories: vertebrates, carrions, plants, fruits, seeds, pollen/nectar and invertebrates**.** The scale considered four possibilities: almost exclusively consumed (1), frequently consumed (0.5), rarely consumed (0.1) and not consumed (0). Categories described as 'chiefly', 'primarily', 'exclusively' or 'mainly' consumed, were given a score of 1; categories described as 'usual' or included in food items' enumerations (e.g. 'variety of foods including [enumeration of foods]', 'diet includes [enumeration of foods]') were given a score of 0.5; and categories reported as 'occasionally', 'opportunistically' or 'rarely' consumed were given a score of 0.1. We considered information at the species level, and therefore gave to each food category the maximum value reported in any of the populations of the species (e.g. if one population only eats fruits but another population of the same species eats fruits and insects, "fruits" was given a score of 1 and insect a score of 0.5). Note however that for the great majority of species, details on diet composition at the population level were not available. We then estimated diet breadth using Rao's quadratic entropy as implemented in the R-package 'indicspecies' (Caceres & Legendre, 2009; Cáceres *et al.*, 2011). This approach estimates diet breadth as the number of categories consumed taking into account that different food items have different degrees of similarity among each other. The approach thus uses the frequency of use of each food category as well as a distance matrix of similarity between categories. Two species including two food categories in their diet might have different diet breadths, depending on how similar these categories are. For example, according to our index of diet breadth, a species that consumes two distant food categories (e.g. fruit and vertebrates) is considered as having a broader diet than another that consumes two more closely related categories (e.g. grass and seeds). The distance matrix used was calculated as a Euclidean distance (Appendix Figure B.8) using published information on water and nutrient content (percentage of sugars, lipids, protein) of each food category: Fruits (Foster, 1977; Herrera, 1987); Plants (Treichler *et al.*, 1946; McLandress & Raveling, 1981); Seeds (Christian & Lederle, 1984; Kelrick *et al.*, 1986; Kerley & Erasmus, 1991); Nectar/Pollen (Baker, 1975; Pyke, 1980); Vertebrates (Bernard & Allen, 1997; Dierenfeld *et al.*, 2002; Özogul *et al.*, 2008); Invertebrates (Bernard & Allen, 1997; Fagbuaro *et al.*, 2006; Deblauwe & Janssens, 2008; Kinyuru *et al.*, 2010; Oonincx & Dierenfeld, 2012). In addition to this continuous index of diet breadth, we included in our dataset two categorical factors describing the consumption of two highly seasonal resources: fruits and insects (Carnicer *et al.*, 2008). We classified each bird species as a fruit consumer (1 = consumer / 0 = not a consumer) or insect consumer (1/0). We consider a species a fruit or insect consumer if that species frequently or only eats the specific food source (1 and 0.5 scores in the diet data detailed before), but not if they consume it occasionally (0.1 score). Third, we took into account whether birds were forest dwellers or not (1/0) because this habitat might buffer seasonal changes (Chesser & Levey, 1998). A species was classified as a forest dweller if it regularly uses forest habitats for breeding. We considered as forest any landscape covered with trees or woody vegetation above three meters. All the information on diet and habitat uses was obtained from the Handbook of Birds of the World Alive (Del Hoyo *et al.*, 2016).

2.4.5 Developmental times, developmental modes and sociality measures.

Length of the incubation and fledging periods were obtained as the number of days between laying to hatching and from hatching to fledging, respectively, and was obtained from various published sources (Bennett, 1986; Szekely *et al.*, 1996; Ricklefs, 2000; Badyaev & Ghalambor, 2001; Jouventin & Dobson, 2002; Lloyd & Martin, 2003; Scheuerlein & Ricklefs, 2004; Figuerola & Green, 2006; Clark & Martin, 2007; Cassey *et al.*, 2012; Galván *et al.*, 2012; Pienaar *et al.*, 2013; Tacutu *et al.*, 2013; Huang *et al.*, 2013; Del Hoyo *et al.*, 2016). Developmental mode was obtained from Iwaniuk's database(Iwaniuk & Nelson, 2003) considering four categories (precocial, semiprecocial, altricial and semialtricial). Superprecocial species were considered precocial to reduce the number of categories. For a few species for which information was available, we used the family value as at this taxonomic level, we found no discrepancies among species in developmental mode. Social mating system was obtained from published sources (Lenington, 1980; Johnsgard, 1981; Cramp *et al.*, 1998; Rubolini, 2004; Liker & Székely, 2005; Poole, 2005; Shultz & Dunbar, 2010a; García-Peña *et al.*, 2013; Del Hoyo *et al.*, 2016), categorizing species as monogamous or polygamous. We considered a species as socially monogamous if it raises offspring with a single mate, even if there are some levels of extra-pair paternity. Other forms of mating systems (e.g., polygyny, polyandry), were therefore considered polygamous. A third category – facultative mating system – was subsequently added for species in which both monogamy and polygamy are reported (e.g. the Boreal Owl (*Aegolius funereus*) is monogamous but there are some cases of polygyny and polyandry reported that coincide with peak periods of voles' abundance). We then defined the Colonial breeding as the degree of nest aggregation during the breeding season: we considered as colonial a species that breeds in a site with multiple nests of the same species close to each other, with no territorial defense; solitary breeders consisted in species that breed within a territory that defend from competing conspesifics. A third category, semi-colonial species, included species that breed in loose colonies (sparse aggregations of nests) or may shift between colonial and territorial breeding (e.g. the White-faced Heron *(Egretta novaehollandiae)* normally breeds solitary but sometimes breeds in colonies). All information for colonial breeding was obtained from the Handbook of the Birds of the World Alive (Del Hoyo *et al.*, 2016). Social foraging was defined by the degree of gregarious foraging behaviour outside of the breeding season. Solitary species were defined as those where birds forage alone. Pairs were defined as those where two reproductively mature adults continue to forage together in the non-breeding period, sometimes with other family parties. Bonded foraging groups were defined by small (<30) and stable group membership, where individuals always forage with the group. Aggregations were defined as species foraging in large numbers (>30) or by cases of highly variable social foraging, where both solitary and group foraging occur. Data for social foraging was obtained from Shultz & Dunbar (Shultz & Dunbar, 2010b) and completed with information from the Handbook of the Birds of the World Alive (Del Hoyo *et al.*, 2016).

2.4.6 Phylogenetic hypotheses

We randomly extracted 100 fully resolved trees from the Bird Tree project (Jetz *et al.*, 2012) for all our species (n = 1217) . With the 100 trees, we built the maximum clade credibility tree (summary tree) using TreeAnnotator (a program included in the software BEAST v1.8.0) (Drummond *et al.*, 2012). Trees from the Bird Tree project include species for which no genetic information is available. Removing the 146 species with no genetic information in our sample does not affect our results.

2.4.7 Phylogenetic correlations

We modelled brain size (log-transformed) as a function of environmental variability and additional covariates by means of Phylogenetic Generalized Least Squares (PGLS) approach (Freckleton *et al.*, 2002). We used the *pgls* function in the R-package ‘caper’ (Orme *et al.*, 2013), which implements GLS models accounting for phylogeny through maximum likelihood estimations of Pagel's λ (Pagel, 1999). We used the consensus phylogenetic tree for all the PGLS analysis, but we re-ran the key analyses with the 100 different trees to account for phylogenetic uncertainty. In birds, enhanced learning abilities are not indicated by absolute brain size, but by the extent to which the brain is either larger or smaller than expected for a given body size (Lefebvre *et al.*, 1997; Lefebvre & Sol, 2008; Overington *et al.*, 2009). Consequently, we always included body size (log-transformed and extracted from the same specimens for which brains were measured) as a co-variate when we modelled brain size as a response. However, we also re-ran the analysis with relative brain size, estimated as the residuals of a log-log PGLS of brain against body size (Appendix Figure B.9), to assess partial R^2.

2.4.8 Phylogenetic reconstructions

To assess whether historical expansions to more seasonal regions can explain differences in brain size, we used the geographic range of the species to reconstruct transitions between tropical and temperate regions (i.e. low-, medium and high-latitude regions) using stochastic character mapping with 'phytools' R-package (Revell, 2012). These latitude categories (see main text and Appendix Figure B.1) integrate several measures of environmental variation and harshness, such as inter-year and seasonal variation and snow cover. Because migration can reduce environmental variation, evolutionary transitions between residency and migration (short and long-distance) were also reconstructed. Consequently, we also categorized species as being residents, short-distance migrants or long-distance migrants. The combination of these two factors leads to the existence of 5 categories (i.e. resident high-latitude, resident medium-latitude, and resident low-latitude, migrant short-distance and migrant long-distance). Evolutionary transitions among these five selective regimes was reconstructed across a phylogeny encompassing all studied species. This was done using a stochastic character mapping (SCM) procedure as implemented in the *simmap* function from R-package 'phytools' (Revell, 2012), which estimates the location of evolutionary transitions between categories on a phylogenetic tree. The SCM method allows changes to take place along the tree branches rather than exclusively at the tree nodes (Garamszegi, 2014). To minimize the potential effects of uncertainty in both tree topologies and phylogenetic reconstructions from the SCM, we used the 100 phylogenies with 10 simulations for each one, resulting in 1000 phylogenetic trees. To estimate the amount and direction of evolutionary transitions between selective regimes, we used the *describe.simmap* function over the 1000 trees and estimated mean and confidence interval for each possible transition (for instance, between Residents medium-latitude and Migrants short-distance).

2.4.9 Fitting evolutionary models of brain size evolution

We used the results of the SCM to test if brain size differences between selective regimes are associated with two different rates of phenotypic evolution (O'Meara *et al.*, 2006) or they are a consequence divergent selective optima for each category (Beaulieu *et al.*, 2012). For this purpose, a random set of 100 stochastic character maps were analysed using the R-package 'OUwie' (Beaulieu & O'Meara, 2012) to test which evolutionary model best explains the evolution of brain size under the different selective regimes. In this case, we also dealt with allometric effects by estimating the residuals of a log-log PGLS of brain against body size. We considered a variety of Ornstein-Uhlenbeck (OU) models (Beaulieu *et al.*, 2012) that test for the existence of phenotypical optima (θ) for relative brain size. OU models test the hypothesis that the evolution of a phenotypic trait is non-random, but rather it is the consequence of selective forces pulling this trait towards an optimal value that is favoured by natural selection. OU models can either include a single optimum (e.g. OU1 model) or consider the possibility that different categories are pulled by natural selection towards different optima. For example, in OUM models smaller brains could be favoured in migratory species while larger brains benefit resident species that experience increased environmental oscillations throughout the year. In the OUMV models, an additional parameter is estimated: the rate of stochastic motion around the optima (σ^2), representing the amount of brain size variation around the phenotypic optimum estimated for each group. We fitted the following OU models: (1) a simple OU model with a single optimum (θ) and the same α and σ^2 parameters for all selective regimes ('OU1' model), (2) an 'OUM' model with different optima, and (3) the same OUM model, but with different σ^2 for each category ('OUMV'). In addition, two Brownian motion (BM) models were also fitted: a single rate 'BM1' model and a 'BMS' model with different rate parameters for each state or phylogeny. Brownian motion models can describe drift, drift-mutation balance and stabilizing selection toward a moving optimum (Beaulieu *et al.*, 2012). To assess the most supported model we calculated the Akaike weights for each model based on AICc scores (Lapiedra *et al.*, 2013). In addition, we also calculated the Bayesian Information Criterion (BIC), which further penalizes for the inclusion of more parameters. Then, the best evolutionary model was identified from both the AICc and BIC scores and we estimated the mean values and the 2.5 and 97.5% confidence intervals for all the parameters. We also tried a more complex model in which another parameter (α) is included as the strength of selection with which natural selection pulls towards a given brain size optimum for each group of species (the so called OUMVA model). However, when using this more complex model, some of the trees gave evolutionary optima that were some orders of magnitude outside the range of existing values of brain size among all bird species and we therefore excluded these models from further analyses. Nevertheless, we obtained similar results in the estimated optima with this model compared to OUMV (see Appendix Table B.16).

Table 2.1. **Brain size (dependent variable) in relation to environmental variables in resident birds.** We use a phylogenetic general least square model (PGLS) while controlling for body size and phylogeny. For each model, λ and R^2 is shown. In brackets, we also show the R^2 of the models once the effect of body size has been removed (see Methods). CV: Coefficient of variation; EVI: Enhanced Vegetation Index (proxy for resource availability); PPC1 and PPC2: Two first axes of a phylogenetic principal component analysis with the environmental variables.

Factor	**Estimate**	**SE**	**t value**	**Pr (>|t|)**
Model 1 (N=835, p-value<0.001, R^2=0.87(0.02), λ=0.92)				
Intercept	-2.53	0.12	-19.86	<0.001
Log(body size)	0.59	0.01	73.24	<0.001
CV (EVI) within the year	2.45	0.01	4.12	<0.001
Model 2 (N=835, p-value<0.001, R^2=0.86(0.02), λ=0.92)				
Intercept	-2.50	0.13	-19.51	<0.001
Log(body size)	0.59	0.01	72.47	<0.001
Log (weeks of snow + 1)	0.04	0.01	3.47	0.001
Model 3 (N= 835, p-value<0.001, R^2=0.87(0.04), λ=0.90)				
Intercept	-2.61	0.13	-20.44	<0.001
Log(body size)	0.59	0.01	72.60	<0.001
CV (EVI) among years	11.18	1.97	5.67	<0.001
Model 4 (N=835, p-value<0.001, R^2=0.87(0.04), λ=0.92)				
Intercept	-2.47	0.13	-19.62	<0.001
Log(body size)	0.59	0.01	73.24	<0.001
Environmental variation PPC1	0.04	0.01	5.69	<0.001
Environmental variation PPC2	0.02	0.01	3.04	0.002

Figure 2.1. Importance of each factor in a model selection approach based on AICc. A model selection process using PGLS models with Log(Brain size) as a response variable and environmental variation axes (PPC1 and PPC2) and all factors included in the full model (See Appendix Table B.8) as explanatory variables in resident species (N=242). Here we show the importance of each factor in terms of AICc weights integrated over all possible combinations of models.

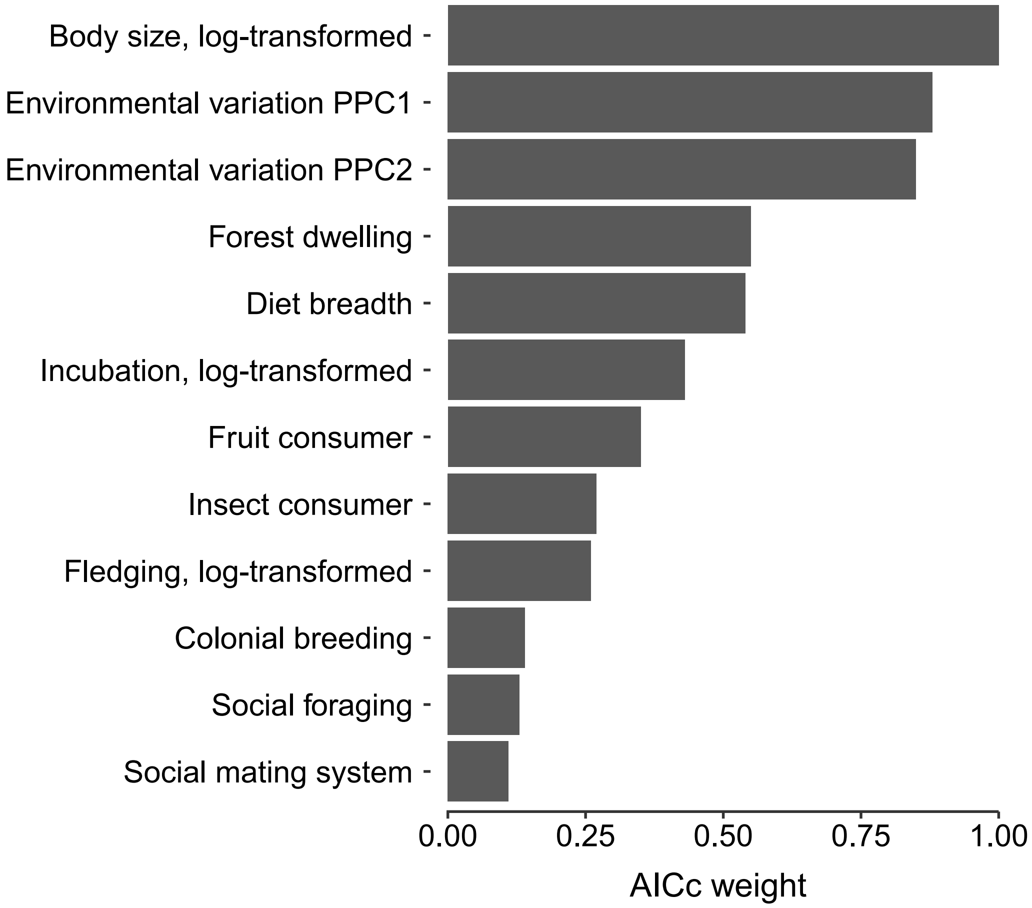


Figure 2.2. Relative brain size along a gradient of environmental variation (PPC1). We tested the effect of environmental variation in four avian orders with representatives in all the latitudinal gradients using PGLS: Relative brain size (Mean±SEM) increase with environmental variation in (A) Passeriformes (0.04±0.01, N=417, p-value=0.01), (B) Strigiformes (0.07±0.02, N=21, p-value=0.001) and (C) Piciformes (0.06±0.02. N=31, p-value=0.008) but not in (D) Galliformes (-0.02±0.01, N=22, p-value=0.097). The fitted line and the standard error in the figure are derived from the raw data.

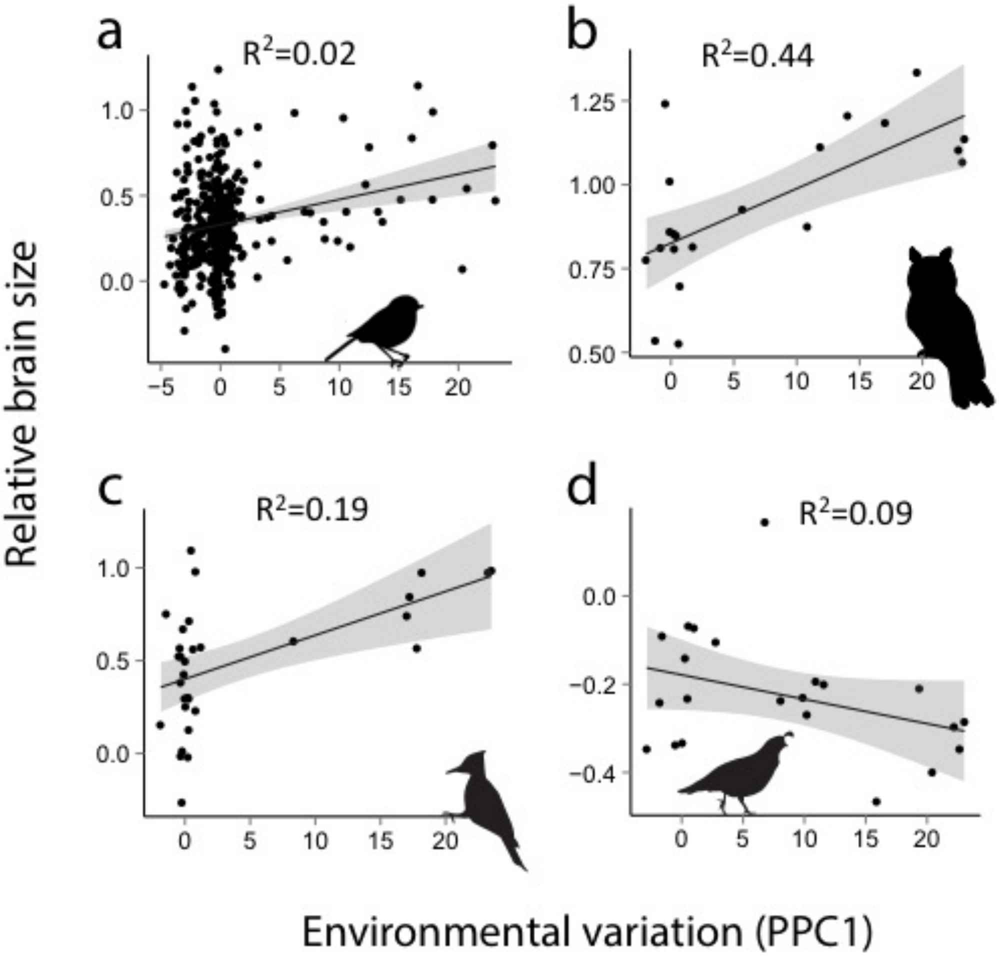


Figure 2.3. Changes in resource availability (Mean ± SEM) during the breeding and non-breeding season. We measured resource availability using the enhanced vegetation index (EVI) in the breeding areas during summer (light grey bars) and winter (dark grey bars). In the breeding areas of residents from higher latitudes (N=50), short-distance (N=230) and long-distance migrants (N=87), there is a larger decrease in EVI during winter (PGLS, p-value<0.001, Appendix Table B.10) compared to residents from mid (N=326) and low (N=459) latitudes. Migratory birds skip this decrease in resource availability by moving to wintering areas in lower latitudes (black bars).

