Title: LONG LIFE EVOLVES IN LARGE BRAINED BIRD LINEAGES

Running title: Large-brained birds live longer

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Abstract

The brain is an energetically costly organ that consumes a disproportionate amount of resources. Species with larger brains relative to their body size have slower life histories, with reduced output per reproductive event and delayed development times that can be offset by increasing behavioral flexibility. The "cognitive buffer" hypothesis maintains that large brain size decreases extrinsic mortality due to greater behavioral flexibility, leading to a longer lifespan. Alternatively, slow life histories, and long lifespan can be a pre-adaptation for the evolution of larger brains. Here we use phylogenetic path analysis to contrast different evolutionary scenarios and disentangle direct and indirect relationships between brain size, body size, life history and longevity across 339 altricial and precocial bird species. Our results support both a direct causal link between brain size and lifespan, and an indirect effect via other life history traits. These results indicate that large brain size engenders longer life, as proposed by the "cognitive buffer" hypothesis.

Keywords: Brain size, longevity, life history, cognitive buffer hypothesis, phylogenetic path analysis.

Introduction

Vertebrates show substantial interspecific variation in brain size in relation to body mass (henceforth relative brain size). Even in organisms of similar body size notable differences in brain size persist, suggesting that part of the variation in brain size must be explained by factors other than body size (Striedter 2005). Processes responsible for generating and maintaining this variation, which apply across a broad spectrum of species, remain elusive. Understanding the causes of variation in brain size is important as differences in brain size influence key processes such as behavioral flexibility

(Benson-Amram et al. 2016; Sol et al. 2016), species' vulnerability to extinction and adaptation to human-modified environments (e. g. Maklakov et al. 2011; Gonzalez-Voyer et al. 2016; Santini et al. 2019).

Enlarged relative brain size in vertebrates has evolved through a balance between costs that constrain its evolution, and the associated benefits that promote it (Niven and Laughlin 2008; Isler and van Schaik 2009; Sol 2009). One such benefit is proposed by the cognitive buffer hypothesis, which suggests that larger relative brain size enhances behavioral flexibility, enabling the construction of novel behavioral responses that buffer individuals against environmental challenges, reducing extrinsic mortality, which results in prolonged (intrinsic) longevity (Allman et al. 1993; Deaner et al. 2003; Sol 2009). Three sources of evidence provide empirical support for the cognitive buffer hypothesis. First, a positive association between relative brain size and maximum longevity has been described in birds and mammals (Allman et al. 1993; Hofman 1993; González-Lagos et al. 2010; Minias and Podlaszczuk 2017). Second, relative brain size is the main predictor of behavioral flexibility, which is advantageous in environments where climate and resource availability can vary drastically throughout the year (Lefebvre et al. 1997; Sol et al. 2005, 2016; Lefebvre and Sol 2008; Overington et al. 2009; Lefebvre 2013; Sayol et al. 2016a). Finally, wild big-brained birds have lower mortality rates compared with their smaller-brained counterparts (Sol et al. 2007).

Notwithstanding the potential benefits proposed for a large brain, the costs of developing and maintaining it can constrain its evolution (Aiello and Wheeler 1995; Isler and van Schaik 2006). The brain is energetically expensive as it consumes more energy per unit weight than other somatic tissues (Mink et al. 1981). This suggests that brain size is restricted by a species' energy budget, and therefore, an increase in brain size must be met by increasing the energy input or by changing the energy allocation patterns to life history traits such as reproductive investment and developmental time (Expensive brain hypothesis; Isler and van Schaik 2009). For example, larger relative brain size is associated with delayed maturity, prolonged parental care, and later ages of first reproduction in birds and mammals (Iwaniuk and Nelson 2003; Barton and Capellini 2011). Similarly, reproductive energetic costs of large brains are associated with higher maternal energy investment, larger neonates, and reduced clutch or litter sizes in fish and mammals (Martin 1996; Deaner et al. 2003; Barrickman et al. 2008; Isler and van Schaik 2009; Barton and Capellini 2011; Kotrschal et al. 2013; Gonzalez-Voyer et al. 2016).

Despite the empirical support for the positive relationship between relative brain size and longevity, an important limitation is that results are of a correlative nature, which does not allow direct from indirect relationships among traits to be disentangled (González-Lagos et al. 2010; Minias and Podlaszczuk 2017). Furthermore, previous studies (with the exception of Sol et al. (2016)) have treated life-history traits, such as development time and offspring number, as potential confounding variables to statistically control for (González-Lagos et al. 2010; Minias and Podlaszczuk 2017). Such an approach excludes the possibility of testing alternative scenarios of relationships between variables, such as large brains favoring slow life-histories, which in turn result in prolonged longevity. Therefore, it is not possible to rule out that the apparent correlation between brain size and longevity is merely a result of a slower pace of life. Alternatively, the brain-longevity relationship could be an indirect product of the common influence of body size, given the overwhelming allometric effects on virtually all life history traits, as well as on brain size (Hallmann and Griebeler 2018; Rogell et al. 2019). Integrating studies of brain size evolution within a life history framework could be helpful to understand why, in many organisms, a large brain is not present despite the potential benefits, and at the same time to understand the evolution of reproductive and developmental trade-offs associated with larger brains. A recent example of the value of such an approach is the work by Sol et al. (2016), whose results suggest that behavioral flexibility might be selected for as part of a life history strategy that prioritizes future over current reproduction.

