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Evolution of brain–body allometry in Lake Tanganyika cichlids

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Brain size is strongly associated with body size in all vertebrates. This relationship has been hypothesized to be an important constraint on adaptive brain size evolution. The essential assumption behind this idea is that static (i.e., within species) brain–body allometry has low ability to evolve. However, recent studies have reported mixed support for this view. Here, we examine brain–body static allometry in Lake Tanganyika cichlids using a phylogenetic comparative framework. We found considerable variation in the static allometric intercept, which explained the majority of variation in absolute and relative brain size. In contrast, the slope of the brain–body static allometry had relatively low variation, which explained less variation in absolute and relative brain size compared to the intercept and body size. Further examination of the tempo and mode of evolution of static allometric parameters confirmed these observations. Moreover, the estimated evolutionary parameters indicate that the limited observed variation in the static allometric slope could be a result of strong stabilizing selection. Overall, our findings suggest that the brain–body static allometric slope may represent an evolutionary constraint in Lake Tanganyika cichlids.

KEY WORDS: **Allometry, brain–body allometry, brain evolution, constraints, Lake Tanganyika cichlid, phylogenetic comparative analysis.**

Brain size varies greatly among vertebrates (Jerison 1973). It is proposed that brain size diversity is produced and maintained through a balance of adaptations to different types of cognitive ability (Striedter 2005; Gonzalez-Voyer et al. 2009b; Kotrschal et al. 2013; MacLean et al. 2014; Bijl et al. 2015; Kotrschal et al. 2015; Benson-Amram et al. 2016; Navarrete et al. 2016) and constraints on adaptive evolution (Jerison 1973; Striedter 2005; Tsuboi et al. 2015). An important form of evolutionary constraint is brain–body allometry; the close association between body size and brain size observed both within and between species across a wide range of taxa (Huxley 1932; Jerison 1973; Lande 1979). The allometric relationship between brain and body sizes is expressed as a power law $Y = aX^b$, where Y is brain size, X is body size. This in turn yields the standard linear allometric equation $\log(Y) = \log(a) + b\log(X)$, where b is the allometric slope. For interspecific data among larger taxonomic groups, the brain–body allometric slope b is near 0.67, which is referred to as *evolutionary allometry* (Cheverud 1982), while b for adults within populations, which is referred to as *static allometry*, often falls within a range between 0.2 and 0.4 (Huxley 1932; Jerison 1973; Striedter 2005). The classic interpretation of such constancy in allometric slopes is that they result from invariant growth regulation mechanisms (Huxley 1932; Maynard Smith et al. 1985). Under the assumption that growth regulation has only a limited ability to evolve, the constant allometric slope was historically interpreted as a constraint that may restrict independent evolution of brain size (Huxley 1932; Simpson 1944; Jerison 1973; Gould and Lewontin 1979; Lande 1979; Cheverud 1982; Deacon 1990).

Over the last few decades, however, the allometric constraint hypothesis has been challenged by the argument that static

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allometric parameters are actually evolutionary labile. It has been suggested that allometric slopes and intercepts of various morphological traits vary substantially among populations or closely related species (Eberhard and Gutierrez 1991; Emlen and Nijhout 2000) and that strong directional selection can alter these parameters (Tobler and Nijhout 2010; Pavlicev et al. 2011; Egset et al. 2012; Bolstad et al. 2015). In the context of brain size evolution, it has been shown that brain and body sizes present markedly different evolutionary patterns in cichlids (Gonzalez-Voyer et al. 2009a) and pinnipeds (Fitzpatrick et al. 2012), and that the degree of uncoupling for bran and body sizes is heterogeneous across major mammalian orders (Smaers et al. 2012). These studies indicate that static allometric parameters (i.e., slope and intercept) are evolvable at least to some extent and thus do not present strict barriers to the evolution of size-related traits such as brain size (e.g., Emlen and Nijhout 2000, p. 663). However, a recent meta-analysis of static allometric parameters showed that most studies that implied evolutionary lability of the static allometric slope did not in fact test the narrow-sense allometric constraints hypothesis (Voje and Hansen 2013; Voje et al. 2014) and that the allometric slope as a constraint on trait adaptation is still a sound hypothesis. Yet, the variance of static allometric slope and intercept is heterogeneous across lineages, trait types, and the time scales in which the hypothesis is tested (Bonduriansky 2007; Voje and Hansen 2013; Voje et al. 2014; Voje 2016). Therefore, these recent findings call for a revision of the classic view of static allometry as a constraint for brain size evolution (i.e., Huxley 1932; Jerison 1973; Gould and Lewontin 1979; Lande 1979; Deacon 1990). In the current study, we investigate how brain–body static allometric parameters evolve, and how they are related to brain size evolution over a macroevolutionary time scale using Lake Tanganyika cichlids as a model system.