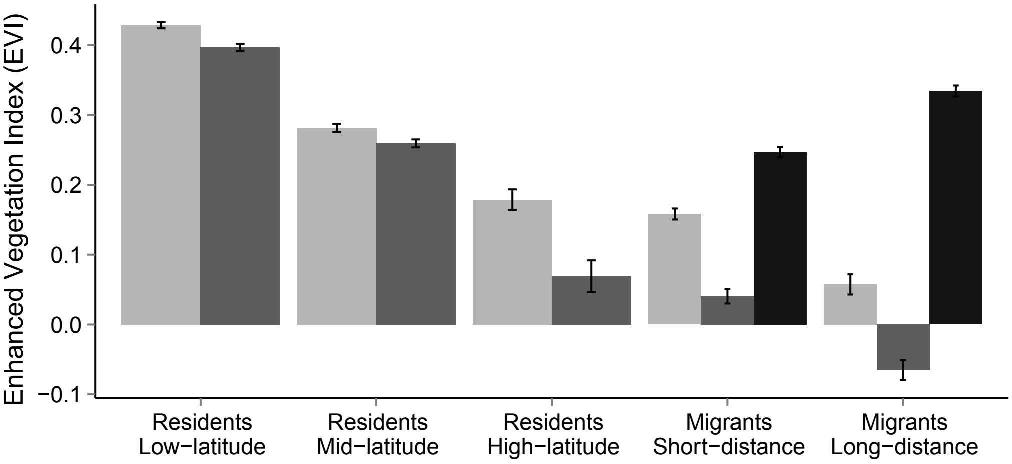


Figure 2.4. Ancestral reconstruction and the evolution of relative brain size. We reconstructed different character states representing different exposures to environmental variation. An example of a single reconstruction of shifts between migratory behaviours and breeding regions is shown in, where each character state is given a distinct colour; outside bars represent the relative brain size of each species, with representatives species from the main orders shown.

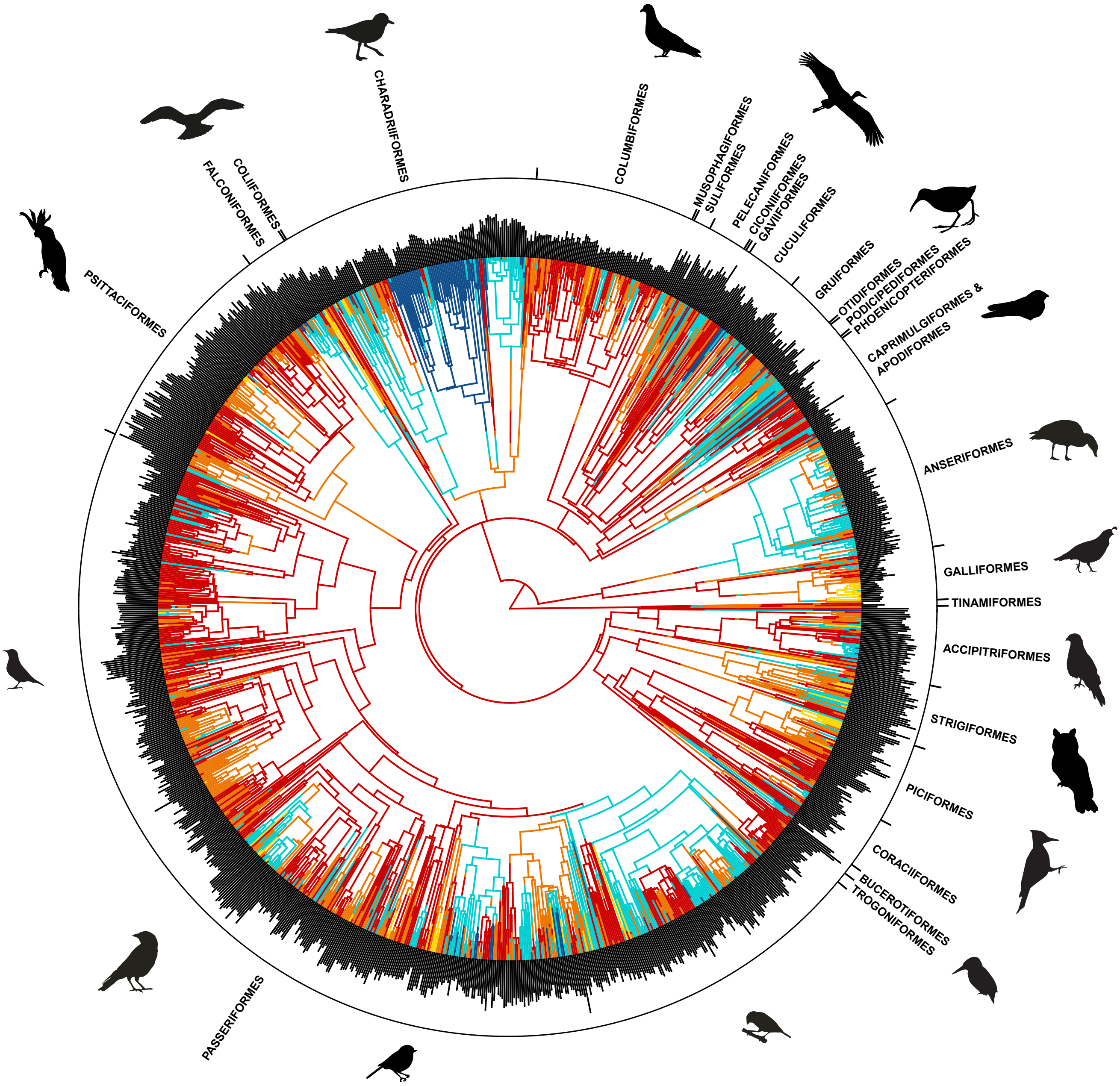
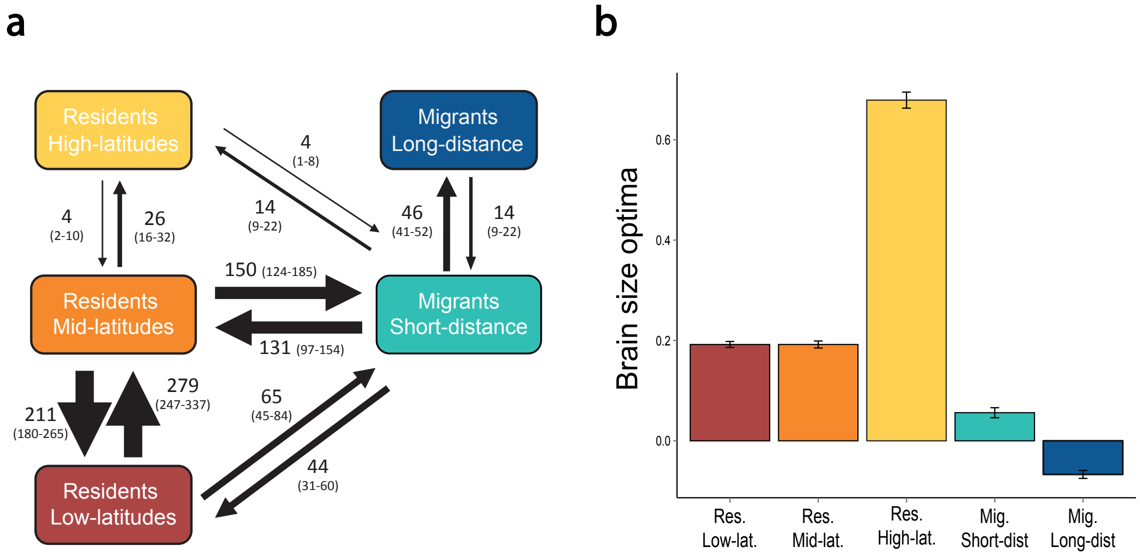


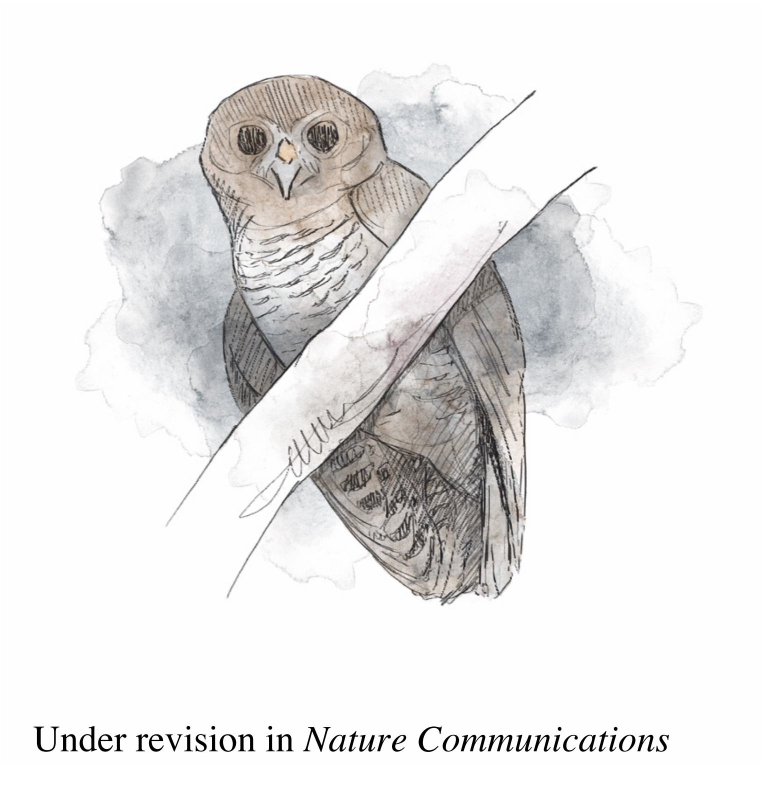
Fig. 2.5. Evolutionary transitions and brain size optima among different character states. The median number of transitions between different character states and the 97.5% and 2.5% confidence intervals are based on 1000 reconstructions (**a**). The mean and SE of the estimated brain optima under an OUMV model for 100 phylogenies is shown for each category (**b**). Silhouette illustrations came from PhyloPic (http://phylopic.org), contributed by various authors under Public domain license.



Chapter 3

Predictable evolution towards larger brains in birds colonizing oceanic islands

SAYOL, F., DOWNING, P.A., IWANIUK, A.N., MASPONS, J., SOL, D.



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Abstract

Theory and evidence suggest that some selective pressures are more common on islands than on adjacent mainland habitats, leading evolution to follow predictable trends. The existence of predictable evolutionary trends has nonetheless been difficult to demonstrate, mainly because of the challenge of separating in situ evolution from sorting processes derived from colonization events. Here, we use brain size measurements of more than 1900 avian species to reveal the existence of one such trend: the increase of the brain in island dwellers. Based on sister-taxa comparisons and phylogenetic ancestral trait estimations, we show that species living on islands have relatively larger brains than their mainland relatives, and that these differences mainly reflect *in situ* evolution rather than varying colonisation success. Although the trend towards larger brains might in part reflect niche expansions and life history constraints, the scenario best supported by phylogenetic path analyses is that selection arises from the need to confront sudden environmental changes under dispersal limitation. These findings reinforce the view that in some instances evolution may be predictable, and yields insight into why some animals evolve larger brains despite substantial energetic and developmental costs.

3.1 Introduction

Islands are classically considered natural laboratories for studying evolution (Grant, 1998; Losos & Ricklefs, 2009). Research on islands has not only documented extraordinary adaptive radiations (Darwin, 1859; Losos, 1998), but it has also provided evidence that evolution can be predictable, rather than idiosyncratic (Gould, 1990). Predictable evolutionary trajectories in islands include: a tendency toward medium body size in vertebrate lineages (Foster, 1964; Lomolino, 1985, 2005; Clegg & Owens, 2002) (the so called "island rule"), convergence towards equivalent eco-morphs in lizards (Losos, 1998; Mahler *et al*., 2013), and reduction of flight capacity (Wright *et al*., 2016), plumage brightness and colour intensity in birds (Doutrelant *et al*., 2016). Although the generality of some of these patterns remains controversial, there is agreement that some distinctive features of islands, such as their depauperate biotas, isolation, smaller size and well defined boundaries, should make some selective pressures more common on islands than on adjacent mainland areas (Wallace, 1881; Carlquist, 1974).

The propensity for tool-use behaviours observed in the New-Caledonian crow (*Corvus moneduloides)* (Rutz & St Clair, 2012), the Hawaiian crow (*Corvus hawaiiensis)* (Rutz *et al*., 2016) and the Galápagos woodpecker finch (*Camarhynchus pallidus*) (Tebbich & Teschke, 2013) suggests that islands may lead to the evolution of advanced cognitive abilities, presumably by enlarging the brain (Cnotka *et al*., 2008; Mehlhorn *et al*., 2010). Three main factors may set the stage for the evolution of enlarged brains when an island is colonized: niche expansions, environmental variability under dispersal constraints, and a slow-down in the pace of life.

Niche expansion is related to the impoverished species richness typical of islands, a consequence of isolation and dispersal constraints. Impoverished species richness is thought to facilitate niche expansion by releasing new colonizers from inter-specific competition (Van Valen, 1965; Roughgarden, 1972) and enemies (Sondaar, 1977; Alcover & McMinn, 1994) while increasing intra-specific competition (MacArthur *et al*., 1972; Wright, 1980). The adoption of new resource opportunities during niche expansions might select for enhanced cognition and larger brains by increasing the fitness value of plastic behaviours, as suggested by the "cognitive buffer hypothesis" (Allman *et al*., 1993; Sol, 2003, 2009b). This may happen even when niche expansions are driven by individual specializations (Scott *et al*., 2003), as resource specializations are often mediated by behaviour (Werner & Sherry, 1987). Recent empirical evidence shows that ecological generalists tend to have relatively larger brains and a higher propensity for behavioural innovation (Overington *et al*., 2009, 2011; Ducatez *et al*., 2014; Sol *et al*., 2016), lending credence to the importance of niche expansions in brain size evolution.

Limits to dispersion which prevent individuals from moving to other places when environmental conditions deteriorate may also facilitate the evolution of larger brains on islands (Greenberg & Danner, 2013). Although large brains are energetically costly and need longer periods to develop, current evidence suggest that they function (and hence may have evolved) to buffer individuals against environmental changes by facilitating the construction of plastic behavioural responses (Schuck-Paim *et al*., 2008; Sol, 2009a; Sayol *et al*., 2016b; Vincze, 2016). Animals may alleviate the effect of food shortages by switching towards novel foods or inventing new foraging techniques (Lefebvre *et al*., 1997; Sol *et al*., 2005b). For example, in woodpecker finches tool use replaces the more usual gleaning technique in years when droughts drive insects from foliage to crevices (Tebbich *et al*., 2002). Environmental variability coupled with dispersal limitations might therefore be a powerful force selecting for enlarged brains on islands.

Finally, the trend towards slower life history strategies often documented in island dwellers (Covas, 2012; Novosolov *et al*., 2013) may facilitate the evolution of larger brains on islands. A slow life history strategy is considered a prerequisite for the evolution of enlarged brains, which require more time to develop (Isler & van Schaik, 2006a, 2009; Weisbecker & Goswami, 2014; Weisbecker & Goldizen, 2015). Moreover, learning is more advantageous in long-lived species than in short-lived species (particularly when predation risk is low) because the former have more time to explore and develop new behaviours, and the acquired behaviours may be used for longer periods (Sol, 2009a; Sol *et al*., 2016). While enhanced cognition is not indispensable for a slow pace-of-life, the possibility that life history acts as a constraint needs to be incorporated into analyses of brain size evolution on islands.

Despite being rooted in sound theoretical arguments, only two studies to date have investigated whether island species differ in relative brain size from continental species. A study on crows and ravens (Corvids) failed to find any association between brain size (relative to body size) and island living (Jønsson *et al*., 2012). Similarly, neither absolute brain mass nor brain mass relative to body size changed with insularity in seven primate species (Montgomery, 2013). However, testing the "brain-island" hypothesis is challenging for two main reasons. First, it requires well-sampled lineages in both islands and continents. Second, and more problematically, interpreting the results is dependent on disentangling whether large brains evolved before or after island colonisation, especially because larger brains facilitate the colonization of novel regions (Sol *et al*., 2005a, 2008). To solve these problems, we assemble the most complete collection of brain measurements currently available for both oceanic island and continental avian species, and test the "brain-island" hypothesis by applying a Bayesian phylogenetic framework to a fully resolved avian phylogeny (Downing *et al*., 2015; Cornwallis *et al*., 2017).

3.2 Results

3.2.1 Relative brain size across island and mainland species

Our analyses are based on 11,519 specimens of 1917 species belonging to 91% of all extant bird families. We classified these species as either inhabiting oceanic islands ($N_{species}$ =108) or not ($N_{species}$ =1809), and used Bayesian Phylogenetic Mixed Models (BPMMs) to ask whether island species have larger brains than mainland species. We found that endemic oceanic island birds tend to have bigger brains than other birds, after controlling for allometric and phylogenetic effects (BPMM: insularity estimate [β]=0.044, credible interval [CI]=0.019 to 0.074, pMCMC=0.002; $N_{species}$=1917; Fig. 1, model 1 in Appendix Table C.1). The insular effect on relative brain size remained even when restricting the analysis to species represented by brain size measurements of at least three individuals (BPMM; insularity β=0.044, CI=0.015 to 0.082; pMCMC=0.004; $N_{species}$ =1510, model 2 in

Appendix Table C.1). Likewise, we still found relatively larger brains on islands after controlling for migratory behaviour(Sol *et al*., 2005b, 2010; Sayol *et al*., 2016b; Vincze, 2016) or developmental mode(Iwaniuk & Nelson, 2003) (BPMM; insularity β=0.030, CI=0.005 to 0.055; pMCMC=0.028; $N_{species}$ =1917; model 4 in Appendix Table C.1).

3.2.2 Relative brain size differences between sister species.

Our previous analyses show general tendencies, and hence put our findings in the context of general brain evolution. However, A stronger test of the "brain-island" hypothesis is to ask whether species that are endemic to oceanic islands have larger relative brains than their phylogenetically-closest continental species. When we compared sister-taxa, we found that island species have relatively larger brains than their closest continental counterparts (BPMM; insularity β=0.036, CI=0.004 to 0.070; pMCMC=0.024; $N_{comparisons}$=108; Model 1 in Appendix Table C.2), although the effect differs among lineages (Appendix Figure C.1).

3.2.3 The allometric influence of body size

A relatively larger brain may be acquired not only through selection for enlarged brains but through selection for smaller body size. Consistent with the island rule (Van Valen, 1973), and in accordance with previous studies on birds (Clegg & Owens, 2002; Boyer & Jetz, 2010), a sister-taxa analysis revealed that small birds exhibit larger size on islands while large birds exhibit smaller size (BPMM; insularity*body size category β=0.353, CI=0.085 to 0.618; pMCMC=0.016; $N_{comparisons}$=108; Appendix Table C.3). However, our finding that relative brain size is larger on island species cannot be explained by selection for smaller body size: differences in relative brain size between island and mainland were largely independent of body size (Model 2 in Appendix Table C.2 and Appendix Figure C.2).

3.2.4 Relative brain size increase: Cause or consequence of island living?

Despite the significant association between relative brain size and island living, our sister-taxa analysis is insufficient to determine whether a relatively larger brain is a cause or consequence of island living. Indeed, past analyses of human-mediated introductions of birds and mammals have revealed that having a relatively large brain increases the likelihood of establishment in novel regions, including islands(Sol *et al.*, 2005a, 2008; Amiel *et al.*, 2011). However, two additional pieces of evidence suggest that the enlarged brains of island birds primarily reflect *in situ* evolution rather than varying colonisation success. First, the occurrence of island-dwelling species was not more probable in families with relatively larger brains (BPMM: relative brain size effect, β=0.010, CI= -1.568 to 1.320, pMCMC=0.998; $N_{families}$=108), reflecting that common colonisers of oceanic islands include both small brained lineages, such as pigeons and rails, and large brained lineages such as parrots. Second, reconstructing evolutionary transitions to oceanic island living using a phylogenetic Bayesian approach(Downing *et al.*, 2015; Cornwallis *et al.*, 2017), we found no difference in relative brain size between the ancestors of species that colonised oceanic islands from the continent and the ancestors of species that did not (Fig. 2; BPMM: Relative brain size difference=0.02, CI=-0.15 to 0.12, pMCMC=0.465, $N_{ancestors}$=3418). In contrast, the descendants of species that colonised islands had relatively bigger brains than their mainland ancestors (Fig. 2; BPMM: Relative brain size difference=0.08, CI=-0.01 to 0.18, pMCMC=0.031, $N_{ancestors}$=286), suggesting *in situ* evolution towards relatively larger brains after island colonization.

3.2.5 Disentangling the mechanisms of brain expansions in islands

Three main interrelated mechanisms might explain why the colonisation of oceanic islands should bring associated increases in relative brain size: niche expansions, environmental variation under limited dispersal and differences in life history (Fig. 3a). We explored how these mechanisms influence the relationship between relative brain size and island living by comparing a number of causal scenarios using phylogenetic path analysis (von Hardenberg & Gonzalez-Voyer, 2013). We described niche expansions in terms of diet breadth(Cáceres *et al.*, 2011), environmental variation as variation in Enhanced Vegetation Index (EVI) and life history as the duration of the period from egg laying to full fledging (as development is the life history trait more closely related to brain size evolution (Iwaniuk & Nelson, 2003)) (Fig S3). In the best-supported causal scenario, the effect of island on relative brain size is indirectly mediated by increases in inter-annual environmental variation (Fig. 3b). Thus, there is a link between islands and higher inter-annual EVI variation (Path coefficient=0.427, pMCMC=0.004, $N_{species}$=1195), and it is this variation that leads to increased brain size (Path coefficient=0.032, pMCMC=0.002,

$N_{species}$=1195). Unlike inter-annual variation, seasonal variation in EVI is lower on islands (Path coefficient= -0.350, pMCMC=0.002, $N_{species}$=1195) and does not explain why island dwellers have larger brains for their body size (Appendix Figure C.4). The best model also suggests a second pathway mediating the effect of island on brain size by means of life history changes. Thus, there is a link between island living and longer developmental period (Path coefficient=0.282, pMCMC=0.001, $N_{species}$=1195), which then translates to relative brain size increases (Path coefficient=0.136, pMCMC=0.001). In addition, there is a direct effect of insularity on relative brain size (Path coefficient=0.108, pMCMC=0.014, $N_{species}$=1195).