Here, using birds as our model system, we employ phylogenetic path analysis (von Hardenberg and Gonzalez-Voyer 2013; Gonzalez-Voyer and von Hardenberg 2014) to explore whether larger brain size effects are directly associated with prolonged longevity, as proposed by the cognitive buffer hypothesis, or rather whether the association is indirect, with larger brains resulting in slower life history, including longer life span, all the while controlling for potential allometric effects. Additionally, given the variation in developmental mode in birds, from altricial chicks that hatch virtually naked, eyes closed and initially fully dependent on parents, to precocial chicks that hatch with a greater degree of development and some able to feed themselves (Starck and Ricklefs 1998; Iwaniuk and Nelson 2003), we also tested whether developmental mode affects the relationship between brain size, life history, and longevity. To this end, we contrast 82 path models, 19 for altricial and 63 for precocial bird species. The models are embedded within three different hypothetical scenarios (Fig. 1), which describe potential relationships between brain size, life history and body size. All three scenarios result in correlations between brain size and longevity, but not all imply direct links between the two traits of interest. The allometric effects scenario (Fig. 1a), proposes that variation in maximum longevity, as well as reproductive investment and development, are only directly linked to body size variation. The brain effects scenario (Fig. 1b) proposes that variation in longevity is directly linked to brain size variation, as proposed by the cognitive buffer hypothesis (Allman et al. 1993; Sol 2009). At the same time, it includes the possibility for indirect effects between brain size and longevity through the reproductive and development costs proposed by the expensive brain hypothesis (Isler and van Schaik 2009). Both direct and indirect brain size effects are considered independent of body size. Finally, the third scenario consists of models combining the predictions of the two previous scenarios (Fig. 1c), with brain size affecting longevity directly and indirectly through life history traits. At the same time, the variation in life history traits, longevity, and brain size, can be influenced by body size.

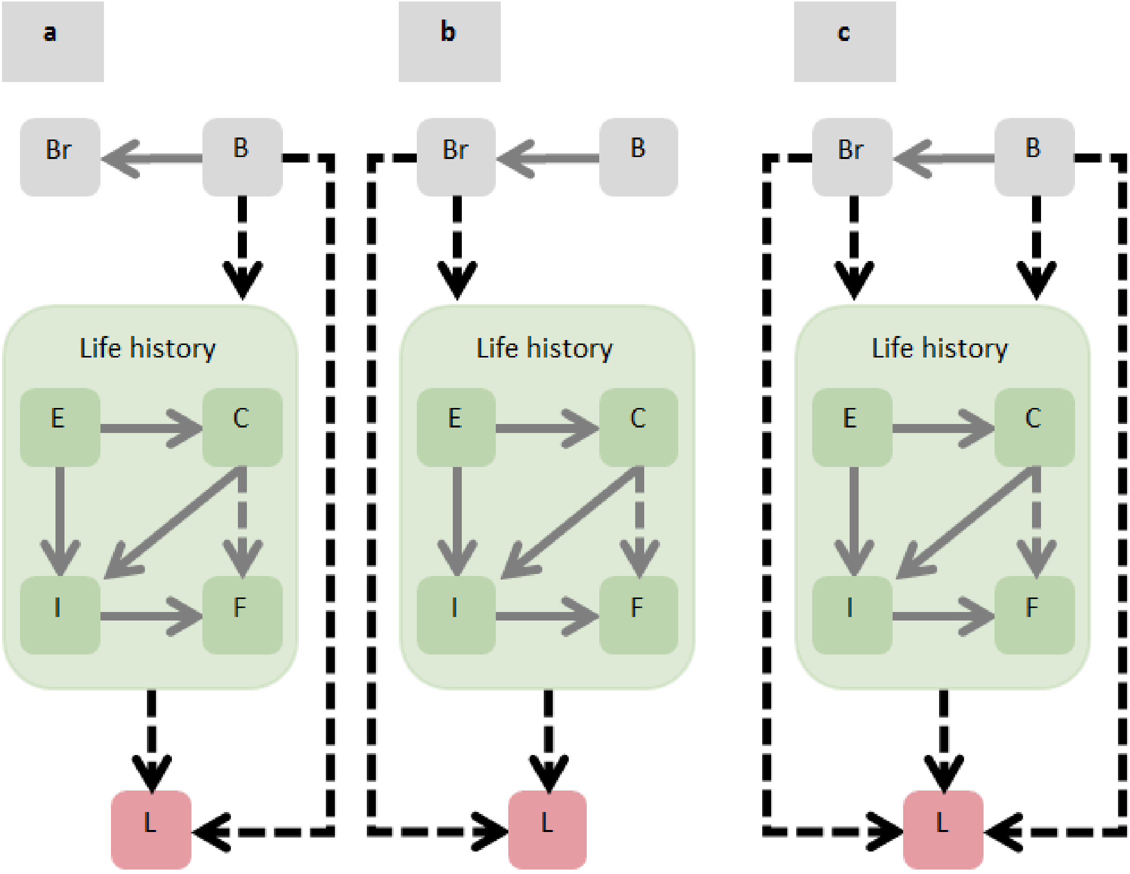

Figure 1. Theoretical framework of the study. **a)** Allometric effects scenario, **b)** Brain effects scenario, and **c)** Combined effects scenario. Arrows indicate proposed direct associations between traits. Dotted lines represent links that were not present in all models (See Supplementary material for the complete set of tested models). Continuous lines represent links present in all models, based on previous evidence supporting the relevance of such relationships (see Methods for details). Br= Brain mass; B= Body mass; E= Egg mass; C= Clutch size; I= Incubation period; F= Fledging age; L= Maximum longevity.