The cichlid fishes of Lake Tanganyika underwent a remarkable diversification to a wide variety of ecological niches within a short time period, forming one of the classic examples of adaptive radiation (Schluter 2000). Brain and body sizes are strongly correlated among cichlid species, but the pattern of brain and body sizes evolution can be markedly different (Gonzalez-Voyer et al. 2009a), suggesting the possibility that brain evolution is, to some extent, decoupled from body size evolution in this lineage. Following from recent contradictory findings for the allometric constraints hypothesis (Gonzalez-Voyer et al. 2009a; Tobler and Nijhout 2010; Pavlicev et al. 2011; Egset et al. 2012; Fitzpatrick et al. 2012; Kotrschal et al. 2013; Voje and Hansen 2013; Bolstad et al. 2015), we propose three scenarios that could underlie the decoupling of brain and body sizes (Fig. 1). First, evolution of brain size could be predominantly a result of evolution in the intercept of within-species brain–body allometric relationships (i.e., static allometry). This scenario, which is described in Figure 1A, corresponds to the central prediction of the allometric constraints hypothesis, which states that the evolution of static allometric slope is strongly constrained and evolutionary changes in brain size occurs strictly through the evolution of the static allometric intercept (Voje et al. 2014). Alternatively, the static allometric slope may be evolvable whereas the intercept is not, and the previously observed partial phenotypic decoupling of brain and body sizes (Gonzalez-Voyer et al. 2009a; Fitzpatrick et al. 2012) could be a consequence of evolution of the slope and its covariation with body size (Fig. 1B). Finally, it is possible that the slope and the intercept are equally evolvable, and a combination of evolution of the static allometric slope and intercept occurs during brain size evolution (Fig. 1C). Using a phylogenetic comparative approach that evaluates the tempo and mode of phenotypic diversification (O'Meara et al. 2006; Beaulieu et al. 2012) and the principle of conditional variance (Hansen and Houle 2008; Voje et al. 2014), this study investigates if and how brain–body static allometry influences brain size evolution over macroevolutionary time scales.

Materials and Methods

DATA ASSEMBLY

We conducted field sampling in the southern part of Lake Tanganyika near Mpulungu, Zambia, during August to September 2012 in compliance with Zambian legislation. Wild fish were obtained while snorkeling or scuba diving using hand nets and monofilament gill nets, with the assistance of local fishermen. After administering deep anesthesia through an overdose of benzocaine, body weight (precision = 1.0 g) was measured and fish were sacrificed by swift decapitation. Fish heads were stored in 4% paraformaldehyde in phosphate-buffered saline for tissue fixation and preservation. Through examination of the gonads, we identified the sex and only sexually mature individuals were included in the analyses. This enabled us to avoid confounding our assessment of static allometry with ontogenetic allometry. Whole brains were obtained from dissected heads. Brain tissue was severed from the spinal cord just posterior to the dorsal medulla. After all cranial nerves, optic nerves, and meningeal membranes were carefully removed, whole brain weight was measured using an electronic scale (precision = 0.01 mg, Precisa Instruments AG, Switzerland). The dataset on body and brain weights consists 505 individuals across 40 species.