3.3 Discussion

Our findings indicate that island birds tend to have larger brains than their mainland close-relatives, and that these differences have evolved *in situ* and independently in several lineages. These findings thus reinforce the view that evolution is not entirely idiosyncratic and, under certain conditions, may follow predictable trajectories.

Although there is a general trend towards the evolution of relatively larger brains on islands across Aves, the effect is stronger in some clades than other (Appendix Figure C.1). This is nonetheless predicted by phenotypic plasticity theory (Price *et al*., 2003), which suggests that moderate levels of behavioural plasticity are optimal in permitting population survival in a new environment and in bringing populations into the realm of attraction of an adaptive peak. For example, if behavioural responses are enough to move a population close to a new adaptive peak, this may hide genetic variation from natural selection and hence inhibit evolutionary change (the Bogert effect; reviewed in Robinson and Dukas 1999; Huey et al. 2003; Price et al. 2003). As Corvids and Primates belong to clades with outstanding behavioural plasticity, the lack of association between brain size and island living found in previous studies (Jønsson *et al*., 2012; Montgomery, 2013) does not necessarily contradict the brain-island hypothesis.

Our results highlight the existence of scenarios where selection is more likely to influence brain size evolution. The best supported scenario suggests that island living makes the environment more unpredictable by increasing environmental resource variation across years, and that this in turn selects for larger brains. On islands, there are limited possibilities to disperse when conditions deteriorate, which can force individuals to explore (Mettke-Hofmann *et al.*, 2002) and rely more on elaborated behavioural responses. Evidence is for instance accumulating that animals may alleviate the effect of food shortages by adopting novel foods or inventing new foraging techniques (Lefebvre *et al.*, 1997; Tebbich *et al.*, 2002; Sol *et al.*, 2005c). The ability to construct behavioural responses to novel challenges is known to be limited by the neural architecture (Lefebvre *et al.*, 1997; Reader *et al.*, 2011; Benson-Amram *et al.*, 2016), particularly the brain areas associated with domain-general cognition (the pallial regions, in birds) (Lefebvre & Sol, 2008; Shanahan *et al.*, 2013). These pallium regions represent a large fraction of the entire brain and have evolved in a concerted way such that overall brain size is an accurate proxy of their relative size (Sayol *et al.*, 2016a). Indeed, growing evidence suggests that larger brains enhance survival of animals confronted with challenging situations (Shultz *et al.*, 2005; Fristoe *et al.*, 2017).

The most plausible causal scenario identified using phylogenetic path analyses also suggests that the evolution of larger brains in islands should be facilitated by the trend towards a slower life history strategies in island dwellers. A slow life history strategy is considered a prerequisite for larger brains, which require more time to develop (Sol *et al.*, 2016), and increases the benefits of exploring and learning by reducing time constraints in developing and using the acquired behaviours. Therefore, our findings fit well with the "island syndrome" theory, which posits that island dwellers have systematic differences in demography, reproduction, behaviour, and morphology when compared to mainland populations (Adler & Levins, 1994).

In contrast to previous studies, we do not find support for diet breadth expansions in island taxa (Alatalo *et al.*, 1986; Scott *et al.*, 2003). However, we cannot rule out that this lack of support reflects limitations in the metrics used to quantify the amplitude of ecological niches, which might ignore subtle changes in niche breadth. For instance, insular populations of coal tits (*Periparus ater*) expand their foraging niche from the branches of trees to the trunks, which are normally occupied by their congeners in the continent

(Alatalo *et al.*, 1986). While this type of detailed analyses is still too rare to be integrated in broad comparative analysis like ours, identifying subtle changes in niche breadth is critical to fully understand the exact importance of niche expansions on the trend towards larger brains in island dwellers.

Our finding that islands tend to promote the evolution of enlarged brains has implications for adaptive radiations on islands. Behavioural shifts combined with geographic isolation may be powerful forces driving evolutionary changes through divergent selection (Mayr, 1963; Lapiedra *et al.*, 2013). However, unlike the flexible stem hypothesis, which predicts that adaptive radiations should be enhanced by behaviourally flexible ancestors able to occupy a broader niche, our results suggest that selection for enhanced flexibility (as measured by brain size increases (Lefebvre *et al.*, 1997, 2004; Benson-Amram *et al.*, 2016)), may also occur on islands instead of being exclusively derived from ancestral species. Ecological opportunities (Schluter, 2000), geographic isolation(Mayr, 1963) and particular gene architectures (Berner & Salzburger, 2015) can influence rapid evolutionary diversification on islands, but our results highlight the need to also consider brain evolution to unravel why some clades have experienced such extraordinary adaptive diversifications on islands.

3.4 Methods

3.4.1 Brain characterization

We used published data on brain size for 1767 bird species measured from museum collections, complemented with new measurements of 150 species from 44 families. The final dataset included 11,519 museum specimens from 1917 species. All specimens were measured by the same researcher (A.I.), using the endocast method(Iwaniuk & Nelson, 2002). In birds, the ability to construct novel behavioural responses is not related to brain size *per se*, but the extent to which the brain is either larger or smaller relative to body size (Lefebvre *et al.*, 1997; Overington *et al.*, 2009). We therefore obtained data on body mass from the same specimens on which brain was measured when available (18% of the species) or taken from the literature otherwise (Dunning, 2008; Del Hoyo *et al.*, 2016). Body mass (log-transformed) was then used as a covariate in models accounting for variation in absolute brain size (Garcia-Berthou & Freckleton, 2001). However, for visual representation of the results as well as in analyses in which brain size was a predictor, we estimated relative brain size as the residual from a log-log phylogenetic Generalised Least Square regression (using the *phyl.resid* function from R-package 'phytools' (Revell, 2012)) of absolute brain size against body mass, to avoid co-linearity between brain and body size. Despite the heterogeneous functional organization of the brain, relative brain size is strongly correlated with the sizes of pallial brain regions responsible for general-domain cognition (Lefebvre & Sol, 2008; Sayol *et al.*, 2016a).

3.4.2 Geographic and ecological characterization

We used distribution maps from BirdLife International (BirdLife International & NatureServe, 2012) to classify each species as either continental or island-dweller. A species was considered to be an endemic island-dweller when exclusively occurring all year-round on islands raised in the middle of the ocean (e.g. from volcanic activity), according to the Island Directory (http://islands.unep.ch/isldir.htm), and that did not reconnect to the continent when sea levels changed during glacial periods, considering the minimum level of 120 meters below current level (Siddall *et al.*, 2003). We considered New Caledonia to be an oceanic island, despite being of continental origin. Geological evidence suggest a complete submersion of New Caledonia between 65 and 37 Ma (Espeland & Murienne, 2011) or until 25 Ma (Trewick *et al.*, 2006), congruent with species radiation estimates (Garcia-Porta & Ord, 2013) and hence it is functionally an oceanic island. To deal with factors potentially confounding the brain-island association, we also obtained information about the breeding latitude centroid and migratory behaviour for each species, considering all the species with a distinct breeding and non-breeding distribution (i.e. full migrant, partial migrant and pelagic birds) as migrants. To characterise environmental fluctuations, we overlapped species' distribution maps with layers of the Enhanced Vegetation Index (EVI) over 15 years. We then estimated annual variation of resources as the coefficient of variation (CV) of EVI mean across years and seasonality variation of resources as the annual EVI amplitude (max-min) averaged across years (see Sayol *et al.*, (2016b) for more details). Date on developmental mode were obtained from Iwaniuk and Nelson (Iwaniuk & Nelson, 2003). We assigned species able to move on their own soon after hatching as precocial and the rest as altricial. Super-precocial and semi-precocial species were lumped with precocial species and semialtricial with altricial species. Developmental period was defined as the sum of incubation and fledging periods. To characterise each species' niche breadth, we retrieved information from the Handbook of the Birds of the World (Del Hoyo *et al.*, 2016) on the frequency of consumption of 10 major food types, following Wilman et al. (2014) and recorded for each species the frequency of use of each food type (1=almost exclusively used, 0.5=often used, 0.1=rarely used). We then built a similarity matrix of nutritional content for each food type (Appendix Figure C.3) and estimated a breadth index using Rao's quadratic entropy as implemented in the R-package 'indicspecies' (Cáceres *et al.*, 2011).

3.4.3 General parameters of the phylogenetic comparative analysis

All of our analyses were based on Markov chain Monte Carlo Bayesian Phylogenetic Mixed Models (BPMMs), implemented in the 'MCMCglmm' R-package v2.20 (Hadfield 2010). In all cases, we used normal priors (V=1, ν=0.002) for fixed effects, and inverse-Wishart priors (V=1, ν=0.002) for random effects. Each model was run for 2,100,000 iterations with a 100,000 burn-in and a thinning interval of 2,000. After running the models, we examined the autocorrelation of samples to make sure that it was less than 0.1, otherwise increasing the thinning intervals and the final number of iterations to obtain 1,000 samples. We repeated each analysis on 10 random phylogenetic hypotheses drawn from the posterior distribution of the global phylogeny of birds (Jetz *et al.*, 2012) available at BirdTree.org. We combined the posterior distributions from the 10 trees resulting in 10,000 samples, for parameter estimation. Parameter estimates from models are presented as the posterior mode and the 95% lower and upper credible intervals (CIs) of the posterior samples. Significance values (pMCMC) reported are the proportion of samples from all the iterations that are greater or less than 0. Model specifications are detailed below.

3.4.4 Evolutionary correlations of mainland-island living

We explored the association between brain size and insularity by constructing a BPMM with brain size as our response (Gaussian error distribution) and insularity, body size, migratory behaviour and developmental mode as fixed factors. We included phylogeny as a random factor. Brain and body size were log-transformed prior to analysis, and the rest of the continuous variables were Z-transformed. For the association between island dwelling frequency and relative brain size among bird families, we modelled the proportion of island and continental species in each family (binomial distribution with a logit function) using a BPMM with mean relative brain size of each family as a fixed effect. Phylogenetic relationships among families were included as a random factor to control for non-independence among clades.

3.4.5 Comparisons of mainland-island sister species.

To check whether island birds have enlarged brains compared to their closest continental counterparts, we calculated the phylogenetic distance between each insular species with all the continental species, and assigned each insular species its closest species or group of continental species. We then included all selected species (insular and their closest sister taxa) in a Gaussian BPMM and included as random factor an identifier for each continent-island comparison, equivalent to a pair-wise test. We first modelled relative brain size as a function of insularity and other confounding factors (body size, migratory behaviour and developmental mode). We additionally tested how body size changes in islands (e.g. the island rule) affect our conclusions. To do this, we modelled body size as our response variable with insularity and a category distinguishing large and small birds (e.g. above or below the median) as fixed factors to test if body size differences in islands depend on body size itself (e.g. bigger birds get smaller and the reverse). We then modelled relative brain size as a function of insularity but including the body size categorization to check whether relative brain size changes in islands are distinct in small and large birds.

3.4.6 Ancestral estimations of island living and relative brain size

To disentangle whether the enlarged brains of island birds primarily reflect *in situ* evolution rather than varying colonisation success, we followed previous studies (Downing *et al.*, 2015; Cornwallis *et al.*, 2017) and examined how relative brain size differed between ancestors of island and continental species using a two-step approach. First, we estimated the ancestral probability of island living by modelling whether contemporary species occurred on either islands or mainland island/continent states with a BPMM including the phylogeny as a random effect. This estimates the posterior probability that each node in the phylogeny is insular. We classified each node as being either island or continental if the posterior probability of the node was > 90%. This resulted in four transition categories: (i) continental ancestors with continental descendants (ii) continental ancestors with island descendants (at least one descendant); (iii) island ancestors whose descendants continued to live on islands (at least one descendant); and (iv) island ancestors with continental descendants. We entered these transition categories as an explanatory variable in a multi-response BPMM with relative brain size as the response traits and a phylogenetic covariance matrix linked to ancestral nodes as a random effect. We removed the global intercept to estimate relative brain size preceding the origin (comparison of classifications i versus ii) and maintenance (comparison of classifications i versus iii) of island living. Brain size changes in the loss of island living (comparison of classifications iii versus iv) were not possible due to the small number of transitions of this type. If brain size increased once the species colonised islands, we should find relatively bigger brains in ancestors already on islands compared to the ancestors that preceded island colonisation. If enlarged brains facilitate island colonisations, we should find larger brains in ancestors preceding island colonization, compared to ancestors that remained on the continent. To incorporate model and phylogenetic uncertainty in the analysis, the chains were run 5 times for each phylogeny across 10 phylogenies, resulting in 50,000 posterior samples that were used to assess the significance value (pMCMC) as the proportion of samples from all the iterations where one level is greater or less than the other.

3.4.6 Phylogenetic path analysis

We used BPMM in a path analysis approach to deconstruct direct, indirect and common causal effects in the relationship between brain size and island occurrence. All explanatory variables were Z-transformed (mean centred with standard deviation=1) prior to analyses so that the relative importance of each path could be assessed. We defined a number of possible causal models including the three factors - diet breadth, variation in EVI and developmental period- potentially influencing the relationship between brain size and island occurrence. We tested variation in EVI within and across years separately as including them in a same model would generate problems of homoscedastic. The R-package ‘gRbase’ (Dethlefsen & Højsgaard, 2005) was then used to test the fit of each model using the d-separation method (von Hardenberg & Gonzalez-Voyer, 2013). This method assesses the minimal set of conditional probabilistic independence constraints (k) expected for the causal model to be correct. Then, the probabilities that the nonadjacent variables in the basic set are statistically independent are used to estimate Fisher's C statistic, which can be approximated to a $\chi 2$ distribution with 2k degrees of freedom. The model was considered to fit the observations if the C statistic was non-significant, meaning that proposed causal relations are dependent and nonadjacent variables are independent. Furthermore, the fit of different models to the data, can be compared using an Information Theory approach based on Fisher's C statistic (CICc): CICc= C+2q x n / n(-q-1), where C is Fisher's C statistic, n is the sample size and q is the number of parameters used to build models plus the number of relationships linking the parameters. If the proposed causal model fits the data, then $P > 0.05$ for the C statistic and the model with the smallest CICc value represents the best candidate model out of the proposed set of models.

Figure 3.1 A. Oceanic island birds have relatively bigger brains than other birds (Mean ± SEM relative brain size are shown). **B.** Consistency of brain size differences across 10 phylogenies randomly selected from the posterior distribution of the global avian phylogeny (combined posterior distribution from BPMMs across 10 trees is plotted).

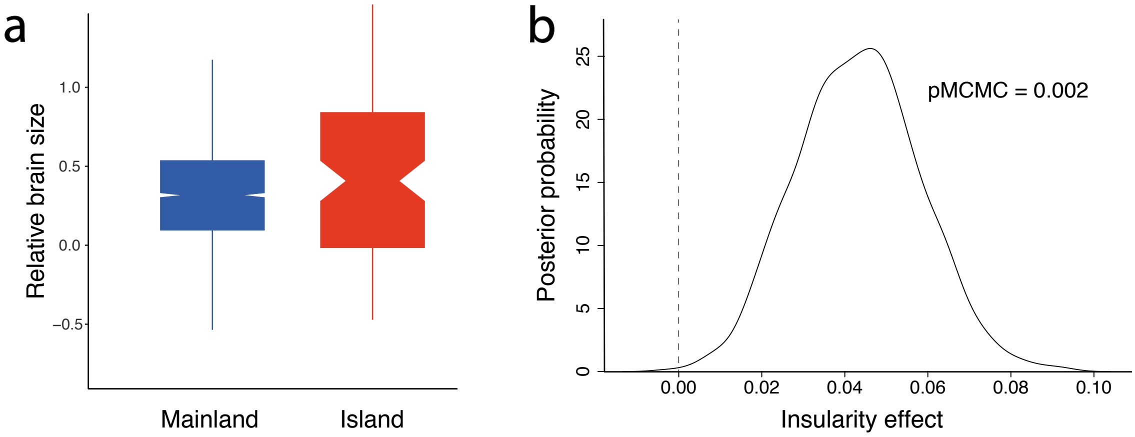


Figure 3.2. A. The phylogenetic distribution of oceanic island-living birds (108 species coloured in red). Internal branches show estimated transitions from island to mainland and vice-versa in one of the ancestral estimations, where red and blue branches represent island and mainland living. Bird silhouettes from PhyloPic (http://phylopic.org), contributed by various authors under public domain license. **B.** We classified different types of transition based on ancestors and descendants: continent to continent (α), continent to islands (β), and islands to islands (γ). **C.** Histograms show the difference in ancestral brain size between different ancestral types, first estimated transitions to all islands and then restricting the analysis to transitions to oceanic islands.

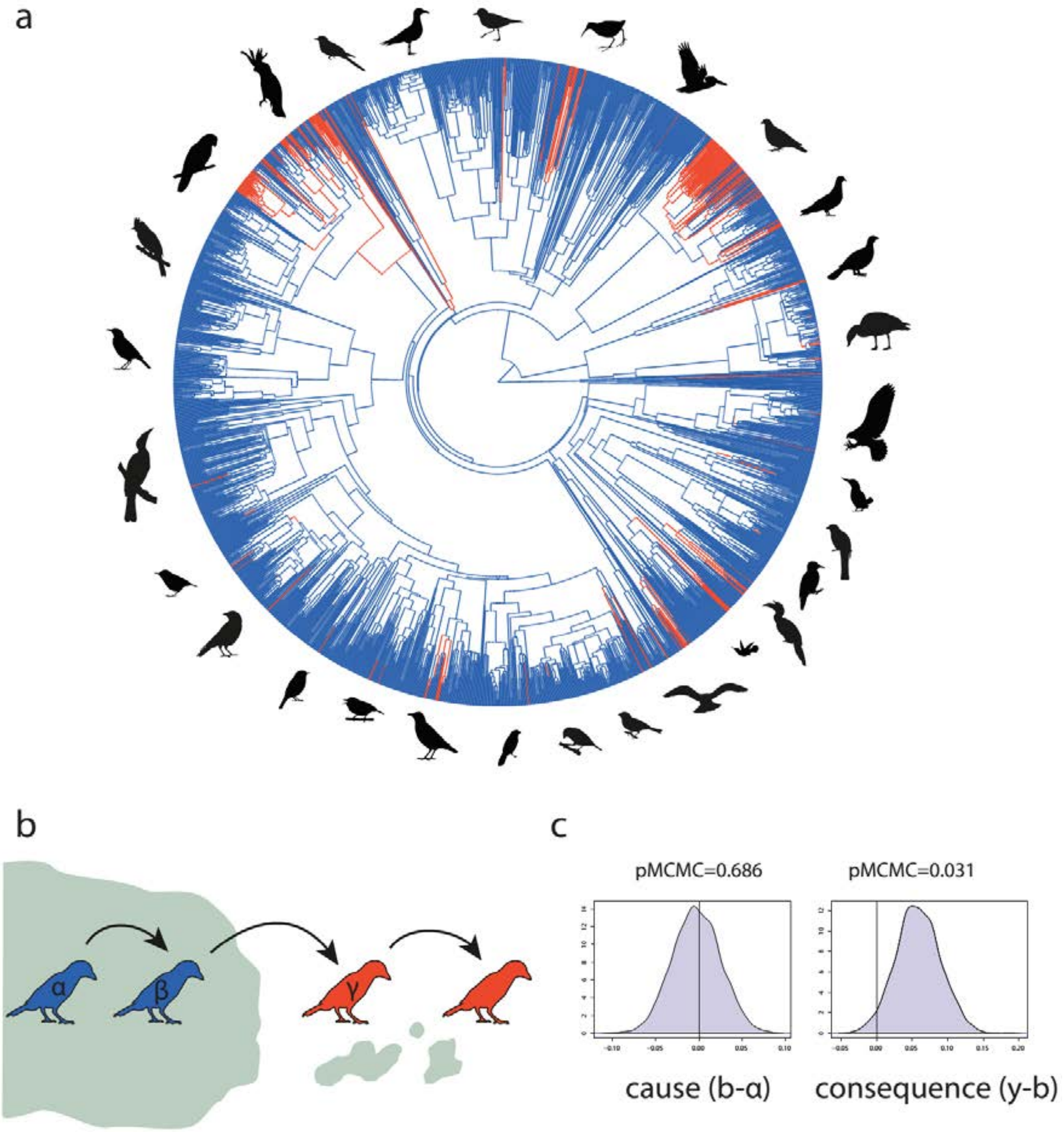
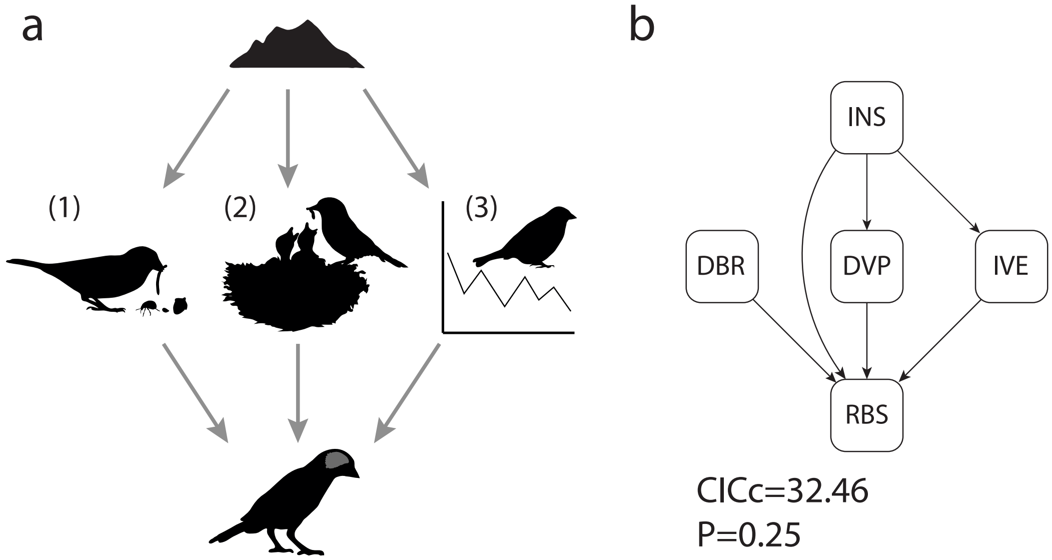


Figure 3.3 Different factors could be mediating the evolution of larger relative brains on islands (**A**): Niche expansions (1), changes in life-history (2) and increased environmental variation (3). The best supported path model suggests that life-history and environmental factors are mainly responsible for brain expansions (**B**). INS, insularity; DBR, diet breadth; DVP, Developmental period; IVE, Inter-annual variation in environmental productivity.