Methods

Brain size

Data for the complete set of variables that we use in this study was available for a total of 339 bird species, of which 219 were altricial and 120 precocial. A complete dataset is necessary for phylogenetic path analysis, thus although data for brain size in bird species is available for a larger number of species, the main limitation was the availability of maximum longevity data in the wild. We used whole brain size in our analysis because data are widely available in the literature. Furthermore, whole brain size is strongly correlated with pallial areas associated with innovation and learning, suggesting that this measure is meaningful for comparative analysis (Timmermans et al. 2000; Sayol et al. 2016a). Second, a growing body of empirical evidence supports the assumption that whole brain size is the main predictor of behavioral flexibility in the wild (Schuck-Paim et al. 2008; Overington et al. 2009; Sayol et al. 2016b; Sol et al. 2016). Because behavioral flexibility requires the integration of cognitive processing with perception and motor ability (Deaner et al. 2003; Lefebvre and Sol 2008), it is not trivial to decide which brain regions best reflect cognitive abilities. Finally, if the energetic costs of brain size are associated with reproductive and developmental costs, then these costs should be easier to detect if we focus on the whole brain rather than on small areas (Sol et al. 2010). Brain size measurements come both from direct measures of brain mass (g), and from indirect measures of endocranial volume obtained by filling the skull with lead shot (see Iwaniuk and Nelson 2003). Nonetheless there is a strong correlation ($r = 0.99$) between the endocranial volume and brain mass in birds, and in order to get the data in the same units, brain volume data were transformed to mass by multiplying by the density of fresh brain tissue (1.036 g/mL; Iwaniuk and Nelson 2002).

Body size

Data for body size come from direct measures of body mass (g) obtained from published sources (Tacutu et al. 2013; Myhrvold et al. 2015). Given that larger species on average tend to have large brains and to live longer (Stearns 1992; Deaner et al. 2003; de Magalhães et al. 2007), it was necessary to statistically control for the allometric effects of body size. We did not use residuals of an allometric relationship between brain size and body size because the use of residuals has been criticized as it can lead to biased parameter estimates (García-Berthou 2001; Freckleton 2002; Rogell et al. 2019). The use of residuals has an additional non negligible problem, since body size is associated with variation in practically all life history traits (Deaner et al. 2003) it is imperative to include it in the models in order to disentangle allometric effects from those of brain size.

Longevity

Lifespan records come from Myhrvold et al. (2015), and the AnAge database (Tacutu et al. 2013). To minimize the potential confounding effects of precision of estimates due to different sample sizes, or combination of records from captive and wild origin (with the potential effect of differential response to captivity of species), we only considered records coded as presenting an “adequate” sample size (as per the AnAge database) and where data were from a “wild origin”. We discarded only outliers with extreme values that we could not validate based on the primary literature. When there was more than one longevity record, the highest value was used.

Life history traits

We included life history traits previously reported to be associated with brain size and/or longevity in birds. Brain size was previously found to be positively associated with egg mass (Isler and van Schaik 2006), incubation period, and fledging age (Iwaniuk and Nelson 2003). Therefore, we collected data for egg mass (in grams), clutch size (average number of eggs per reproductive event), incubation period (the time between egg laying and hatching, in days) and fledging age (days from hatching to the time the bird is capable of flight; Myhrvold et al. 2015). As mentioned above, we also included developmental mode to describe the variation in developmental patterns in birds, associated with differences in whole brain size (Iwaniuk and Nelson 2003). Some studies have classified birds within four (Bennett and Harvey 1985) and five categories (Iwaniuk and Nelson 2003) including altricial, semialtricial, precocial, semiprecocial, and superprecocial species. We use two categories, combining altricial and semialtricial as altricial and precocial and semiprecocial as precocial species, which allowed us to increase the sample size in each category.

All life history trait data were collected from AnAge (Tacutu et al. 2013), Myhrvold et al. (2015), and Iwaniuk and Nelson (2003). Data from different sources for the same variable were transformed to a weighted mean based on the sample size. Taxonomy was homogenized following Jetz et al. (2012). We discarded species considered as extinct, and subspecies when data for the main species was available. All continuous variables were transformed to logarithm base 10 in order to adjust to parametric statistic assumptions and to the Brownian model of trait evolution (Felsenstein 1985). The complete dataset used for the present study is available as supplementary material.

Phylogeny

We use the most recent, complete, time-calibrated avian phylogeny (Jetz et al. 2012). We used trees that were estimated based on the backbone developed by Ericson et al. (2006) including species with molecular data as well as those placed in the tree based on taxonomic information so as to maximize our sample size. We generated a maximum clade credibility tree (MCCT) in the *phangorn* (Schliep 2011) R package (R Core Team 2017) from a sample of 1000 trees from the pseudo-posterior distribution from the BirdTree database available online (http://www.birdtree.org; Jetz et al. 2012) which we used for all analyses. As a test of the sensitivity of our results to phylogenetic uncertainty, we repeated the analyses using a MCCT obtained from a subsample of trees estimated using the Hackett et al. (2008) backbone used by Jetz et al. (2012). The results were qualitatively the same and are presented in the Supplementary Material (Tab. S4, Fig. S7 for altricials, and Tab. S5, Fig. S8 for precocials).