Chapter 4

Larger brains spur species diversification in birds

SAYOL, F., LAPIEDRA, O., DUCATEZ, S., SOL, D.

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Abstract

Key innovations are phenotypic adaptations that spur evolutionary diversification by facilitating the invasion of previously inaccessible niches. In this study, we ask whether a large brain may be a key adaptation in birds. Previous work has shown that larger brains, relative to body size, facilitate the construction of novel behaviours that allow reaching new adaptive peaks. Yet whether they also enhance evolutionary diversification is less clear. Here we take advantage of a complete phylogeny of extant birds and a large brain size database of >1900 worldwide species to show that relative brain size is associated with fast levels of diversification rates. This finding supports the 'Behavioural drive' notion that animals are not passive agents of selection but, instead, they can influence their pace of evolution by actively altering the way they interact with their environment.

4.1 Introduction

Understanding why some lineages have diversified more than others is a central question in evolutionary biology. According to the ecological theory of speciation, one of the factors that may explain these differences is variation in the exposure to ecological opportunities (Simpson, 1944, 1953). Ecological opportunities, either associated with environmental changes or colonisation events, may enhance evolutionary diversification by facilitating adaptation into a variety of ecological niches (Schluter, 2000; Losos, 2010; Yoder *et al.*, 2010). Consequently, the high diversification rates observed in some clades may simply result from being at the right place at the right time to take advantage of ecological opportunities (Ricklefs, 2003). However, it is increasingly appreciated that the use of novel ecological opportunities can be facilitated by the emergence of key innovations (Miller, 1949; Hunter, 1998; de Queiroz, 2002; Losos, 2009). Here we ask whether a large brain represents a key innovation promoting evolutionary diversification.

The possibility that relatively large brains could promote evolutionary diversification was first postulated by Wyles et al. (1983) in their "behavioural drive hypothesis". The hypothesis is based on the idea that an enlarged brain may facilitate the development and transmission of new behaviours that expose individuals to new selective pressures promoting rapid diversification (Hardy, 1965; Wyles *et al.*, 1983). A large brain might also favour evolutionary diversification by other mechanisms, however. For instance, larger brains could promote range expansions that lead to reproductive isolation and facilitate divergent selection (Sol *et al.*, 2005c) and reduce the risk of extinction (Fristoe, Iwaniuk, & Botero, 2017; Shultz, B. Bradbury, L. Evans, D. Gregory, & M. Blackburn, 2005; but see Nicolakakis, Sol, & Lefebvre, 2003).

The assumptions behind the idea that large-brained clades should experience enhanced diversification rates have been the focus of recent investigations. Enlarged brains have been found to facilitate the production and transmission of novel behaviours (Lefebvre *et al.*, 2004), to favour niche expansions (Ducatez *et al.*, 2014; Sol *et al.*, 2016) and to increase the likelihood of colonizing new areas (Sol *et al.*, 2005a, 2008). However, the importance of enlarged brains as a factor in the evolutionary diversification of animals is backed by insufficient evidence (but see Nicolakakis et al., 2003; Sol et al. 2005, Sol & Price 2008). Moreover, if animals overcome the challenges associated with new ecological pressures through flexible changes in behaviour, as suggested by the cognitive buffer hypothesis, this may hide genetic variation from natural selection and hence inhibit evolutionary change (the Bogert effect; reviewed in Huey, Hertz, & Sinervo, 2003; Price, Qvarnström, Irwin, Qvarnstrom, & Irwin, 2003; Robinson & Dukas, 1999).

The recent development phylogenetic approaches to quantify diversification rates, combined with the availability of fully resolved phylogenies, provide now an opportunity to revisit the role of the brain in evolution with more powerful analytical approaches. We used two of these new methods to test whether a large brain represents a key innovation promoting evolutionary diversification in birds, using a large dataset on brains encompassing over 1,900 species. First, we used a Quantitative-trait speciation extinction model (QuaSSE) that allows to test whether speciation and extinction rates have been influenced by brain size. Second, we tested the effect of brain size on a recently proposed diversification metric, the net diversification rate (DR) (Redding & Mooers, 2006; Jetz *et al.*, 2012). The DR metric has the advantage that can be estimated for the complete phylogeny of extant birds, avoiding possible biases of using the subset tree for which trait measurements are available. We tested the effect of brain size on DR by means of phylogenetic-based linear models, controlling for a suite of extrinsic and intrinsic factors known that can also influence evolutionary diversification (Emerson, 2002; Jablonski & Roy, 2003; Phillimore *et al.*, 2006; Ricklefs & Bermingham, 2007; Pinto *et al.*, 2008; Tebbich *et al.*, 2010; Price *et al.*, 2014). In addition, we tested weather the relation between relative brain size and species diversification rate is more pronounced in islands, as predicted by the "flexible stem hypothesis" (Tebbich *et al.*, 2010). This hypothesis predicts that ancestors with enhanced behavioural flexibility should give rise to more daughter species after island colonization and hence predicts a positive correlation between relative brain size and diversification rate in island dwellers.

4.2 Methods

4.2.1 Brain measurements and relative brain size metric

Brain size was retrieved from an extensive dataset on endocast volumes for 1917 species, measured in 11,519 museum specimens by Andrew Iwaniuk and collaborators. This method has been shown to be a reliable proxy of fresh brain size (Iwaniuk & Nelson, 2002) and accurately predicts variation in associative brain regions (Sayol *et al.*, 2016a). Because large birds also tend to have large brains, we estimated a relative measure of brain size independent of body size. To that aim, we obtained body size from published sources (Dunning, 2008; Del Hoyo *et al.*, 2016) and extracted the residuals from a model between Log(Body size) and Log(Brain size) with a phylogenetic corrected least-squares regression, using the function *phyl.resid* from the R-package 'phytools' (Revell, 2012). This method, compared to a non-corrected regression, reduces possible biases derived from the non-random sampling of species. In our case, we used a Brownian motion model to estimate the phylogenetic signal in our data. We then extracted the residuals of the model and we used them as Relative Brain size. Values greater than 0 correspond to species which brains are relatively large as compared to their body size, and values lower than 0 correspond to species which brains are relatively small relatively to their body size.

4.2.2 Species biogeographical and ecological traits

We extracted information on each species distribution from BirdLife International Maps (BirdLife International & NatureServe, 2012). The insularity of each species (Strict island endemic vs. Mainland species) was assessed with the previously mentioned maps, considering a species as island endemic if the species distribution was restricted to an island or group of islands that has never been in contact with the continent (e.g. oceanic islands). When a species was encountered in both island and mainland, it was considered as a mainland species. To define migratory behaviour, we classified each species as migratory or resident, considering as migratory species that have part or the entire population moving to a different region in the non-breeding season (thus, both full migrants and partial migrants are considered migratory species). Habitat and Diet breadth were estimated using Rao's quadratic entropy (Cáceres *et al.*, 2011), as implemented in the R-package 'indicspecies' developed by De Caceres (Cáceres *et al.*, 2011). This method allows to weight the frequency of use of each diet or habitat type by a similarity matrix between category types. In the case of Diet breadth we followed Wilman et al. (2014) by considering 10 food categories (Carrion, Vertebrates-Fish, Vertebrates-Ecthotherms, Verterbartes-Endoterms, Invertebrates, Fruit, Seeds, Pollen&Nectar, Fruits&Berries and Plant material) and we recorded for each species the frequency of use of each category (1=almost exclusively used, 0.5=often used, 0.1=rarely used). We then used a similarity matrix based on nutritional content of each diet type to weight the compositional differences between food categories (**Appendix Figure D.1**). In the case of habitat breadth, we obtained information on each species presence/absence in 82 different habitat subtypes provided by IUCN (http://www.iucnredlist.org/). We excluded artificial habitats and we built an habitat distance matrix between habitat types, based on some habitat characteristics: terrestrially (1 for terrestrial habitats, 0.5 for wetlands and 0 for marine habitats), vegetation cover (1 for deserts and rocky areas, 2 for grasslands, 3 for shrublands, 4 for savannas, 5 for forests), climate (1 for hot, tropical and subtropical habitats; 2 for temperate; 3 for boreal and tundra habitats; 4 for subarctic, subantarctic and mountain peaks) and distance to the continent (0 for inland wetlands and terrestrial habitats, 1 for coastal habitats, 2 for marine intertidal habitats, 3 for marine neritic habitats and 4 for marine oceanic habitats). In marine and wetland habitat types we scored 0 for climate and vegetation cover, unless a specific description was provided (e.g. Shrub dominated wetlands, scored 3 for vegetation cover or Tundra wetlands, scored 3 for climate). We then scaled this scores and calculated the Euclidian distance between each pair of habitats, used as the similarity matrix between habitat types (**Appendix Figure D.2**).

4.2.3 Phylogenetic hypothesis used

We extracted 100 trees from each of the backbones (Hackett *et al.*, 2008; Ericson, 2012) provided in the Bird Tree Project (Jetz *et al.*, 2012) and we built a maximum clade credibility tree (summary tree) using TreeAnnotator (a program included in the software BEAST v1.8.0) (Drummond *et al.*, 2012) for each of the backbones.

4.2.4 Speciation-Extinction models dependent on relative brain size:

We used the quantitative state speciation and extinction model (QuaSSE) implemented in the R-package ‘diversitree’ (Fitzjohn, 2012). This method models diversification as a birth–death process in which speciation and extinction rates are arbitrary functions of a continuous trait. The method simultaneously evaluates trait evolution and species diversification using maximum-likelihood, avoiding the problems when the two are estimated separately (Maddison 2006). We compared a model where speciation (λ) and extinction (μ) rates are independent of relative brain size (e.g. constant along the tree) with a model where λ is a linear function of relative brain size. We also run a third model where a directional tendency of relative brain size evolution (diffusion parameter: ∂) is fitted. The model fits a slope, showing either a positive or negative relationship between relative brain size with λ. In the case of the null model, this slope is set to zero and λ is constant. To reduce the number of parameters, and following Hardy & Otto (2014), we assume that the extinction rate (μ) is constant in all the models, so the effect of brain size on speciation is equivalent to a net change in diversification rate (λ – μ). We compared the three different models using the corrected Akaike information criterion (AICc) and AICc weights in the two summary trees. For the best-fit QuaSSE model, we then run the model with 50 phylogenies from each of the posterior distributions to account for phylogenetic uncertainty in the parameter estimates. QuaSSE requires an estimate of the standard deviation (SD) for the continuous trait within species (here, relative brain size), so we used the SD estimate from the model from which we obtained brain residuals (SD=0.14)

4.2.5 Measuring species-level diversification rates

We calculated a diversification rate metric (DR) for each species based on the inverse of the Equal Splits (ES) metric of evolutionary isolation (Redding & Mooers, 2006). The ES metric distributes the evolutionary history represented by branches lengths among all species. The ES measure for a single species is the sum of the edge lengths from the species to the root, with each consecutive edge discounted by a factor of ½. The ES measure represents the phylogenetic distinctiveness of a species relative to the other species. The function *evol.distinct* from R-package 'picante' (Kembel *et al.*, 2010) was used to calculate the evolutionary distinctiveness for all species by equal splits. For this purpose, we used a set of 100 trees of 9993 species (Jetz *et al.*, 2012), half of each built using two different backbones from two independent phylogenetic studies (Hackett *et al.*, 2008; Ericson, 2012) as a way to integrate phylogenetic uncertainty in the analysis. The inverse of the ES measure can be interpreted as the splitting rate of species from the root to the edge, and is termed diversification rate or DR (Jetz *et al.*, 2012). Species in rapidly-diversifying clades will have short branch lengths shared among many species resulting in high levels of DR, while species in slowly-diversifying clades will have long branches and hence low DR **(Figure 4.1)**. We took the median of the DR value of each species for 100 trees. The median values for Ericson and Hackett backbones were highly congruent, indicating that the measure was robust to the effects of phylogenetic uncertainties.

4.2.6 The effect of relative brain size on Diversification rate (DR) measure

To assess phylogenetic correlations, we used Bayesian Phylogenetic Mixed Models (BPMM) implemented in the R-package 'MCMCglmm' (Hadfield, 2009). For fixed effects, we used a normal prior ($V = 1$, $\nu = 0.002$) and for random effects we used an inverse-Wishart prior ($V = 1$, $\nu = 0.002$). We explored the effect of relative brain size on DR by means of Gaussian BPMM, including phylogeny as a random factor and further controlling for other factors that have been suggested to affect diversification in previous studies, including niche breadth (Phillimore *et al.*, 2006; Price *et al.*, 2014), migratory behaviour, geographic isolation (Emerson, 2002; Jablonski & Roy, 2003; Ricklefs & Bermingham, 2007; Pinto *et al.*, 2008) and the interaction between insularity and behavioural flexibility (e.g. the flexible stem hypothesis) (Tebbich *et al.*, 2010). DR was log-transformed to provide normality and continuous fix factors such as habitat and diet breadth were Z-transformed. Each model was run for 1,010,000 iterations with a 10,000 burn-in and chains sampled every 1,000 iterations unless otherwise specified. After running the models, we examined the autocorrelation of samples to make sure that it was less than 0.1, otherwise increasing the thinning intervals and the final number of iterations to obtain 1000 samples. Parameter estimates from models are as the 95% lower and upper credible intervals (CIs) of the posterior samples. Significance values (pMCMC) reported in correlation analysis are the proportion of samples from all the iterations that are greater or less than 0. Note that combining all the factors resulted in 1701 species for which all traits are available, thus the MCMC models were run in this subset of species.

4.3 Results

Our two approaches yielded firm support for the hypothesis that diversification rates are enhanced in lineages with relatively larger brains. First, quantitative state speciation and extinction models (QuaSSE) revealed a positive effect of relative brain size on speciation rate (0.017-0.035). Although there is always uncertainty regarding the phylogenetic trees used, the linear model was always better supported than the null model (increase in AICc > 27) irrespective of the phylogenetic backbone used.

Second, species with larger relative brains exhibited enhanced diversification rates, as measured with the DR metric (pMCMC=0.020). Diversification rates are known to be influenced by niche breadth (Phillimore *et al.*, 2006; Price *et al.*, 2014), migratory behaviour (Rolland *et al.*, 2014) and geographic isolation (Emerson, 2002; Jablonski & Roy, 2003; Ricklefs & Bermingham, 2007; Pinto *et al.*, 2008), yet the finding that large-brained birds exhibit higher diversification rates was robust to the effect of these factors (**Figure 2**). Migratory behaviour, together with relative brain size, was the other significant factor in this analysis, confirming previous studies that found higher speciation and lower extinction in migratory birds (Rolland *et al.*, 2014).

Finally, we explored the idea that behavioural flexibility could be one of the explanations for island radiations, the so called the "flexible stem hypothesis" (Tebbich *et al.*, 2010). Contradicting the hypothesis, the interaction of island living and relative brain size was found non-significant (pMCMC=0.504).

4.3 Discussion

Previous studies in birds have found that brain size is positively related to species richness (Nicolakakis *et al.*, 2003), subspecies numbers (Sol *et al.*, 2005c), morphological diversification (Sol & Price 2008) and genetic diversity (Vachon *et al.*, 2018). We extend here these results by showing with two conceptually different methods that large brains are positively associated with diversification. Admittedly, our two approaches to explore the role of brain size in evolutionary diversification have limitations. The QuaSSE models, for example, have been criticized for being prone to high type I errors (Rabosky & Goldberg, 2015) and cannot be used in a fully sampled phylogeny, which could lead to biases in the estimation of extinction and speciation rates. Moreover, QuaSSE models do not allow to accommodate alternative factors influencing diversification rates. These limitations are nonetheless solved by the DR approach. Thus, the consistency of the results from the two approaches points towards the existence of a biologically meaningful association between relative brain size and enhanced diversification rates.

The finding that a relatively larger brain contributes to enhance diversification rates can be interpreted in terms of the behavioural drive hypothesis (Mayr, 1963; Wyles *et al.*, 1983): By enhancing the production of novel behavioural variants, a large brain might more frequently expose individuals to conditions favouring speciation (Wyles *et al.*, 1983). Evidence is indeed accumulating that species with relatively larger brains are more prone to change their behaviour to cope with environmental challenges (Reader & Laland, 2002; Lefebvre *et al.*, 2004) and that behavioural changes may facilitate divergent selection (Losos *et al.*, 2004; Lapiedra *et al.*, 2013). Darwin himself was convinced that behavioural changes could lead to changes in morphology when he wrote that "*It is of utmost importance to show that habits sometimes go before structures*" (Darwin, Notebook C) and that "*As we sometimes see individuals of a species following habits widely different from those of their own species (...), such individuals would occasionally have given rise to new species*".

Besides the behavioural drive hypothesis, other non-exclusive mechanisms may also explain the association between brain size and diversification. For instance, behavioural flexibility might promote evolutionary divergence from the ancestor by facilitating range expansions (Sol *et al.*, 2005a, 2008), (Rosenzweig, 1995; Zink *et al.*, 2008). Alternatively, a large brain may buffer individuals against extrinsic mortality, reducing the chances that the population dies out when the environment changes. There is indeed evidence that big brained birds experience lower population declines (Shultz *et al.*, 2005) and are more stable against environmental variation (Fristoe et al., 2017; but See Nicolakakis et al., 2003). Further investigations of the effects of behavioural flexibility and brain size on response to environmental changes are needed to better disentangle these alternative mechanisms.

Altogether, our study significantly contributes to clarify the debate over the role of the brain as key innovation. Although some degree of chance is likely involved in processes leading to speciation events (Ricklefs, 2003), our results emphasize that being at the correct place at the right time is not enough to explain diversification processes. Rather, diversification seems to be higher in lineages that have an enhanced ability to exploit new ecological opportunities (Simpson, 1944, 1953). By allowing to take an active role in the way animals utilize their environment, a relatively large brain may enhance animals' potential to shape their own evolutionary routes.

Table 4.1. QUASSE model comparison in two different phylogenetic summary trees. In each case, we compared the fit (AICc) of a null model with another model including a linear effect of brain size to speciation rates and a model including a linear effect plus a directional tendency of brain size evolution.

Model	df	lnLik	AICc	P>Chi	λ	μ	slope	drift
Ericson summary tree								
Null	3	-6761.0	13528		0.052	<0.001	-	-
Linear	4	-6750.6	13509	<0.001	0.048	<0.001	0.017	-
Linear with drift	5	-6659.2	13328	<0.001	0.021	<0.001	0.033	-0.055
Hackett summary tree								
Null	3	-6747.7	13501		0.053	<0.001	-	-
Linear	4	-6735.3	13478	<0.001	0.048	<0.001	0.019	-
Linear with drift	5	-6634.2	13278	<0.001	0.018	<0.001	0.035	-0.060

Figure 4.1. The diversification rate measure (DR) takes into account both the number of splits and the length of the branches from root to tip (a), where highly diversifying clades have high values of DR, as we can see in a phylogenetic tree containing the species of this study (b).