Differences in life history traits between altricials and precocials

We analyzed differences in the allometric relationship of life history traits between developmental modes –altricial or precocial– using phylogenetic generalized least squares models (PGLS; Martins and Hansen 1997) in the *caper* (Orme et al. 2013) R package (R Core Team 2017). The results confirmed the presence of significant interactions between developmental mode and the allometric relationships with life history traits (Tab. 1). These results justify testing the fit of the different phylogenetic path models separately for altricial and precocial species.

Table 1. Results of phylogenetic ANCOVA models testing whether the allometric relationship of the different life history traits differs based on the developmental mode (i.e. whether species are altricial or precocial). Analyses were run with 339 species. Significant interactions are shown in bold type.

Model	*Coefficients*	*SE*	*t*	*p*	*λ*
Response: Longevity					
Intercept	1.092	0.067	16.172	<0.001	0.599
Developmental mode (precocials)	0.075	0.062	1.212	0.226	
Body mass	0.229	0.028	8.026	<0.001	
Developmental mode*body mass	-0.053	0.046	-1.151	0.250	
Response: Brain mass					
Intercept	0.249	0.047	5.291	<0.001	0.902
Developmental mode (precocials)	-0.099	0.039	-2.514	0.012	
	0.64	0.015	41.952	<0.001	

Body mass	-0.068	0.022	-3.004	**0.002**	
Developmental mode*body mass					
Response: Fledging age					
Intercept	1.392	0.075	18.568	<0.001	0.918
Developmental mode (precocials)	0.042	0.062	0.679	0.497	
Body mass	0.187	0.023	7.857	<0.001	
Developmental mode*body mass	-0.008	0.035	-0.255	0.799	
Response: Incubation					
Intercept	1.281	0.015	84.744	<0.001	0.088
Developmental mode (precocials)	0.111	0.015	7.381	<0.001	
Body mass	0.193	0.010	18.85	<0.001	
Developmental mode*body mass	-0.103	0.019	-5.216	**<0.001**	
Response: Clutch size					
Intercept	0.634	0.104	6.086	<0.001	1
Developmental mode (precocials)	-0.091	0.084	-1.074	0.283	
Body mass	-0.059	0.028	-2.089	0.037	
Developmental mode*body mass	0.042	0.036	1.171	0.242	
Response: Egg mass					
Intercept	0.936	0.055	16.923	<0.001	0.975
Developmental mode (precocials)	0.192	0.045	4.214	<0.001	
	0.681	0.016	42.260	<0.001	

Body mass Developmental mode*body mass	-0.020	0.022	-0.875	0.382	

Relationships between life history variables

We conducted PGLS analyses to confirm that previously reported relationships between life history traits were also observed in our sample. For example, previous studies have described a negative association between egg size and clutch size (Blackburn 1991; Figuerola and Green 2005), a positive relationship between egg size and incubation period (Rahn and Ar 1974; Deeming et al. 2006), associations between variables reflecting development time, i.e. incubation period and fledging age, (Bennett and Owens 2002; Iwaniuk and Nelson 2003), and finally the well-known positive allometric relationship between brain and body size (Nealen and Ricklefs 2001; Sol and Price 2008). As our dataset reflected the aforementioned associations between life history traits (Table S1), we decided to fix these relationships in our proposed models (i.e. direct links between these traits were present in all models; Figs. S1-S6) so as to reduce the number of models.

Phylogenetic path analysis

To test the hypothetical causal relationship between brain size and maximum longevity in a life history framework, we used phylogenetic path analysis (von Hardenberg and Gonzalez-Voyer 2013; Gonzalez-Voyer and von Hardenberg 2014) to compare the three hypothetical scenarios described above (Fig. 1). We tested a total of 82 models, 19 for altricial and 63 for precocial species. Path analysis is an extension of multiple regression allowing to test the relative fit of alternative causal models, which include different hypothetical causal links between variables (Shipley 2000; Gonzalez-Voyer and von Hardenberg 2014). A causal model is represented as a directed acyclic graph (DAG). Model fit is tested based on the minimum set of conditional independences that must be true not to reject the causal model (Shipley 2000; von Hardenberg and Gonzalez-Voyer 2013). The *p* values of the conditional independences in one particular model can be combined to obtain the Fisher's C statistic, which represents a measure of the goodness of fit of the model to the data (Shipley 2000). The C statistics follows a X^2 distribution with 2k degrees of freedom, k being the number of conditional independences in the model. Goodness of fit of the model is based on conditional independencies being met, thus a C statistic with a p value < 0.05 indicates that the model fits the data poorly, and cannot be considered a candidate causal model (Shipley 2000). Different, non-nested models, can be compared by means of the C statistic information criterium (CIC; analogous to the Akaike information criterion, AIC; (von Hardenberg and Gonzalez-Voyer 2013)). For all models we present the C statistic, CICc, ΔCICc and w_i (weight). All models were run in the *phylopath* (van der Bijl 2018) R package (R Core Team 2017). Tests of the conditional independencies are run using PGLS including an estimate of the λ parameter (Freckleton et al. 2002), which provides an estimate of the amount of phylogenetic signal in the residuals of the linear model. All path models were tested separately for altricial and precocial bird species. Finally, we calculated the average model from selected models that met two main criteria. First, given our interest in identifying potential causal models, we only considered models where the C statistic was non-significant (p > 0.05), i.e. where all conditional independencies in the minimum set are met. Second, we included models whose summed weights were ≥ 0.95 (Burnham and Anderson 2002). Standardized path coefficients were calculated following standardization of all variables, with slopes averaged by the weight (w) of the model. When two variables were not linked by a causal path in a given model, it was assigned a value of zero when calculating the average model (Symonds and Moussalli 2011).

Results

Our phylogenetic comparative analyses indicate that for both altricial and precocial bird species there is a direct as well as an indirect association between brain size and longevity. The best-fitting models were all within the combined effects scenario (Fig. 1a) in both altricial (Table 2 for the first eleven models and ΔCICc range: 0 – 39.518; Table S2 for all tested models; see Figs. S1-S3 for the complete set of tested models on altricial bird species) and precocial species (Table 3 for the first eleven models and ΔCICc range: 0 – 31.528; Table S3 for all tested models; see Figs. S4-S6 for the complete set of models tested on precocial bird species). On the other hand, the models in the allometric effects (altricials ΔCICc range: 7.76 – 547.365; Table S2; precocials ΔCICc range: 22.525 – 322.747; Table S3) and the brain size effects scenarios (altricials ΔCICc range: 148.411 – 562.691; Table S2; precocials ΔCICc range: 101.136 – 343.026; Table S3) provided a very poor fit to the data. The best-fitting models provide consistent evidence for an effect of brain size on maximum longevity, both directly and indirectly through life history traits (Figs. 2 and 3). The models also point to an important influence of body size on maximum longevity, which highlights the importance of using a path analysis framework to disentangle direct from indirect associations between these two traits.

The first six models for altricials (Fig. 2; Table 2) and first eight models for precocials (Fig. 3; Table 3) meet the criteria to be averaged (C statistics $p > 0.05$, and summed weights (w) ≥ 0.95). Interestingly, average models were qualitatively similar regardless of the development mode; the main particularities arose from the different set of conditional independences tested in altricial and precocial bird species (Figs. S1-S6). In altricial species, for instance, the models include a direct relationship from clutch size to fledging age (Fig. 2), which is absent in precocial species. On the other hand, in precocial species we include additional relationships among life-history traits to ensure conditional independences were met. These relationships are between body size and incubation period, egg size and maximum longevity, and between clutch size and maximum longevity (Fig. 3). These results suggest that in precocial species, the indirect pathway of influence from body size or brain size to maximum longevity, could be through the egg and clutch sizes, both variables associated with reproductive investment (Blackburn 1991; Sibly et al. 2012). Whereas in altricial species, the indirect pathway of influence from brain or body size to maximum longevity, is through fledging age, a variable that reflects development time (Iwaniuk and Nelson 2003; Sibly et al. 2012).

Note that the apparently negative association between body mass and maximum longevity in the averaged model for precocial species is most likely an artefact arising from the estimate of the standardized slopes for the average model (Rogell et al. 2019); as in bivariate models body mass is positively associated with longevity, furthermore both egg size and brain size (strongly positively correlated with body size) are positively associated with longevity. Finally, it is worth noting the fact that the standardized slopes for the relationship between body size and longevity and brain size and longevity are of similar magnitude in the averaged models, particularly so for altricial species, which also points to synergistic effects of these two key traits on longevity.

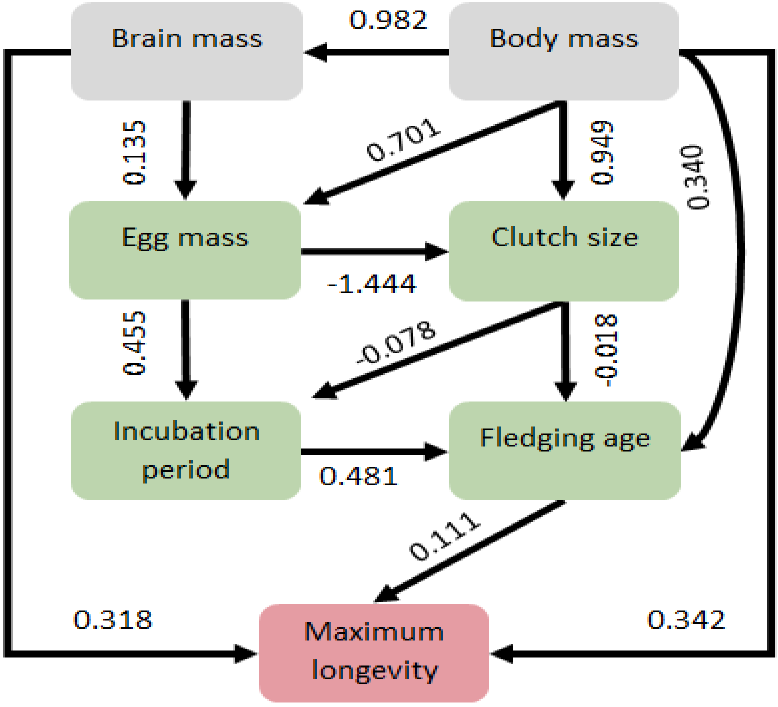

Figure 2. Average model for the altricial species based on the six best-supported models. Arrows represent hypothetical causal links; values represent the standardized average coefficients.