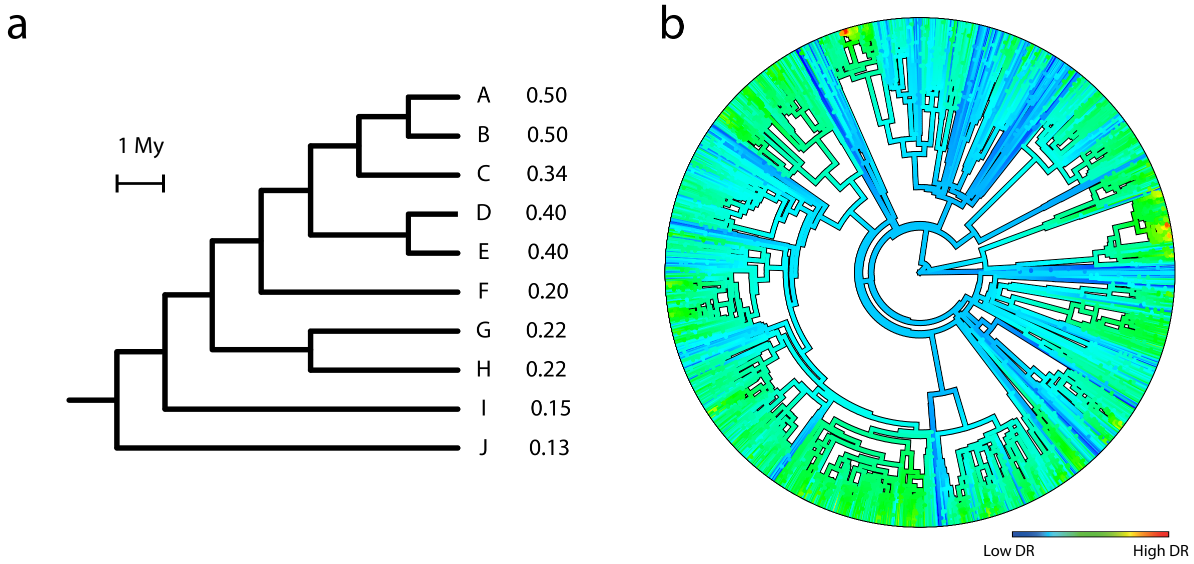
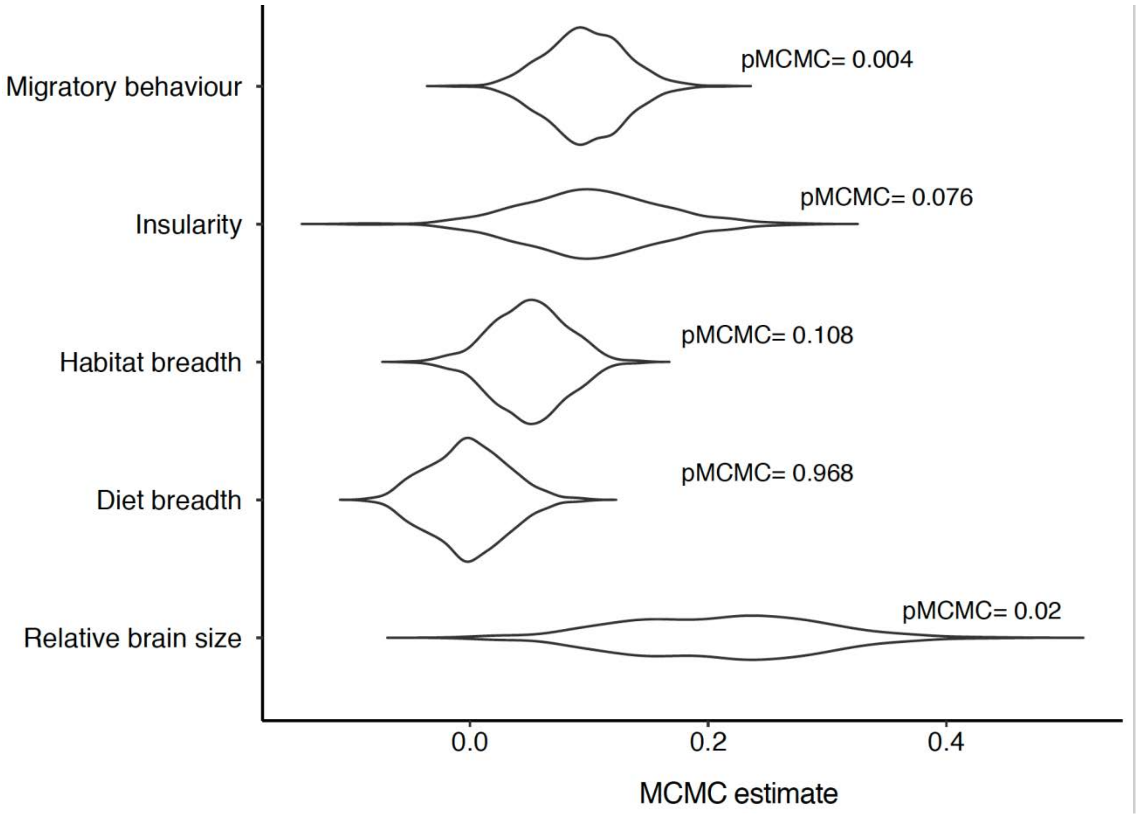


Figure 4.2. Distribution of the effect of each factor on diversification rate (DR) in 1000 samples of a Phylogenetic Bayesian mixed model (N=1701 species), where pMCMC is the number of times that the sample was greater than zero.



General discussion and Conclusions

Relatively to their body size, our human ancestors evolved the largest brain of any mammal. However, restricting the analyses to humans when investigating brain size evolution runs the risk of generalizing from a single case. The discovery that other animals stand out for their intelligence while having also evolved a relatively large brain raises thus major interest to investigate the circumstances that have favoured the evolution of large brains. This thesis explores the causes and consequences of the evolution of large brains in birds. First, we show that a large brain results from an expansion of the associative areas (**Chapter 1**), which are responsible of the integration of stimuli and the development of novel behaviours. Such large brains seem to have evolved in places characterized by higher levels of environmental variation, including high latitudinal regions (**Chapter 2**) and oceanic islands (**Chapter 3**). These regions experience an especially high uncertainty in resource availability. Finally, the evolution of large brains may enhance the rate of evolutionary diversification (**Chapter 4**). In the next paragraphs, I discuss these main findings in light of the current literature knowledge.

The use of whole brain size as a measure for cognitive abilities has been questioned for some authors (Healy & Rowe, 2007). The main argument is that brain is structured in functionally distinct areas and hence two brains of similar size may be built by increasing different brain areas, making comparisons of the entire brain biologically meaningless. However, two lines of evidence support the use of whole brain size as a valid measure for cognition capacities. First, comparative evidence show that relatively large brains are related to better performance in cognitive measures such as the propensity for behavioural innovation in birds (Lefebvre *et al*., 1997, 2004) and primates (Reader & Laland, 2002), and problem solving in carnivores (Benson-Amram *et al*., 2016). Second, artificial selection for whole brain size shows that relatively large brained guppies have better learning abilities in experimental tests, at least in females (Kotrschal *et al*., 2013; Buechel *et al*., 2018). One of the explanations proposed for why the whole brain size predicts cognitive performance, even if brain is composed by different areas controlling distinct behaviour (Devoogd *et al.*, 1993), is that enlarged brains are not the result of increases in different brain areas in different lineages but are characterized by the enlargement of the associative areas (the frontal cortex in primates and the pallium in birds). In **Chapter 1** we show that the increase in relative brain size is indeed mainly caused by a disproportionate enlargement of the associative pallium, formed by two areas that control advanced cognition such as tool use (Lefebvre *et al.*, 2002) and behavioural innovation (Timmermans *et al.*, 2000). This result supports the use of relative brain size as a proxy of cognitive abilities, and hence validate the use of relative brain size in broader studies of the ecological causes of brain size variation.

The cognitive buffer hypothesis is based on the idea that big brains allow individuals to buffer environmental changes, thereby enhancing survival rates. Supporting evidence comes from studies in birds showing that species with relatively bigger brains are more likely to establish themselves in novel environments (Sol & Lefebvre, 2000; Sol *et al.*, 2005a), suffer lower mortality rates in their native ranges (Sol *et al.*, 2007), and their populations are less likely to decline (Shultz *et al.*, 2005) or fluctuate (Fristoe *et al.*, 2017) over time. In primates, the comparison of daily food intake with variation in the environment shows that species with relatively larger brains have a greater capacity to compensate the drop in food availability (van Woerden *et al.*, 2010, 2011, 2014).

Nevertheless, the crucial prediction of the CBH that enlarged brains have primarily evolved in lineages exposed to high environmental variation has received far less support. In birds, the finding that migratory birds have relatively smaller brains than resident species (Winkler *et al.*, 2004; Sol *et al.*, 2005b, 2010; Vincze, 2016) may be interpreted as resident species having been selected for larger brains to respond to the environmental variation. However, the alternative that the smaller brain of migratory species reflect constraints cannot be rule out (See later discussion on constraints). Work on primates also led some authors to suggest that increased seasonality could constrain rather than favour the evolution of large brains if growing and maintaining the brain during periods of food scarcity is excessively costly (van Woerden *et al.*, 2010, 2011, 2014). In **Chapter 2**, we used birds as a study model to provide a general test for a link between brain size and environmental variability. First, we confirm the trend for smaller brains in migratory species. Second, and more importantly, we find that residents from higher latitudes, which experience both seasonal and between-year changes in resource availability, have larger brains than both residents from lower latitudes and migratory species. Previous works in parrots already found that seasonal changes in temperatures and precipitations are associated with relatively larger brains (Schuck-Paim *et al.*, 2008), but in **Chapter 2** we generalize this result to all birds and we additionally find an association between environmental uncertainty (e.g. changes from year to year) and brain size. In **Chapter 3**, we further show that colonization of oceanic islands was followed by an increase in relative brain size, in part because of the more frequent environmental changes across years on these islands as compared to the closest continent. Therefore, among-year changes in resources appear to be the common environmental driver affecting brain size in higher latitudes (**Chapter 2**) and islands (**Chapter 3**), suggesting an important role of environmental uncertainty in the evolution of large brains and in line with theoretical models (Dridi & Lehmann, 2016; Dunlap *et al.*, 2016). Future work will have to disentangle whether it is seasonality, unpredictability or both what selects for enhanced cognition and how they interact on other selective pressures such as the social environment (Overington *et al.*, 2008).

The results of **Chapter 2 & 3** suggest that relatively large brains evolved as a result of selection for coping with environmental variation, as predicted by the cognitive buffer hypothesis. However, the presence of species with relatively larger brains in more variable regions can also result if a large brain has facilitated the colonization of regions with higher environmental variation (Sol *et al.*, 2005b, 2010; Fristoe *et al.*, 2017). Indeed, there is ample evidence that large brained species are better colonizers of novel environments (Sol *et al.*, 2005a, 2008; Amiel *et al.*, 2011). The expansion of the human lineage has also been associated with changes in brain size, which potentially favoured the colonization of new environments (Wells & Stock, 2007; Lefebvre, 2013). Disentangling both alternatives requires to separate in situ evolution from sorting processes derived from colonization events, which cannot be achieved with traditional correlative analyses. However, a retrospective approach that allows reconstructing ancestral states along the phylogeny can give clues on causality. In **Chapter 2**, a character stochastic mapping approach (Huelsenbeck *et al.*, 2003) and a subsequent fitting of evolutionary models (Beaulieu *et al.*, 2012) show that species living in higher latitudes have a higher optimum value of relative brain size compared to resident species from other regions. Although this is not sufficient to conclude that brain size evolved after the colonization events, intra-group differences also suggest that the global association between higher environmental variation and relative brain size does not come from a sorting process of large brained lineages colonizing higher latitudes. In a similar vein, **Chapter 3** shows differences in relative brain size between sister species from islands and continents, suggesting that *in situ* evolution could better explain the relatively bigger brains of island birds. Additional reconstructions of ancestral node states using a Bayesian approach also suggest that insularity drives the evolution of larger brains. Despite the inferred causal link, we still have to be careful in the interpretation of the results as there is no guarantee that the evolutionary processes currently operating are the same that operated in the past (Losos, 1994).

Apart from the outlined benefits, brain size evolution also is also affected by important constraints, as the development and maintenance of a large brain requires substantial time and high amounts of energy. In energetic terms, brain tissues are nearly an order of magnitude more expensive than most other somatic tissues (Mink *et al.*, 1981). According to the expensive brain hypothesis (Isler & van Schaik, 2009), this metabolic cost can be afforded by either increasing the total energy budget or by compensating changes in energy allocation to other maintenance functions. Therefore, the hypothesis predicts that the brain should be smaller if more energy needs to be allocated into other functions such as locomotion (Isler & van Schaik, 2006a; Navarrete *et al.*, 2011). Evidence for this hypothesis was found in **Chapter 2**, as brain size decreases with migratory distance, presumably because of the energy needs associated with long-distance migration (Sol *et al.*, 2010). However, developmental constraint could also be in part responsible for a decrease in brain size if migrating longer distances reduces the time available for the development of a larger brain. Relative brain size is indeed associated with the length of the developmental period (Iwaniuk & Nelson, 2003; Barton & Capellini, 2011), presumably because a large brain takes longer to grow. We confirm such a relationship in **Chapters 2 & 3**, further supporting the idea that a slow life history strategy is a prerequisite for the evolution of enlarged brains (Isler & van Schaik, 2006a, 2009; Weisbecker & Goswami, 2014; Weisbecker & Goldizen, 2015). In this sense, a slow pace of life would give parents the chance of a prolonged investment in offspring (Covas & Griesser, 2007) and allow more time for the brain to grow (Walker *et al.*, 2006). Indeed, longer developmental periods could also explain the disproportionate associative areas in large brained birds found in **Chapter 1**. A delay in the neurogenesis onset and offset during the fledging period characterizes large brained lineages, causing an increase in the association areas by delaying and prolonging the production and maturation of neurons (Charvet *et al.*, 2011). The association between brain size and slower life history, however, is also expected if investing in a larger brain provides long term benefits for species with a long lifespan. The cognitive buffer hypothesis predicts that if brains allow to construct behavioural responses during periods of environmental stress, this should reduce mortality (Sol *et al.*, 2007) and finally select for longer lives (González-Lagos *et al.*, 2010; Minias & Podlaszczuk, 2017). In primates, the relation between lifespan and brain size has been found to be independent of the maternal investment effect (Street *et al.*, 2017), suggesting a direct effect of relative brain size on survival. In addition, an extended lifespan would increase the benefits of flexible behaviours, as the chances that an individual encounters severe crises during its lifetime are higher and, thus, longevity should favour selection for enlarged brains in order to sustain animals through the periods of environmental stress (Allman *et al.*, 1993; Sol, 2009a). The association we found between brain size and resource variation among years in **Chapters 2 & 3** supports the idea of an advantage of developing a large brain in species that live longer and hence have more chances to experience important changes from year to year. Moreover, if large brained species have more time to explore and develop new behavioural responses, the acquired behaviours may be used for longer periods (Sol, 2009a; Sol *et al.*, 2016). This might be especially important in places with low predatory pressures, such as islands (**Chapter 3**), where the development of novel behaviours may be facilitated by the reduced costs of exploration (Mettke-Hofmann *et al.*, 2002).

The results of this thesis can help to explain how large brains have evolved independently, with implications for understanding human evolution. Human recent evolution was characterized by a fast increase in relative brain size, presumably explaining why we managed to colonize almost all available environments on earth (Martin, 1983). However, the debate is still open on which selective pressures shaped our brains. Our finding that enlarged brains are associated with higher environmental variation in birds provides credibility to the classic view that environmental changes were one of the main factors of favouring enlarged brains in humans (Vrba, 1985; Potts, 1998; Richerson & Boyd, 2000; Lefebvre, 2013).

Finally, the thesis has implications on how animals will respond to human-induced environmental changes in the future, an issue of particular relevance in the Anthropocene era. If relative brain size has evolved as response to environmental challenges, it should also protect animals from human-induced environmental changes such as habitat alteration and climate change. Given the increased concern over human impacts on biodiversity loss, this issue will be an important avenue for future research.

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Appendix A

Relative brain size and its relation with the associative pallium in birds

Table A.1. Correlation matrix between the raw volume of the six major brain parts controlling for phylogenetic non-independence of the species.

	Nidopallium	**Mesopallium**	**Hyperpallium**	**Diencephalon**	**Cerebellum**
Mesopallium	0.975	-	-	-	-
Hyperpallium	0.864	0.872	-	-	-
Diencephalon	0.896	0.907	0.869	-	-
Cerebellum	0.756	0.823	0.853	0.911	-
Brainstem	0.649	0.728	0.759	0.863	0.940

Table A.2. Relationships between log body mass and different encephalization metrics used in other studies. Ndp: Nidopallium; Brn: Brainstem.

Brain Measure	Predictor	Intercept ±SE	Slope ±SE	Pr(>|t|)	R^2	Lambda
Absolute measures						
Log (absolute Ndp)	Log (body size)	1.43 ±0.40	0.66 ±0.04	<0.001	0.82	1.00
Residuals						
Ndp residual (against Brn)	Log (body size)	-343.97 ±477.59	0.00 ±0.01	0.935	0.00	1.00
Ndp residual (against body)	Log (body size)	-326.93 ±582.85	0.05 ±0.05	0.374	0.00	1.00
Proportions						
Ndp / brain	Log (body size)	0.24 ±0.05	0.01 ±0.05	0.001	0.09	1.00
Log (Ndp) / Log (brain)	Log (body size)	0.73 ±0.02	0.02 ±0.02	<0.001	0.48	1.00
Fractions						
Ndp / brain - Ndp	Log (body size)	0.23 ±0.15	0.04 ±0.02	0.001	0.09	1.00
Log (Ndp) / Log (brain - Ndp)	Log (body size)	0.79 ±0.03	0.02 ±0.00	<0.001	0.27	1.00
Executive ratios						
Ndp / Brn	Log (body size)	-0.65 ±1.39	0.36 ±0.14	0.010	0.08	0.97
Log (Ndp) / Log (Brn)	Log (body size)	1.06 ±0.07	0.01 ±0.01	0.319	0.00	0.98

Table A.3. Correlation matrix between the six major brain parts after removing the allometric effect of body mass by means of residuals and controlling for phylogenetic non-independence of the species.

	Nidopallium	**Mesopallium**	**Hyperpallium**	**Diencephalon**	**Cerebellum**
Mesopallium	0.942	-	-	-	-
Hyperpallium	0.737	0.664	-	-	-
Diencephalon	0.796	0.726	0.710	-	-
Cerebellum	0.609	0.572	0.573	0.713	-
Brainstem	0.273	0.297	0.232	0.490	0.434

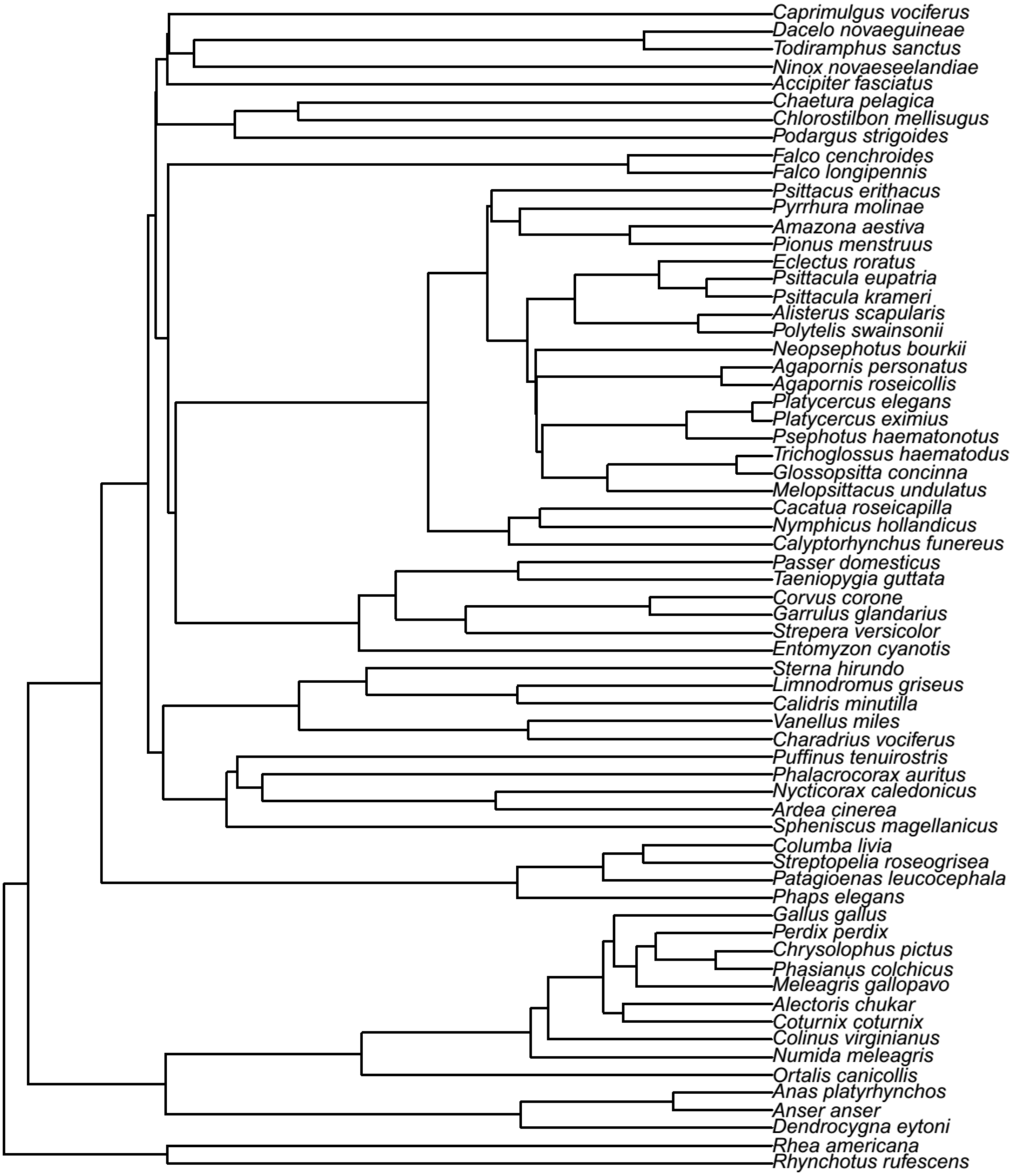
Table A.4. Body size and brainstem size as predictors of whole brain size and the different brain parts, using PGLS models.

Brain area	**Predictor**	**Intercept ±SE**	**Slope ±SE**	**Pr(>|t|)**	**Adj R^2**	**lambda**
Log (whole brain)	Log(Body size)	4.24±0.24	0.63±0.03	<0.001	0.85	0.97
Log (Nidopallium)	Log(Body size)	2.72 ±0.33	0.65 ±0.04	<0.001	0.81	0.98
Log(Mesopallium)	Log(Body size)	1.49 ±0.35	0.69 ±0.04	<0.001	0.80	0.91
Log(Hyperpallium)	Log(Body size)	1.32 ±0.48	0.68 ±0.05	<0.001	0.71	1.00
Log(Cerebellum)	Log(Body size)	2.23 ±0.24	0.62 ±0.03	<0.001	0.85	0.69
Log(Diencephalon)	Log(Body size)	1.48 ±0.26	0.53 ±0.03	<0.001	0.82	0.87
Log(Brainstem)	Log(Body size)	2.94 ±0.15	0.55 ±0.02	<0.001	0.89	0.19
Log(Nidopallium)	Log(Brainstem)	0.01 ±0.49	1.07 ±0.07	<0.001	0.80	1.00
Log(Mesopallium)	Log(Brainstem)	-1.57 ±0.49	1.15 ±0.07	<0.001	0.82	0.97
Log(Hyperpallium)	Log(Brainstem)	-1.61 ±0.72	1.13 ±0.10	<0.001	0.66	0.96
Log(Cerebellum)	Log(Brainstem)	-0.59 ±0.32	1.06 ±0.05	<0.001	0.88	0.50
Log(Diencephalon)	Log(Brainstem)	-1.14 ±0.35	0.96 ±0.05	<0.001	0.85	0.83

Table A.5. Relationship of different brain parts with brain size after removing allometry by means of residuals from body size or brainstem size and using PGLS models to control for phylogenetic non-independence of the species.