Table 2. Eleven of the tested models for altricial species ordered based on their ΔCICc value. Most of the models correspond to the combined effects scenario (Fig. 1c), except models ranked from 7 to 10, which correspond to the allometric effects scenario (Fig 1a). Shown are *k*, the number of parameters, *q*, the number of tested conditional independencies, the C statistic with its *p* value, the CICc and corresponding ΔCICc and weight (*w*). All models and their parameter values are shown in Table S2, Figures S1-S3 show all models tested on altricial bird species.

Model		*k*	*q*	*C*	*p*	*CICc*	*ΔCICc*	*w*
1	C2	9	19	16.065	0.588	57.884	0	**0.342**
2	C7	10	18	18.756	0.538	58.176	0.293	**0.296**
3	C3	9	19	18.265	0.438	60.084	2.201	**0.114**
4	C1	8	20	16.265	0.435	60.507	2.624	**0.092**
5	C6	10	18	21.246	0.383	60.666	2.783	**0.085**
6	C5	9	19	19.471	0.363	61.29	3.407	**0.062**
7	A1	10	18	26.223	0.159	65.643	7.76	0.007
8	A4	11	17	32.225	0.074	69.27	11.386	0.001
9	A2	11	17	35.816	0.032	72.861	14.977	0
10	A3	11	17	54.364	0	91.409	33.525	0
11	C4	10	18	57.982	0	97.402	39.518	0

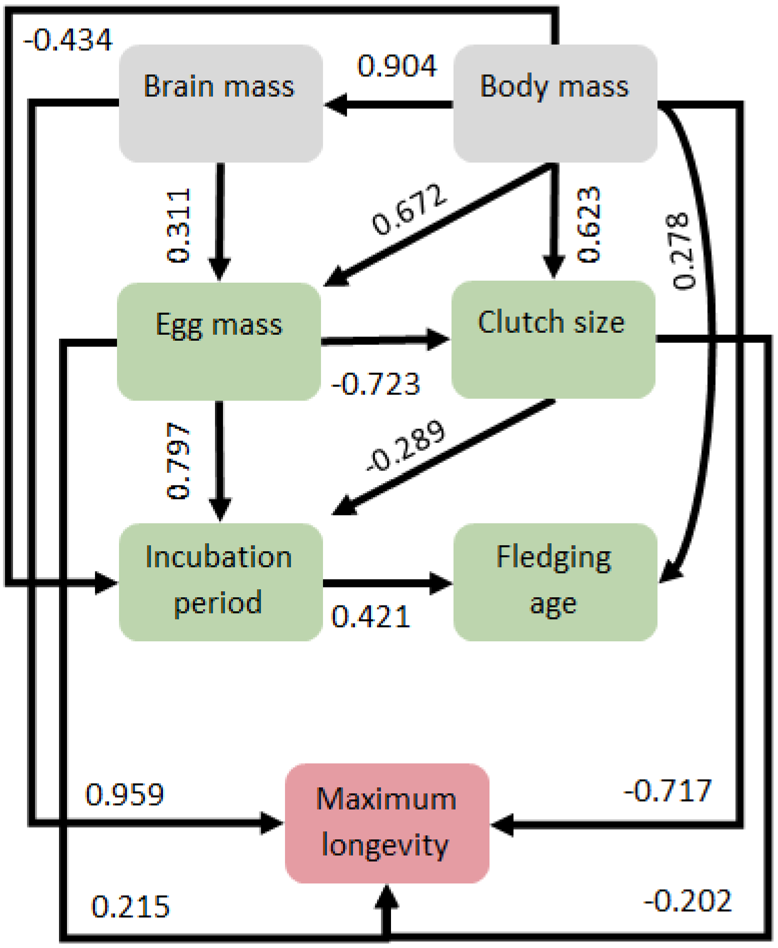

Figure 3. Average model for the precocial bird species based on the eight best-supported models. Arrows represent the hypothetical causal links; values represent the standardized average coefficients.

Table 3. Eleven of the tested models for precocial species ordered based on their ∆CICc values. All models correspond to the combined effects scenario (Fig. 1c). Shown are *k*, the number of parameters, *q*, the number of tested conditional independencies, the C statistic with its *p* value, the CICc and corresponding ΔCICc and weight (*w*). All models and their parameter values are shown in Table S3, Figures S4-S6 show all models tested on precocial bird species.