Response	Predictor	Intercept ±SE	Slope ±SE	Pr(>|t|)	Adj R^2	lambda
(Residuals from Body size)						
Brain size	Nidopallium	0.00 ±0.05	0.76 ±0.03	<0.001	0.90	0.72
Brain size	Mesopallium	0.00 ±0.06	0.70 ±0.04	<0.001	0.84	0.71
Brain size	Hyperpallium	0.01 ±0.09	0.46 ±0.04	<0.001	0.65	0.74
Brain size	Diencephalon	0.00 ±0.08	0.88 ±0.06	<0.001	0.79	1.00
Brain size	Cerebellum	-0.01 ±0.11	0.77 ±0.06	<0.001	0.70	1.00
Brain size	Brainstem	0.00 ±0.16	0.58 ±0.09	<0.001	0.36	1.00
(Residuals from Brainstem size)						
Brain size	Nidopallium	-0.03 ±0.13	0.48 ±0.07	<0.001	0.39	0.59
Brain size	Mesopallium	-0.04 ±0.14	0.46 ±0.08	<0.001	0.34	0.67
Brain size	Hyperpallium	-0.05 ±0.15	0.29 ±0.05	<0.001	0.29	0.72
Brain size	Diencephalon	0.00 ±0.13	0.57 ±0.11	<0.001	0.27	0.72
Brain size	Cerebellum	-0.01 ±0.17	0.29 ±0.12	<0.001	0.07	0.87

Figure A.1. Example of one of the 20 phylogenetic hypotheses used in the analyses



Appendix B

Environmental variation and the evolution of enlarged brains in birds

Table B.1. PGLS modelling variation in brain size (log-transformed) as a function of body size and latitude (with Low latitudes taken as reference for comparisons) for resident species.

Factor (N=855, p-value<0.001)	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Intercept	-2.62	0.17	-15.07	<0.001	0.86(0.02)	0.90
Log (body size)	0.59	0.01	73.05	<0.001		
Resident mid-latitude	0.00	0.01	0.12	0.901		
Resident high-latitude	0.06	0.03	2.44	0.015		

Table B.2. Correlation matrix for the environmental variables in resident birds (N=835). Values represent the Pearson's correlation coefficients, with the R^2 of the corresponding PGLS models with the two variables in parenthesis. The R^2 were used to calculate the variance inflator factor of the three variables (VIF=6.6).

	EVI among	EVI within
Snow	0.51 (0.25)	0.89 (0.74)
Evi within	0.53 (0.27)	-

Table B.3. PGLS modelling variation in brain size (log-transformed) as a function of body size, two environmental axes from a PPCA and including ecological categories such as fruit consumption, insect consumption and forest dwelling for resident birds.

Factor (N=827, p-value<0.001)	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Intercept	-2.52	0.13	-19.99	<0.001	0.87(0.05)	0.91
Log (body size)	0.59	0.01	72.18	<0.001		
Environmental variation (PPC1)	0.04	0.01	5.03	<0.001		
Environmental variation (PPC2)	0.02	0.01	2.10	0.036		
Fruit consumer	0.01	0.02	0.69	0.492		
Insect consumer	0.02	0.02	0.96	0.336		
Forest dwelling	0.04	0.01	2.79	0.005		

Table B.4. PGLS modelling variation in brain size (log-transformed) as a function of body size, two environmental axes from a PPCA and diet breadth in resident birds.

Factor (N=827, p-value<0.001)	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Intercept	-2.49	0.13	-19.75	<0.001	0.87(0.05)	0.92
Log (body size)	0.59	0.01	72.82	<0.001		
Environmental variation (PPC1)	0.04	0.01	5.03	<0.001		
Environmental variation (PPC2)	0.02	0.01	3.32	0.001		
Diet breadth	0.20	0.10	2.10	0.035		

Table B.5. PGLS modelling variation in brain size (log-transformed) as a function of body size, two environmental axes from a PPCA and including developmental periods (Model 1) and developmental modes (Model 2) as confound factors in resident birds.

Factor	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Model 1 (N=468, p-value<0.001)						
Intercept	-2.75	0.23	-12.06	<0.001	0.88(0.12)	0.95
Log (body size)	0.58	0.01	42.60	<0.001		
Environmental variation (PPC1)	0.04	0.01	4.94	<0.001		
Environmental variation (PPC2)	0.04	0.01	4.11	<0.001		
Log (Incubation)	0.07	0.03	2.55	0.022		
Log (Fledging)	0.02	0.01	1.78	0.492		
Model 2 (N=835, p-value<0.001)						
Intercept	-2.29	0.14	-16.97	<0.001	0.87(0.07)	0.90
Log (body size)	0.59	0.01	74.01	<0.001		
Environmental variation (PPC1)	0.04	0.01	5.76	<0.001		
Environmental variation (PPC2)	0.02	0.01	3.19	0.001		
Dev.mode (Precocial)	-0.37	0.11	-3.45	0.001		
Dev.mode (Semialtricial)	0.23	0.09	2.03	0.008		
Dev.mode (Semiprecocial)	-0.15	0.12	-1.88	0.206		

Table B.6. PGLS modelling variation in brain size (log-transformed) as a function of body size, two environmental axes from a PPCA and including the social mating system (Model 1), degree of colonial breeding (Model 2) and social foraging (Model 3) as confound factors in resident birds. Monogamy is taken as the reference level in social mating system and solitary is taken as reference level in the case of colonial breeding and social foraging.

Factor	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Model 1 (p-value<0.001, N=590)						
Intercept	-2.25	0.15	-14.96	<0.001	0.87(0.03)	0.91
Log (body size)	0.59	0.01	60.75	<0.001		
Environmental variation (PPC1)	0.04	0.01	4.62	<0.001		
Environmental variation (PPC2)	0.03	0.01	3.16	0.002		
Mating system (Facultative)	0.03	0.06	0.48	0.626		
Mating system (Polygamous)	-0.04	0.04	-1.17	0.242		
Model 2 (N=443, p-value<0.001)						
Intercept	-2.29	0.16	-14.50	<0.001	0.87(0.02)	0.97
Log (body size)	0.60	0.01	54.46	<0.001		
Environmental variation (PPC1)	0.03	0.01	3.61	<0.001		
Environmental variation (PPC2)	0.02	0.01	2.31	0.002		
Colonial Breeding (Colonial)	0.00	0.04	0.04	0.969		
Colonial Breeding (Semi-colonial)	0.00	0.03	0.12	0.904		
Model 3 (N=302, p-value<0.001)						
Intercept	-2.36	0.18	-13.00	<0.001	0.89(0.04)	0.95
Log (body size)	0.59	0.01	45.18	<0.001		
Environmental variation (PPC1)	0.05	0.01	4.18	0.002		
Environmental variation (PPC2)	0.04	0.01	3.12	0.001		
Social Foraging (Pairs)	0.04	0.04	0.88	0.378		
Social Foraging (Bonded Groups)	0.01	0.04	0.35	0.730		
Social Foraging (Aggregations)	0.01	0.04	0.19	0.846		

Table B.7. PGLS modelling variation in brain size (log-transformed) as a function of body size, two environmental axes from a PPCA and including ecological categories, diet breadth, developmental periods, mating system, degree of colonial breeding and social foraging as confound factors in resident birds. Monogamy is taken as the reference level in social mating system and solitary is taken as reference level in the case of colonial breeding and social foraging.

Factor (N=242, p-value <0.001)	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**ʎ**
Intercept	-2.90	0.32	-9.14	<0.001	0.87(0.43)	1.0
Log (body size)	0.58	0.02	33.01	<0.001		
Environmental variation (PPC1)	0.03	0.01	2.39	0.018		
Environmental variation (PPC2)	0.05	0.02	3.31	0.001		
Fruit consumer	-0.05	0.03	-1.69	0.092		
Insect consumer	-0.02	0.03	-0.61	0.541		
Forest dwelling	0.03	0.03	0.95	0.342		
Diet breadth	0.48	0.16	3.31	0.003		
Log (Incubation)	0.23	0.09	2.47	0.014		
Log (Fledging)	-0.01	0.01	-1.81	0.072		
Mating system (Facultative)	0.00	0.07	0.00	0.998		
Mating system (Polygamous)	0.02	0.05	0.36	0.718		
Colonial Breeding (Semi-colonial)	0.07	0.02	3.05	0.003		
Colonial Breeding (Colonial)	0.07	0.07	1.06	0.291		
Social Foraging (Pair)	0.04	0.05	0.88	0.378		
Social Foraging (Bonded group)	0.05	0.04	1.26	0.211		
Social Foraging (Aggregation)	0.03	0.04	0.84	0.406		

Table B.8. Model selection table including the beta estimate for each predictor included in the best models (increase in AICc<2) of Log (Brain size) as a response of body size, two environmental axes from a PPCA and all confound factors (N=242) with the importance in terms of AICc weight of each factor below. social mating system, colonial breeding and social foraging do not appear in the table because they do not enter in any of the best models.

Intercept	Body size	Env. var. (PPC1)	Env. var. (PPC2)	Diet Breadth	Incubation	Fledging	Forest Dweller	Fruit Consumer	Insect Consumer	df	AICc	delta	weight
-2.744	0.594	0.009	0.021	0.263	0.1508	-	-	-	-	6	-97.8	0.00	0.105
-2.703	0.597	0.008	0.021	-	0.1377	-	-	-	-	5	-97.8	0.00	0.105
-2.345	0.611	0.009	0.022	-	-	-	-	-	-	4	-97.5	0.27	0.092
-2.376	0.613	0.007	0.019	-	-	-	0.040	-	-	5	-97.5	0.32	0.09
-2.690	0.601	0.007	0.018	-	0.1226	-	0.035	-	-	6	-97.2	0.58	0.079
-2.352	0.609	0.009	0.022	0.234	-	-	-	-	-	5	-97.1	0.72	0.073
-2.729	0.598	0.007	0.019	0.254	0.1356	-	0.033	-	-	7	-97.1	0.73	0.073
-2.381	0.612	0.007	0.019	0.227	-	-	0.039	-	-	6	-96.9	0.86	0.068
-2.787	0.595	0.008	0.020	0.272	0.1685	-0.009	-	-	-	7	-96.6	1.22	0.057
-2.739	0.598	0.008	0.020	-	0.1524	-0.009	-	-	-	6	-96.4	1.36	0.053
-2.728	0.602	0.007	0.017	-	0.1379	-0.010	0.037	-	-	7	-96.0	1.78	0.043
-2.775	0.599	0.007	0.018	0.263	0.1538	-0.010	0.035	-	-	8	-96.0	1.79	0.043
-2.375	0.616	0.007	0.018	-	-	-0.007	0.042	-	-	6	-95.9	1.93	0.040
-2.715	0.598	0.009	0.021	-	0.1377	-	-	-	0.011	6	-95.8	1.98	0.039
-2.741	0.594	0.009	0.021	0.291	0.1492	-	-	-0.012	-	7	-95.8	1.99	0.039

Table B.9. PGLS modelling the EVI amplitude (difference between summer and winter in the breeding regions) as a function of latitude and migratory distance categories (with low latitudes residents as reference level to compare them with residents from other regions and with migratory birds moving short and long distances).

Factor (N=1159)	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Intercept	-0.03	0.02	-1.72	0.085	0.25	0.35
Resident mid-latitude	0.01	<0.01	1.61	0.107		
Resident high-latitude	-0.07	0.01	-7.65	<0.001		
Migrant short-distance	-0.08	0.01	-15.93	<0.001		
Migrant long-distance	-0.08	0.01	-9.82	<0.001		

Table B.10. PGLS modelling variation in brain size (log-transformed) as a function of body size and coefficient of variation of EVI along the year (Model 1) or body size and coefficient of variation of EVI between years (Model 2) in migratory birds.

Factor	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Model 1 (N=317, p-value<0.001)						
Intercept	-2.39	0.12	-20.47	<0.001	0.90(0.00)	0.88
Log (body size)	0.61	0.01	52.85	<0.001		
CV (EVI along the year)	-0.05	0.20	-0.24	0.809		
Model (N=317, p-value<0.001)						
Intercept	-2.38	0.12	-19.32	<0.001	0.90(0.00)	0.89
Log (body size)	0.61	0.01	52.64	<0.001		
CV (EVI among years)	-1.46	3.34	-0.43	0.666		

Table B.11. PGLS modelling variation in brain size (log-transformed) as a function of body size, latitude and migratory distance categories (with middle latitudes residents as reference level to compare them with residents from other regions and with migratory birds moving short and long distances).

Factor (N=1217, p-value<0.001)	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Intercept	-2.48	0.12	-20.66	<0.001	0.86(0.02)	0.90
Log (body size)	0.59	0.01	86.38	<0.001		
Resident low-latitude	0.01	0.01	2.30	0.527		
Resident high-latitude	0.06	0.02	2.51	0.022		
Migrant short-distance	-0.03	0.01	-1.81	0.023		
Migrant long-distance	-0.06	0.02	-2.29	0.020		

Table B.12. PGLS modelling variation in brain size (log-transformed) as a function of body size, migratory distance and including developmental periods (Model 1) and developmental modes (Model 2) as confound factors in migratory birds.

Factor	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**λ**
Model 1 (N=314, p-value<0.001)						
Intercept	-2.32	0.12	-18.79	<0.001	0.90(0.13)	0.90
Log (body size)	0.59	0.01	42.93	<0.001		
Log (Migratory distance)	-0.03	0.01	-2.55	0.011		
Log (Incubation)	0.19	0.08	2.41	0.017		
Log (Fledging)	0.02	0.01	1.78	0.085		
Model 2 (N=362, p-value<0.001)						
Intercept	-2.27	0.12	-19.91	<0.001	0.91(0.08)	0.85
Log (body size)	0.61	0.01	56.64	<0.001		
Log (Migratory distance)	-0.03	0.01	-2.68	0.008		
Dev.mode (Precocial)	-0.32	0.09	-3.49	0.001		
Dev.mode (Semialtricial)	0.18	0.09	2.03	0.043		
Dev.mode (Semiprecocial)	-0.20	0.11	-1.88	0.061		

Table B.13. PGLS modelling variation in brain size (log-transformed) as a function of body size, migratory distance and including the social mating system (Model 1), degree of colonial breeding (Model 2) and social foraging (Model 3) as confound factors in migratory birds. Monogamy is taken as the reference level in social mating system and solitary is taken as reference level in the case of colonial breeding and social foraging.

Factor	**Estimate**	**SE**	**t value**	**Pr (>|t|)**	**R^2**	**ʎ**
Model 1 (N=311, p-value<0.001)						
Intercept	-2.13	0.16	-12.96	<0.001	0.90(0.02)	0.89
Log (body size)	0.61	0.01	50.38	<0.001		
Log (Migratory distance)	-0.03	0.01	-2.28	0.023		
Mating system (Facultative)	0.02	0.03	0.74	0.460		
Mating system (Polygamous)	-0.01	0.04	-0.13	0.897		
Model 2 (N=296, p-value<0.001)						
Intercept	-2.08	0.17	-12.14	<0.001	0.90(0.03)	0.89
Log (body size)	0.61	0.01	50.59	<0.001		
Log (Migratory distance)	-0.04	0.01	-2.55	0.001		
Colonial Breeding (Colonial)	-0.02	0.03	-0.50	0.618		
Colonial Breeding (Semi-colonial)	-0.04	0.02	-1.85	0.065		
Model 3 (N=228, p-value<0.001)						
Intercept	-2.24	0.19	-11.82	<0.001	0.91(0.01)	0.90
Log (body size)	0.60	0.01	45.76	<0.001		
Log (Migratory distance)	-0.02	0.02	-0.94	0.344		
Social Foraging (Pairs)	0.04	0.06	0.69	0.490		
Social Foraging (Bonded Groups)	-0.01	0.05	-0.17	0.862		
Social Foraging (Aggregations)	-0.03	0.03	-1.17	0.245		

Table B.14. Support for alternative models of brain size evolution (i.e. two Brownian-motion models and five Orstein-Uhlebeck models) using the mean absolute value of Akaike information criteria (AICc) and the mean Bayesian Information Criterion (BIC) to identify the best model. Models are based on 100 randomly selected phylogenies from the stochastic character mapping of different selective regimes.

	BM1	**BMS**	**OU1**	**OUM**	**OUMV**
AICc	9.12	-161.26	-160.52	-166.87	**-247.41**
BIC	19.31	-130.71	-145.23	-131.24	**-191.50**

Table B.15. Mean estimates and confidence intervals (2.5 and 97.5%) for the parameters (optimum, strength of selection and variation around the optimum) of the OUMV model for different selective regimes of environmental variability integrated over 100 character stochastic map trees. In the last two columns, we report in how many of the 100 trees residents from higher latitudes have higher values than other residents and long distance migrants have lower values than short distance migrants.

OUMV Model (N=100)	**Res High Latitudes**	**Res Medium Latitudes**	**Res Low Latitudes**	**Short-distance migrant**	**Long-distance migrants**	**Models with Resident High lat. > Other residents**	**Models with Long-dist. migrant < Short-dist. migrant**
Brain optima (θ)	0.68 (0.43/0.99)	0.19 (0.12/0.30)	0.19 (0.09/0.33)	0.06 (-0.09/0.26)	-0.07 (-0.21/0.06)	100 %	96 %
Variation around optima (σ^2)	0.07 (0.00/1.35)	0.05 (0.01/0.84)	0.04 (0.01/0.83)	0.03 (0.00/0.32)	0.02 (0.02/0.47)	76 %	1 %

Table B.16. Mean estimates and confidence intervals (2.5 and 97.5%) for the parameters (optimum, strength of selection and variation around the optimum) of the OUMVA model for different selective regimes of environmental variability integrated over 100 character stochastic map trees. In the last two columns, we report in how many of the 100 trees residents from higher latitudes have higher values than other residents and long distance migrants have lower values than short distance migrants.

OUMVA Model (N=100)	**Res High Latitudes**	**Res Medium Latitudes**	**Res Low Latitudes**	**Short-distance migrant**	**Long-distance migrants**	**Models with Resident High lat. > Other residents**	**Models with Long-dist. migrant < Short-dist. migrant**
Brain optima (θ)	0.42 (0.00/0.75)	0.10 (-0.36/0.29)	0.19 (-0.32/0.28)	0.05 (-0.31/0.20)	0.00 (-0.12/0.14)	81 %	70 %
Strength of selection (α)	0.03 (0.00/2.51)	0.01 (0.00/2.81)	0.02 (0.01/3.19)	0.02 (0.00/2.89)	0.02 (0.00/1.95)	79 %	33 %
Variation around optima (σ^2)	<0.01 (0.00/1.21)	<0.01 (0.00/0.98)	<0.01 (0.00/0.76)	<0.01 (0.00/0.49)	<0.01 (0.00/0.45)	17 %	30 %

Figure B.1. Differences in enhanced vegetation index (EVI) variation within and among years and weeks of snow in the breeding site of resident birds at high (N=50), mid (N=326) and low (N=459) latitudes (**a-c**). Phylogenetic PCA (PPCA) with the three variables (**d**) and their co-variation with latitude (**e-f**). In all the bar plots the mean±SEM of the corresponding environmental factor is shown. Residents from higher, mid and low latitudes are represented by black, dark-grey and light-grey bars, respectively.

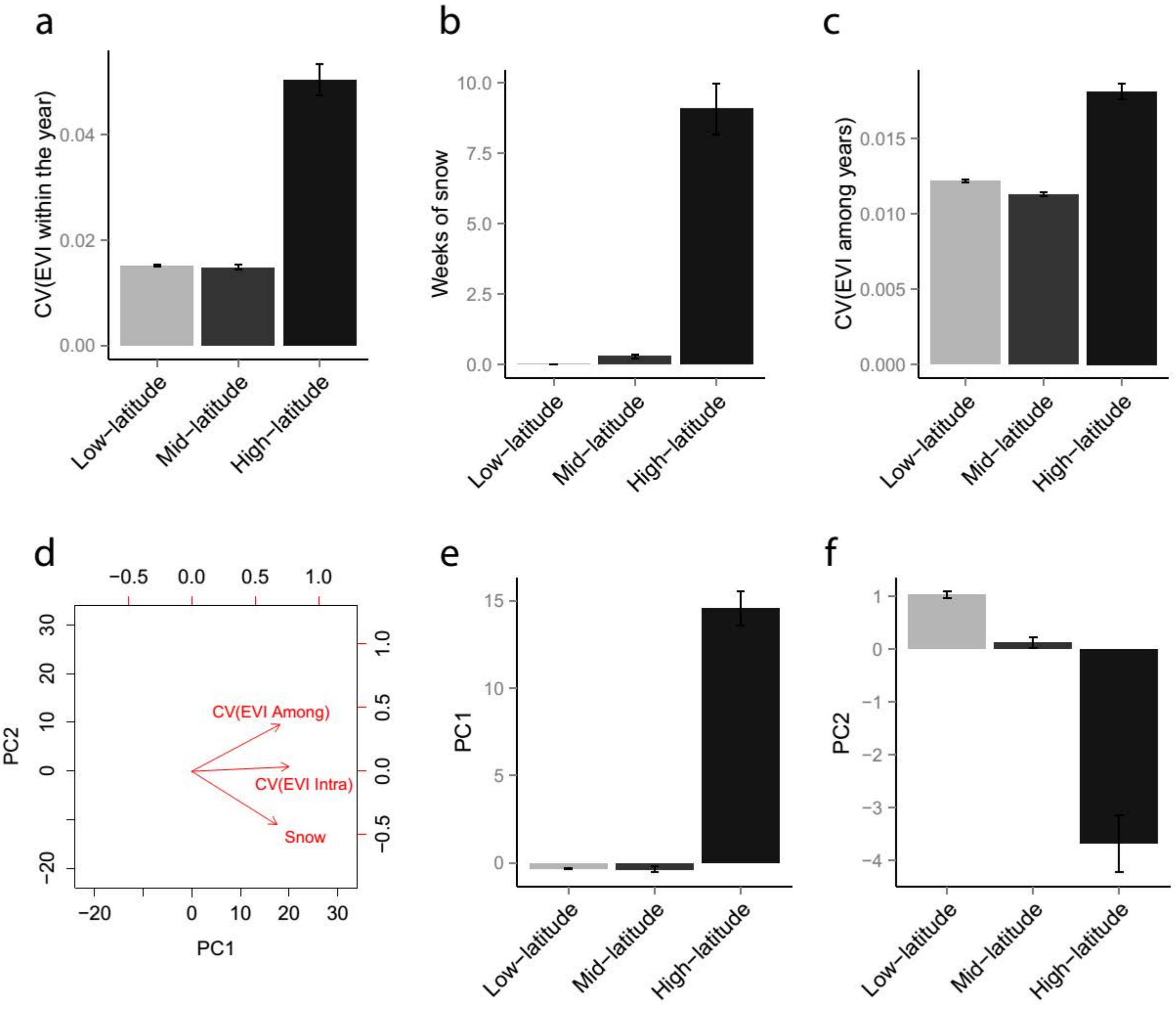


Figure B.2. Relative brain size (Mean ± SEM) in resident species as a function of latitude of the region where they occur. Residents from Higher latitude have larger brains than residents from lower latitudes (PGLS: p = 0.015, N=855, See Table B.1). Residents from higher (N=53), mid (N=335) and low (N=467) latitudes are represented by black, dark-grey and light-grey bars, respectively.

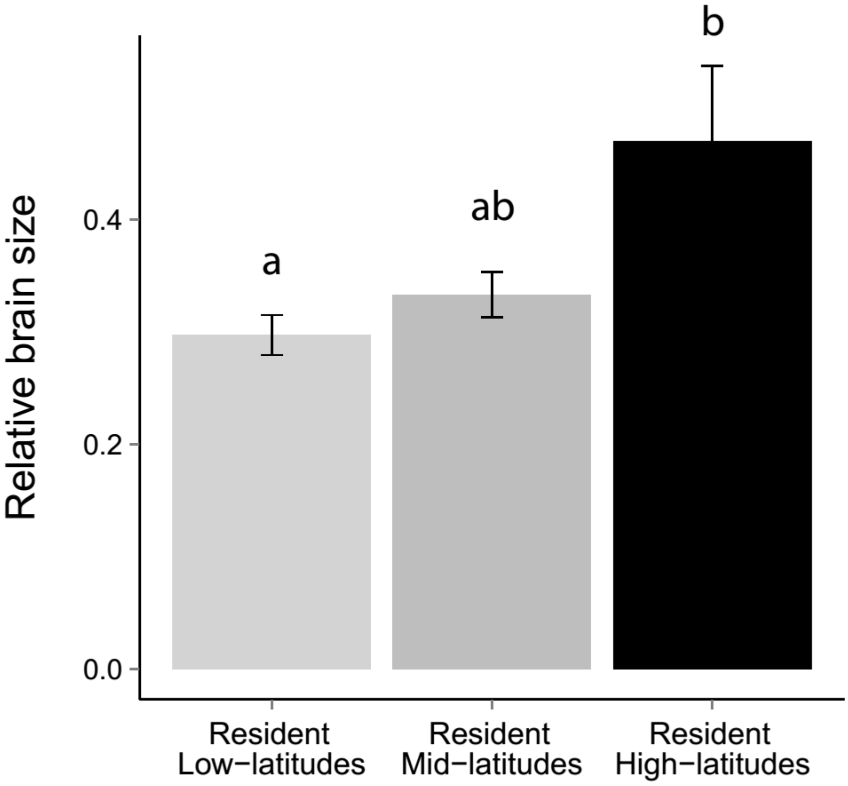


Figure B.3. Distribution of slopes (blue histograms) and p-values (red histograms) of PGLS models using 100 different phylogenetic trees linking brain size with PPC1 (**a-b**) and PPC2 (**c-d**), while controlling for Log (body size).

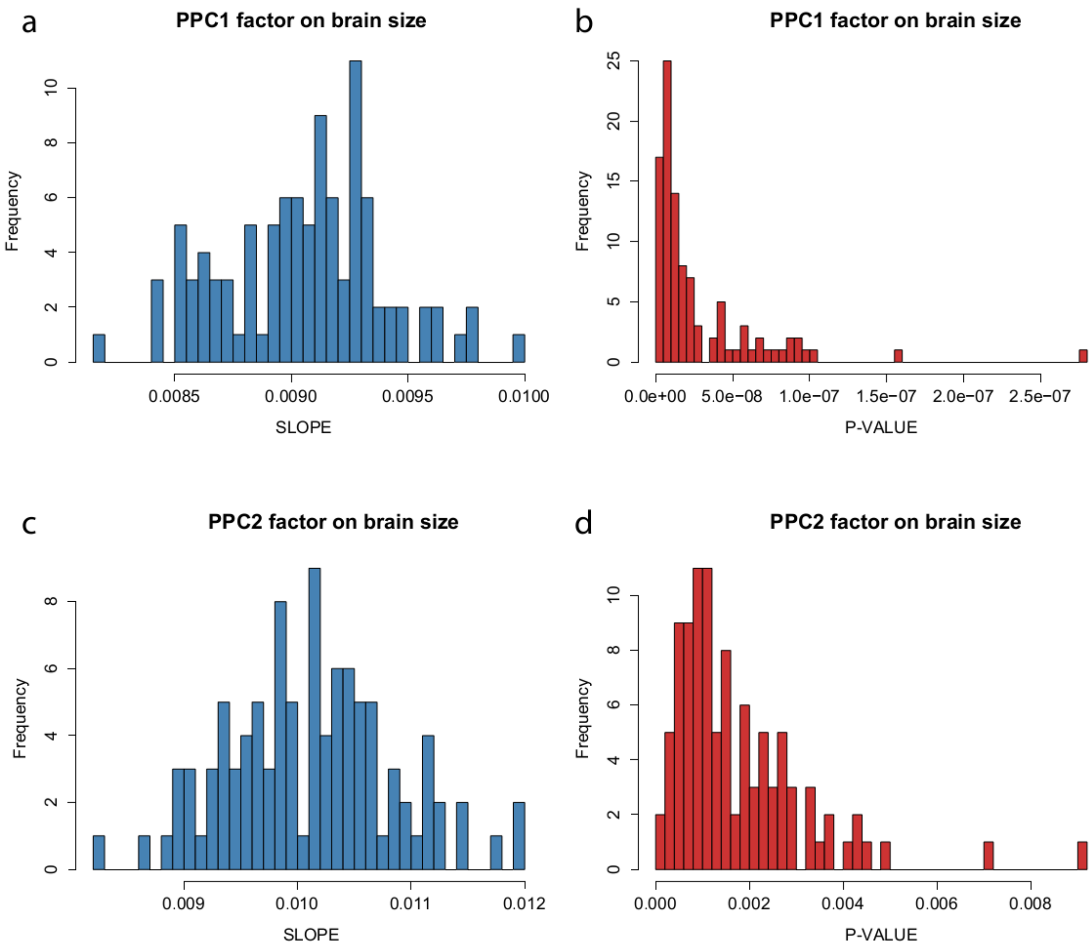


Figure B.4. Variation in productivity (Mean ± SEM), measured by the coefficient of variation of enhanced vegetation index (EVI) across 15 years during breeding season in the breeding distribution range (light grey) and during non-breeding season in the non-breeding distribution range (dark grey) of bird species exposed to different degree of environmental variation.

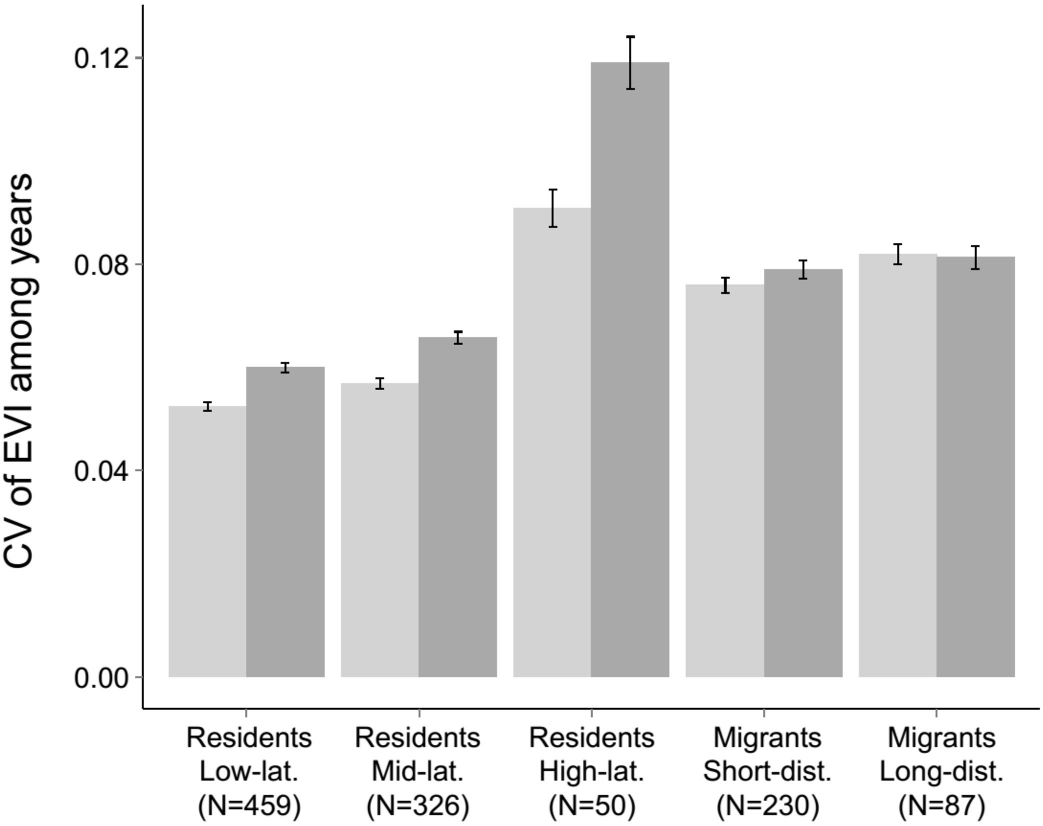


Figure B.5. Relationship between relative brain size and migratory distance within avian orders. The lines are fitted on raw data, with a SEM interval; p-values and R^2 are derived from PGLS models. Only orders with at least 10 species are presented.

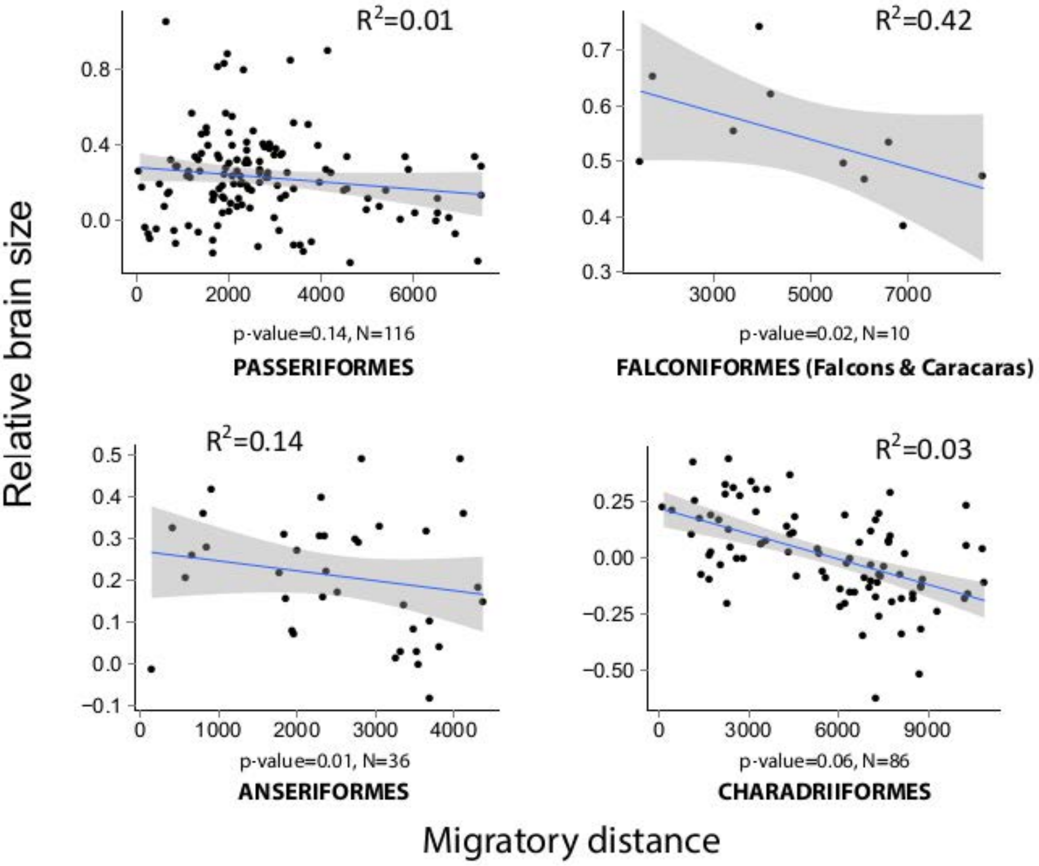


Figure B.6. Histogram of migratory distance in migratory birds (N=362 species)

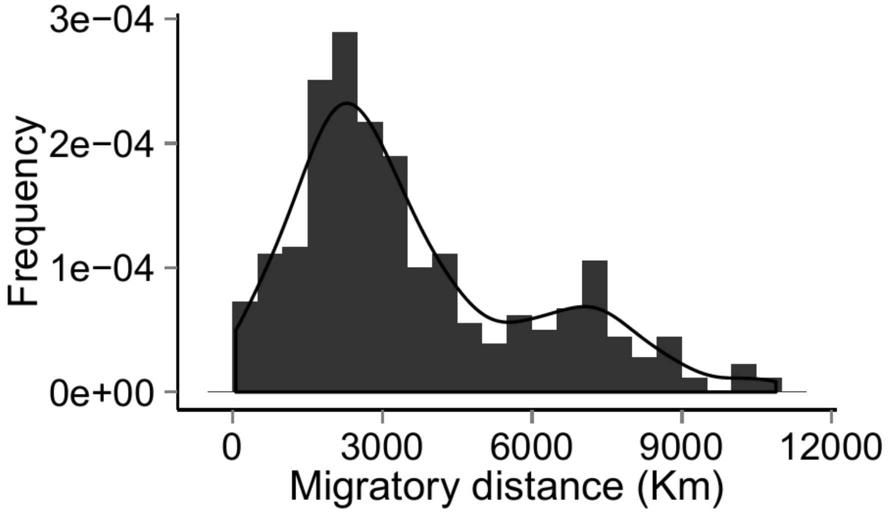


Figure B.7. Distribution of the species used in the study exposed to different degrees of seasonality, divided in those residing the entire year at higher (yellow circles), medium (orange circles) and low latitudes (red circles). An alternative strategy to avoid seasonal changes is to migrate every year to avoid harsh winters, exhibiting long-distance migrations (dark-blue triangles) or short-distance travels (light-blue triangles). Each dot is plotted in the breeding centroid of the distribution area using the *worldHires* map from ‘mapdata’ R-package.

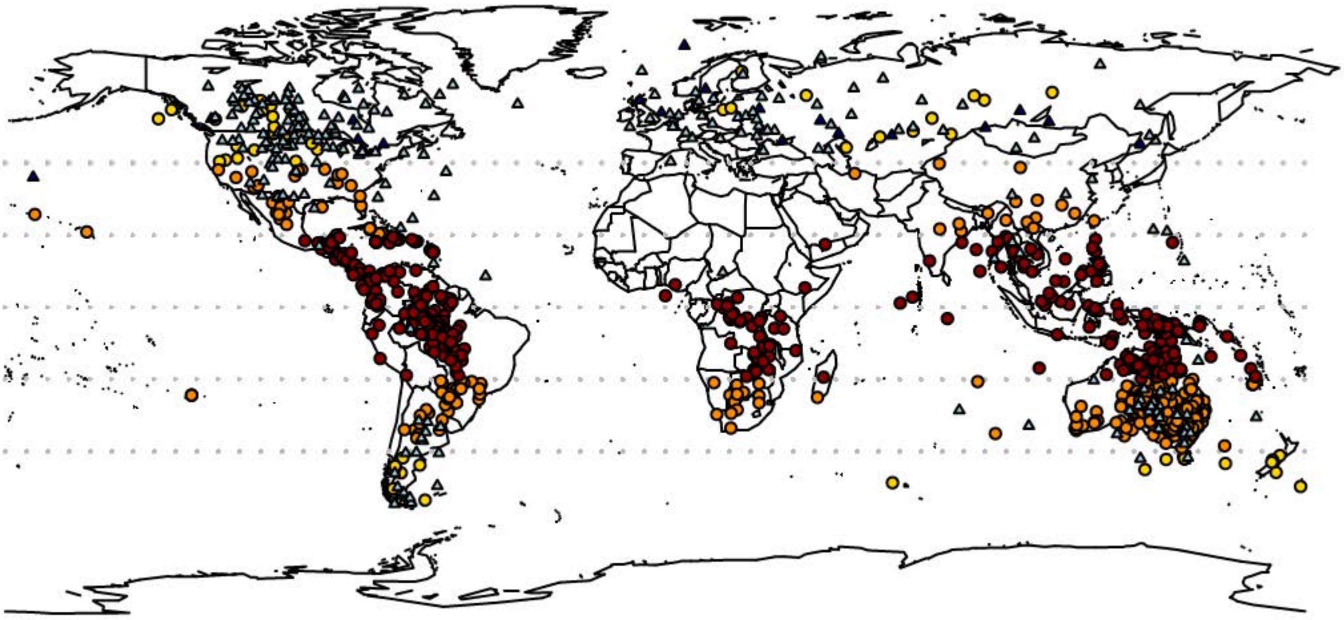


Figure B.8. Resource similarity representation used to calculate diet breadth index: (**a**) nutrient contents estimated for each food item (PT: Proteins; CH: Carbohydrates; LP: Lipids; W: Water content; O: Other), and (**b**) cluster diagram to assess similarity between diet types.

a

Diet Type	PT	CH	LP	W	O
Carrion	16	0	5	75	4
Fruit	2	30.5	7	59	1.5
Invertebrates	17	3	5.5	70	4.5
Nectar	0	20.5	0	79.5	0
Seed	9	72	3	8	8
Vertebrates	16	0	5	75	4
Plant	4.5	34.5	3	55	3

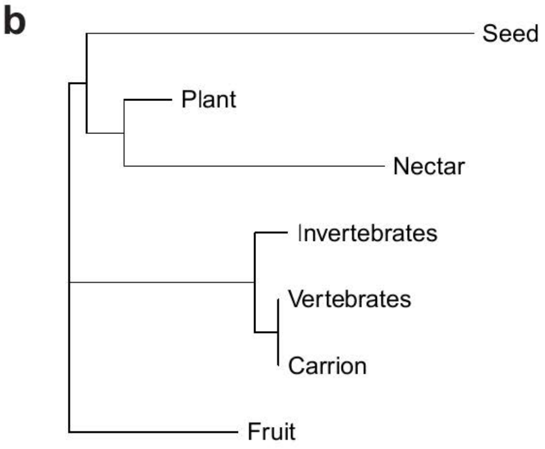
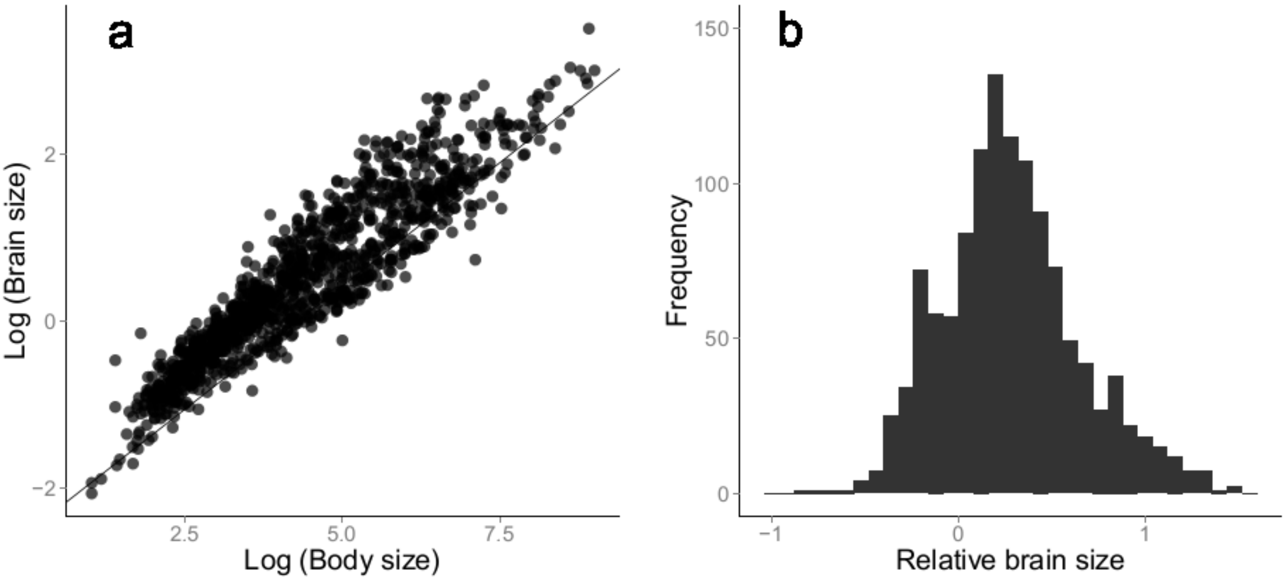


Figure B.9. Phylogenetic regression between body and brain size (**a**), used to take into account allometric effects in brain size and obtain a relative measure based on the residuals (**b**).