Model		*k*	*q*	*C*	*p*	*CICc*	*ΔCICc*	*w*
1	C13	8	20	19.222	0.257	67.707	0	**0.429**
2	C9	7	21	18.027	0.206	69.456	1.749	**0.179**
3	C5	8	20	21.021	0.178	69.506	1.8	**0.174**
4	C6	9	19	26.086	0.098	71.686	3.979	**0.059**
5	C1	7	21	20.973	0.102	72.402	4.695	**0.041**
6	C15	9	19	26.97	0.08	72.57	4.863	**0.038**
7	C21	9	19	27.996	0.062	73.596	5.889	**0.023**
8	C11	8	20	25.557	0.061	74.041	6.335	**0.018**
9	C2	8	20	26.081	0.053	74.566	6.86	0.014
10	C8	10	18	32.895	0.035	75.667	7.961	0.008
11	C17	8	20	27.451	0.037	75.936	8.229	0.007

Discussion

Our main goal here was to test if prolonged longevity in birds is directly associated with larger brain size, beyond life-history and allometric effects, as predicted by the cognitive buffer hypothesis (Allman et al. 1993; Deaner et al. 2003; Sol 2009). We found clear support for a direct link between brain size and longevity for both altricial and precocial species (Figs. 2 and 3). Models which only included indirect links between brain size and longevity, such as through changes in life history, provided a poor fit to the data (see Suplementary Material Figs S1-S6). The best supported models were all from the combined effects scenario (Fig. 1c, Tables 2 and 3), which considers synergistic direct effects of brain size and body size on longevity, as well as indirect effects of life-history traits, in accordance with results from previous studies (Iwaniuk and Nelson 2003; Isler and van Schaik 2009; Sol et al. 2016; Minias and Podlaszczuk 2017). Models considering independent effects of brain size (Fig. 1b; Figs. S2 and S5), or body size (Fig. 1a; Figs. S1 and S4), on life-history and longevity provided a poor fit to the data, highlighting the importance of considering the synergistic effects of these two key traits. Furthermore, by analyzing the relationship between brain size and longevity in both altricial and precocial species, we were able to show that the effects are consistent regardless of developmental mode, even when there were some differences in relationships among traits between the two developmental modes.

Consistent correlation between brain size and longevity across vertebrates

The finding that brain size is positively associated with maximum longevity for both precocial and altricial species is consistent with previous studies in birds (Sol et al. 2016; Minias and Podlaszczuk 2017), mammals (Allman et al. 1993; González-Lagos et al. 2010), and anurans (Yu et al. 2018) that have found a positive correlation between these two traits. The cognitive buffer hypothesis originated from studies mainly in primates, where a positive association between brain size and longevity was found even when controlling for the effects of social structure, life history, body size and metabolic rate (Allman et al. 1993; Hofman 1993). However, these early studies did not consider the evolutionary relationships between species. More recent evidence confirmed the correlation between brain size and longevity while accounting for allometric effects as well as phylogenetic non-independence in diverse vertebrate clades (González-Lagos et al. 2010; Sol et al. 2016; Minias and Podlaszczuk 2017). It is interesting to note that in mammals previous results suggest the correlation between brain size and longevity possibly stems from an indirect effect through life-history, as a significant correlation between brain size and longevity is no longer significant when maternal investment is included as an additional predictor (Barton and Capellini 2011). Nonetheless, these previous results could not distinguish between direct or indirect associations. Our results support the presence of a direct, causal link between brain size and longevity in birds even when accounting for life-history effects.

Brain size affects life history traits

Two non-mutually exclusive mechanisms may explain how larger brain size may prolong longevity. First, intrinsic life span could be prolonged as a result of better homeostatic control, which may reduce reactive oxygen species-related (ROS) senescence and counter organismal aging (Monaghan et al. 2009). In support of this hypothesis, a recent study found that large brained birds suffer less oxidative damage in membrane lipids, suggesting a potential link between ROS damage and brain size (Vágási et al. 2016). However, in guppies (*Poecilia reticulata*) from an artificial selection experiment on relative brain size (up and down selected lines), fish with enlarged brain size showed reduced longevity in a laboratory setting (i.e. most likely reflecting intrinsic mortality as extrinsic mortality is reduced), which points to potential increased costs of enlarged brain size (Kotrschal et al. 2019). Second, life span could increase as a result of greater behavioral flexibility, which enables individuals to reduce extrinsic mortality allowing for natural selection to act on intrinsic mortality resulting in a longer life span (Allman et al. 1993; Deaner et al. 2003; Sol 2009; Sol et al. 2016). There is ample evidence for the association between brain size and behavioral flexibility in birds and mammals (Lefebvre et al. 1997, 2004; Sol et al. 2008; Overington et al. 2009; Benson-Amram et al. 2016; Sayol et al. 2016a). In addition, in the guppy (*Poecilia reticulata*), females (but not males) from experimental lines selected for large brains showed greater survival when faced with a natural predator in a common-garden experiment in semi-natural conditions, than females from lines selected for small brains (Kotrschal et al. 2015). Our results do not allow us to identify the mechanism responsible for the prolonged longevity observed in large-brained bird lineages, although the cognitive buffer hypothesis considers both potential mechanisms. It is interesting to note that we also identified indirect effects through life history traits, which influence longevity and are affected by brain size. The presence of these indirect effects suggests that larger brain size is associated with a reduction in the pace-of-life, by affecting key life-history traits associated with reproductive investment (e.g. egg size or clutch size) or development rate (e.g. fledging age).