Appendix C

Predictable evolution towards larger brains in birds colonizing oceanic islands

Appendix C

Table C.1. BPMMS of brain size (log-transformed) as a function of oceanic island living and body size including all the species of our study (model 1), only including species with at least 3 brain measurements (model 2), including interactions (model 3) and confounding factors (model 4). For migratory behaviour and developmental mode, residency and altricialiity are respectively the reference levels.

Model	**Response**	**Predictor**	**Estimate**	**95% CI**	**pMCMC**
Model 1	Log(Brain)	Intercept	-2.556	[-2.755; -2.353]	<0.001
(N=1917)		Log (Body)	0.600	[0.591; 0.610]	<0.001
		Insularity	0.044	[0.019; 0.074]	0.002
Model 2	Log(Brain)	Intercept	-2.576	[-2.811; -2.383]	<0.001
(N=1510)		Log (Body)	0.605	[0.595; 0.617]	<0.001
		Insularity	0.048	[0.015; 0.082]	0.004
Model 3	Log(Brain)	Intercept	-2.382	[-2.593; -2.163]	<0.002
(N=1917)		Log (Body)	0.600	[0.592; 0.611]	<0.002
		Insularity	0.030	[0.005; 0.055]	0.028
		Developmental mode (Precocial)	-0.266	[-0.071; -0.161]	<0.002
		Migratory behavior (Migrant)	-0.051	[-0.067; -0.032]	<0.002

Table C.2. BPMMS of relative brain size as a function of oceanic island living and confound factors, including each insular species and their closest continental taxa and an identifier of each comparison as a random factor in the model. For migratory behaviour and developmental mode, resident and altricial are respectively the reference level. For body size category, big size is the reference level (N_c=Number of comparisons).

Response	**Predictor**	**Estimate**	**95% CI**	**pMCMC**
Model 1				
Relative brain size	Intercept	0.380	[0.060; 0.775]	0.044
(N_c=108)	Insularity	0.036	[0.004; 0.070]	0.024
	Developmental mode (Precocial)	-0.334	[-0.672; 0.071]	0.076
	Migratory behavior (Migrant)	-0.050	[-0.011; -0.088]	0.008
Model 2				
Relative brain size	Intercept	0.377	[-0.004; 0.757]	0.048
(N_c=108)	Insularity	0.046	[0.005; 0.089]	0.024
	Body category (Small)	-0.025	[-0.093; 0.061]	0.556
	Insularity : Body category (Small)	-0.021	[-0.075;0.051]	0.532
	Developmental mode (Precocial)	-0.329	[-0.672; 0.029]	0.062
	Migratory behavior (Migrant)	-0.054	[-0.010; -0.090]	0.012

Table C.3. BPMMS of body size (log-transformed) as a function of oceanic island living and body size category including each insular species and their closest continental taxa and an identifier of each comparison as a random factor in the model. For body size category, big size is the reference level. (N_c=Number of comparisons).

Response	Predictor	Estimate	95% CI	pMCMC
Log(Body)	Intercept	6.411	[4.731; 7.857]	<0.002
(N_c=108)	Body category (Small)	-1.303	[-1.624; -0.966]	<0.002
	Insularity	-0.201	[-0.343; -0.031]	0.002
	Insularity : Small Body	0.353	[0.085; 0.618]	0.016

Figure C.1. Relative brain size differences between island and mainland sister species in different Avian clades. The posterior mode and 95% CI from a BPMM comparing the relative brain size of island species with their group of closest mainland species in each clade are shown. Parameter estimates are averaged across 10 phylogenetic trees. The order Passeriformes was split into infraorders Meliphaga, Corvoida and Passerida. (* pMCMC <0.05). The number of island species measured in each clade is given in parenthesis.

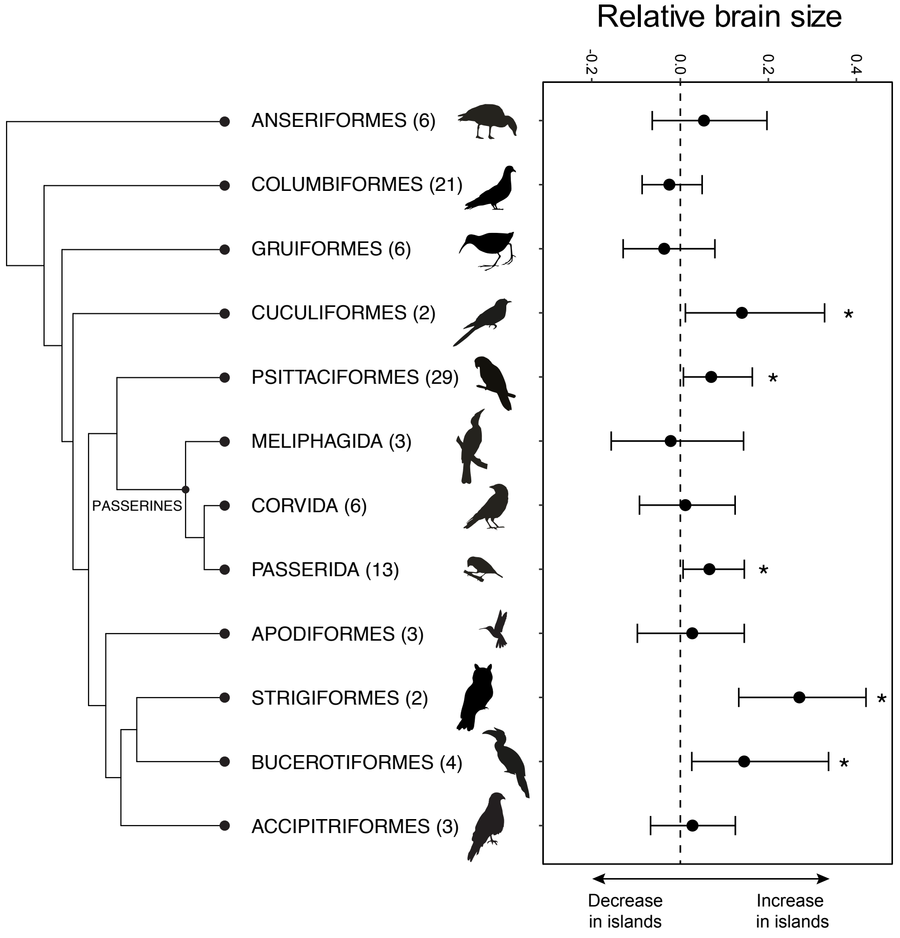


Figure C.2. Body size evolution does not explain why island species have relatively larger brains than mainland species. Neither body size of continental species (**A**) or the difference in body size between island and mainland species (**B**) was associated with relative brain size differences between island and mainland sister species.

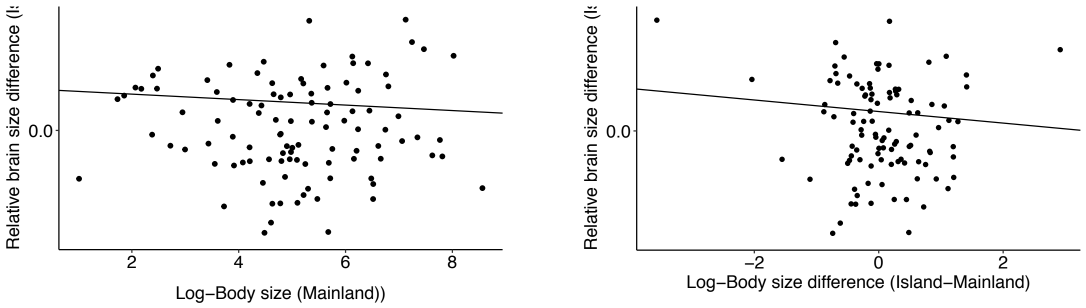


Figure C.3. Alternative models tested to explore the mechanisms underlying the relationship between relative brain size and island living. INS, insularity; DBR, diet breadth; DVP, Developmental period; IVE, Inter-annual variation in environmental productivity.

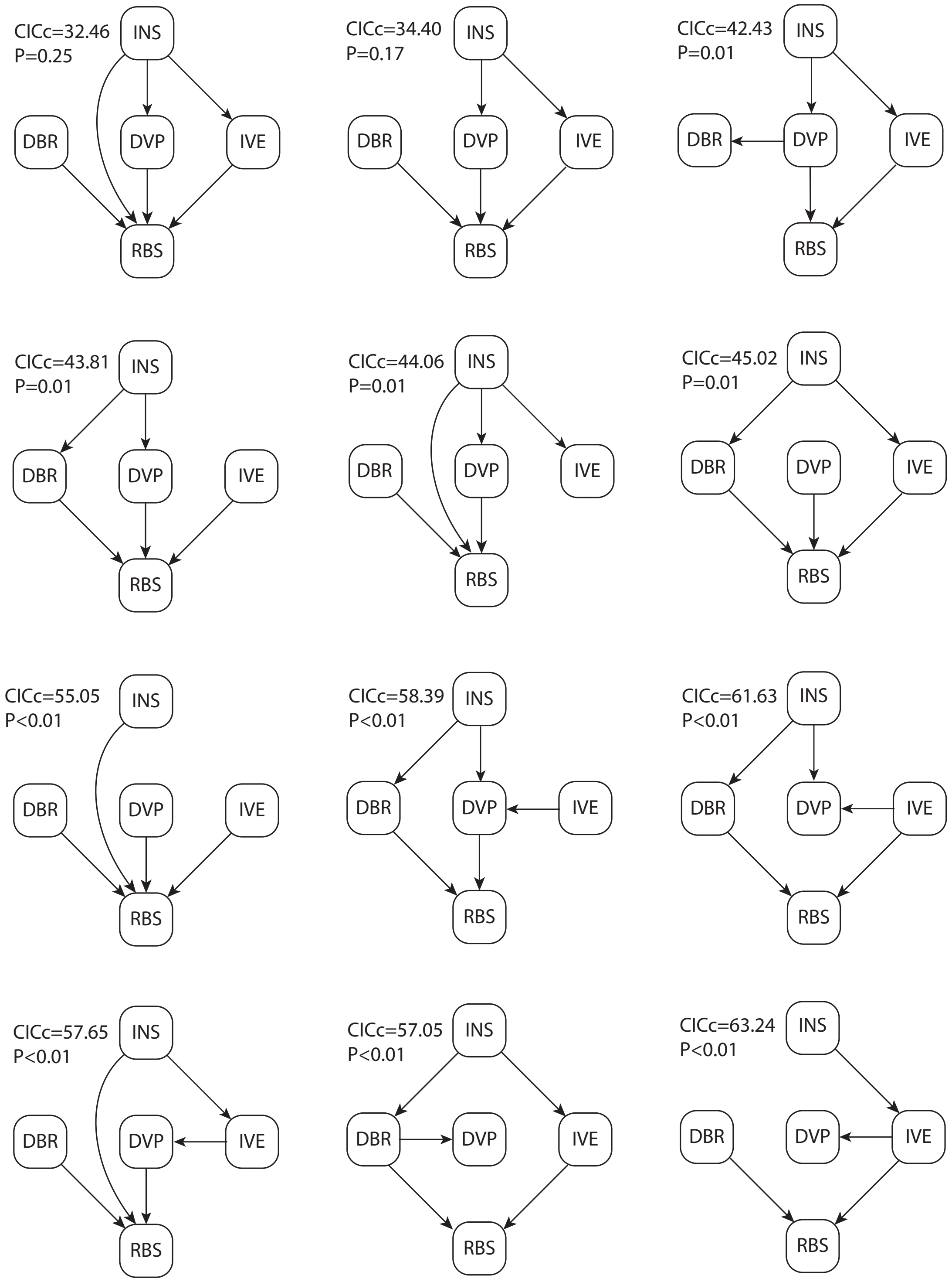


Figure B.4. Alternative models tested to explore the mechanisms underlying the relationship between relative brain size and island living. INS, insularity; DBR, diet breadth; DVP, Developmental period; SVE, Seasonal variation in environmental productivity.

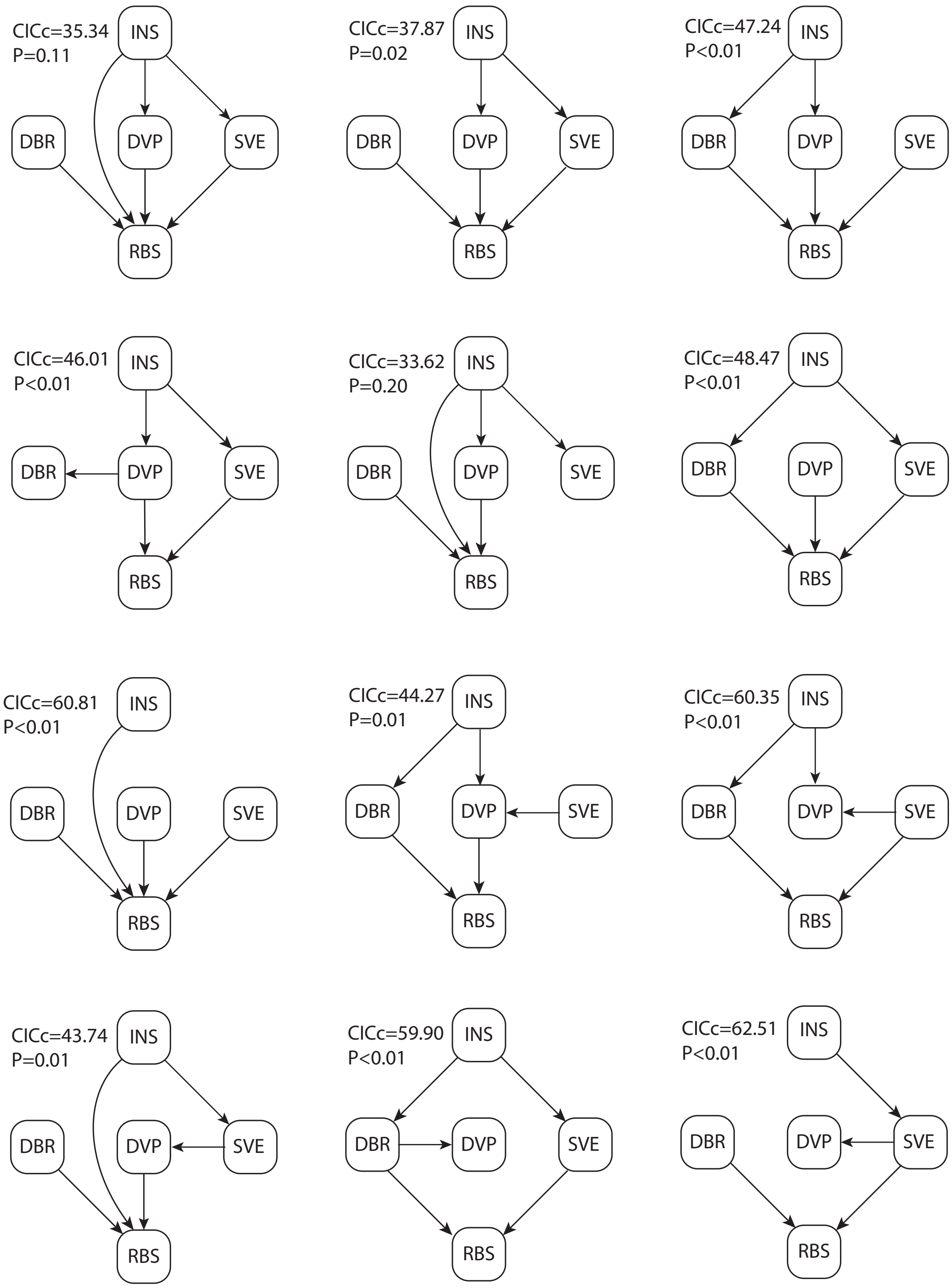
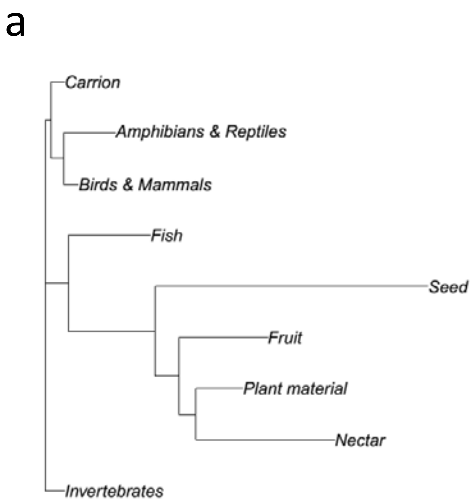


Figure C.5. Resource similarity between food sources, used to calculate diet breadth index (**A**), based on nutritional content for each food item estimated from various sources (**B**) (P: Proteins; G: Carbohydrates- Glucides; F: Carbohydrates-Fiber; L: Lipids; W: Water content; O: Other).



b

	P	G	F	L	W	O	Ref.
Carrion	16	0	0	5	75	4	(1)
Birds & Mammals	15	0	0	4.5	75.5	5	(1)
Amphibians & Reptiles	17.2	0	0	2.7	75.6	4.5	(2)
Fish	15	0	0	8	74.5	2.5	(3)
Invertebrates	17	0	3	5.5	70	4.5	(4-7)
Fruit	2	24	6.5	7	59	1.5	(8-9)
Seeds	9	28	44	3	8	8	(10-12)
Nectar	0	20.5	0	0	79.5	0	(13-14)
Plant material	4.5	26.5	8	3	55	3	(15-16)

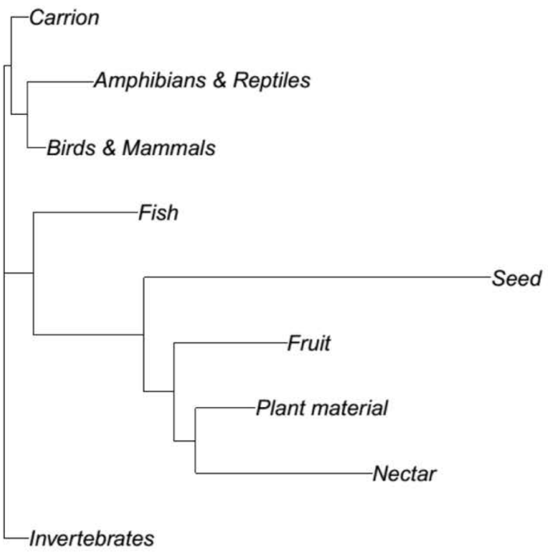
Appendix D

Larger brains spur species diversification in birds

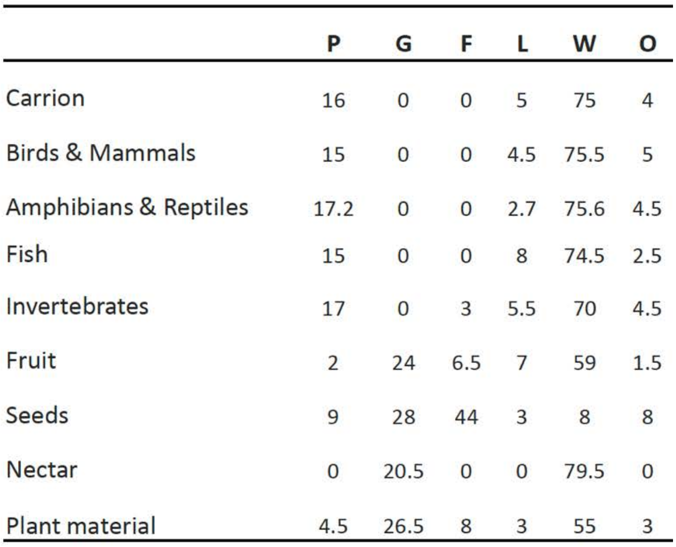
Appendix D

Figure D.1. Resource similarity between food sources, used to calculate diet breadth index (a), based on nutritional content for each food item estimated from various sources (b) (P: Proteins; G: Carbohydrates- Glucides; F: Carbohydrates-Fiber; L: Lipids; W: Water content; O: Other).

a



b



	P	G	F	L	W	O
Carrion	16	0	0	5	75	4
Birds & Mammals	15	0	0	4.5	75.5	5
Amphibians & Reptiles	17.2	0	0	2.7	75.6	4.5
Fish	15	0	0	8	74.5	2.5
Invertebrates	17	0	3	5.5	70	4.5
Fruit	2	24	6.5	7	59	1.5
Seeds	9	28	44	3	8	8
Nectar	0	20.5	0	0	79.5	0
Plant material	4.5	26.5	8	3	55	3

Figure D.2. Tree representation of the similarity between 67 IUCN habitat types. The distance matrix depicted by this cladogram is used to calculate the habitat breadth of each species, taking into account that some habitat types are more different than others.