Our results are in line with those of a recent work that proposes that innovative behavior is selected as part of a slow pace-of-life, as it is primarily under such circumstances where individuals can reap the associated benefits (Sol et al. 2016). Furthermore, the aforementioned study shows that innovation and slow life histories (including prolonged longevity) are influenced by brain size (Sol et al. 2016). These results fit well with the main predictions of life-history theory, which proposed that extrinsic mortality at a given age is the main factor explaining among-species differences in life history traits (Promislow and Harvey 1990; Reznick et al. 1990; Martin 2015). According to this theory, reduced adult extrinsic mortality would select for prioritizing future reproduction, with delayed ages of sexual maturity, reduced investment per reproductive event and prolonged longevity. Therefore, we propose that brain size should be considered as a key trait influencing life-history, as changes in brain size have direct effects on traits such as egg size, or neonate size, development time (Iwaniuk and Nelson 2003), and age at sexual maturity, in mammals (Deaner et al. 2003; Barrickman et al. 2008; Barton and Capellini 2011; Sol et al. 2016; Minias and Podlaszczuk

2017). An example of this is the association between brain size and parental care patterns in carnivores and cichlid fishes (Gittleman 1994; Gonzalez-Voyer et al. 2009).

Our results highlight interesting links between brain size and life history traits beyond the association with longevity. For example, in both altricial and precocial species, larger brain sizes are associated with larger egg size. These results suggest that the widely described trade-off between egg mass and clutch size (Blackburn 1991; Figuerola and Green 2005) may be, at least in part, mediated by brain size. In fish and mammals, neonate size increases with larger brain sizes, which results in reduced clutch or litter sizes per reproductive event (Barrickman et al. 2008; Barton and Capellini 2011; Kotrschal et al. 2013). Further effects of brain size on other life history traits are indirect. For example, in altricial and precocial species, our results suggest a positive relationship between egg size and incubation period, which is concomitant with a negative relationship between clutch size and incubation period. This finding supports the idea that as birds produce bigger eggs and therefore smaller clutches, the embryo development time increases (Martin et al. 2000; Martin 2002). Interestingly, only in the case of altricial species, our results also suggest a trade-off between clutch size and fledging age, which reveals that as clutch size decreases, the investment in development time increases. This is potentially the result of a longer and more intense reproductive effort in altricial bird species (Starck and Ricklefs 1998; Iwaniuk and Nelson 2003; Jetz et al. 2008). In other words, given our finding of an association between clutch size and egg size, it is possible that larger clutches are composed of smaller eggs with small-brained and hence faster developing nestlings. On the other hand, small clutches are composed of large eggs, with large-brained offspring that develop more slowly (Iwaniuk and Nelson 2003).

We did not find support for a direct relationship between brain size and fledging age in either developmental modes, contrary to previous studies in birds and mammals (Iwaniuk and Nelson 2003; Barrickman et al. 2008; Barton and Capellini 2011). Previous results with birds suggested that brain size is positively associated not only with fledging age, but also with variables reflecting total development time (i.e. incubation period, duration of postfledging parental care and total period of parental care (Iwaniuk and Nelson 2003)). Prolonged developmental periods were suggested to be associated with larger brain size as it is during the parental care stage that young acquire and tune the skills associated with a mature nervous systems, such as better foraging skills, predator evasion and social interaction (Grüebler and Naef-Daenzer 2010; Sol et al. 2016). Our results, however, suggest that the indirect effects of brain size on longevity, present in both altricial and precocial species, are not associated with prolonged development but rather parental investment. In precocial species, egg size and clutch size have direct effects on longevity, suggesting it is mainly reproductive investment (i.e. egg-clutch size trade-off; Blackburn 1991; Sibly et al. 2012) which influences maximum longevity. On the other hand, in altricial species, fledging age directly influences lifespan. This in turn suggests that in altricial species, both the reproductive and the developmental investment mainly determine the indirect pathway between brain size and maximum longevity (Iwaniuk and Nelson 2003; Sibly et al. 2012; Sol et al. 2016). Finally, it is worth noting that our analyses do not allow us to distinguish between direct associations between brain size or body size and fledging age, as that was not the main aim of our study.

Although our results are consistent with both direct and indirect effects of brain size on longevity of birds, the directionality of the causal relationship is prone to debate (Ratikainen and Kokko 2019). It is likely that the relationship is not only unidirectional, and that prolonged longevity also facilitates increased brain size. Indeed, as discussed above, prolonged longevity would favor prioritizing future reproduction and reducing investment per reproductive event, with concomitant slower development times, which in turn would allow for larger brain sizes to evolve (Covas and Griesser 2007; Sol et al. 2016; DeCasien et al. 2018).

In conclusion, our results are consistent with a direct causal link between brain size and longevity, beyond body size effects, in support of the cognitive buffer hypothesis (Allman et al. 1993). Additionally, we found evidence for an indirect relationship between brain size and longevity through development and reproductive life history traits. These results suggest that the cognitive buffer hypothesis could provide an overarching explanation for the evolution of brain size across vertebrates. Prolonged life-span could enable species to offset the energetic costs of enlarged brain size by slowing down their pace of life, through prolonged development times, delayed ages of first reproduction and prioritizing future reproduction (Barrickman et al. 2008). As also suggested elsewhere (Sol et al. 2016), a longer life-span would allow species to make the most of the investment in brain size as long life allows both for learning, and using behavioral flexibility to deal with environmental challenges, such as reduced food availability or increased predation risk. Larger brain size could also promote longer life spans through more refined homeostatic control. Indeed, the differential resource allocation to life history components is strongly influenced by physiological processes that change throughout the life cycle (Ricklefs and Wikelski 2002; Selman et al. 2012; Lendvai et al. 2013). Studies of the relationship between brain size and physiology are likely a fruitful avenue for further research.

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