STATIC ALLOMETRY AND RELATIVE BRAIN SIZE

All statistical analyses were performed using (R Foundation for Statistical Computing, Vienna, Austria) version 3.2.1 (R Development Core Team 2011). Among the three types of allometry discussed in the literature, ontogenetic allometry, static allometry, and evolutionary allometry (Cheverud 1982), we investigate static allometry, that is, the relationship between brain and body sizes

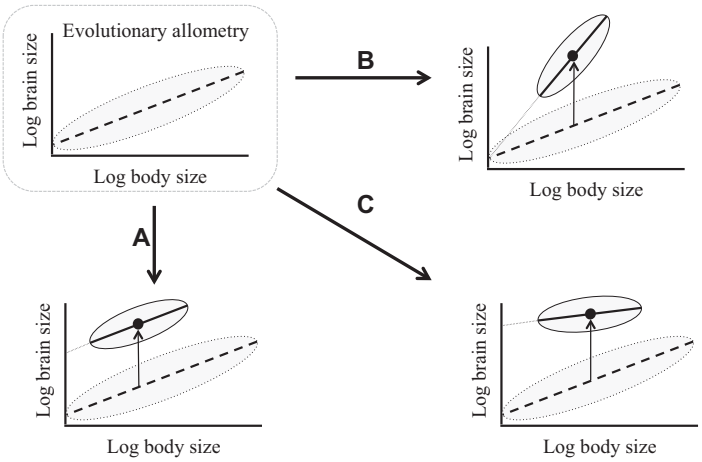

Figure 1. **Graphical illustration of how variation in static allometric intercept, slope, or combination of both produce deviations of relative brain size from evolutionary allometry. The gray ellipses with dashed outline represent variation in brain size and body size in log scales across species. The dashed line in these ellipses thus indicates evolutionary allometry. The gray ellipses with solid outline represent variation across adult individuals of a single species. The solid line in ellipses surrounded by solid lines thus indicates static allometry, and solid dots represent species means of body size and brain size. (A) Evolution of relative brain size away from evolutionary allometry arises only due to evolutionary change in static allometric intercept. (B) The evolution of relative brain size occurs by evolution in static allometric slope while the intercept remains constant. (C) Both the static allometric slope and intercept evolved, and relative brain size changes as a combined result.**

among adult individuals of a single population. Static allometry was estimated using the linear version of the allometric equation $\log_{10}(Y) = \log_{10}(a) + b\log_{10}(X)$ with ordinary least squares of brain weight against body weight for individuals of the same species (Table 1). To circumvent the inherent negative correlation between static allometric slope and intercept (White and Gould 1965; Gould 1966), we centered $\log_{10}$ body size to the mean $\log_{10}$ body size of all included samples in estimating static allometric intercept (Egset et al. 2011; Voje et al. 2014). We calculated relative brain size as residuals of a phylogenetic generalized least-square regression (PGLS; Grafen 1989) between species-average $\log_{10}$ brain and $\log_{10}$ body weights, which we use to define a categorical selective regimes for subset of phylogeny in subsequent analysis (see below for details). Using a consensus molecular phylogeny drawn from a Bayesian phylogenetic reconstruction based on mitochondrial sequences downloaded from Genbank (Fig. S1, Amcoff et al. 2013), PGLS regression estimates a maximum-likelihood value of the phylogenetic scaling parameter, λ, simultaneously with the regression parameters ($\beta \pm \mathrm{SE} = 0.50 \pm 0.03$, $\lambda = 0.90$). PGLS was performed using the caper package version 0.5.2 (Orme et al. 2011).

ASSESSING THE VARIABILITY OF BRAIN-BODY STATIC ALLOMETRY

To evaluate the degree to which brain–body static allometric parameters have evolved and are linked to brain size evolution, we employed two approaches. First, we calculated the among-species variances in static allometric parameters, the slope, and the intercept, and compared them with those reported in Voje et al. (2014). Second, we investigated the relative contribution of allometric parameters and body size on brain size using the principle of conditional variance (Hansen and Houle 2008; Voje et al. 2014). This technique evaluates the proportion of variance in brain size explained by variation in static allometric intercept, variation in static allometric slope, or variation in body size by estimating the decrease in variance in brain size when one of the allometric parameters or body size was held constant (Voje et al. 2014). Furthermore, by holding both body size and one of the static allometric parameters constant, this method measures relative contribution of either slope or intercept of static allometry to explain variance in relative brain size. Therefore, this approach can quantify the relative contributions of static allometric parameters to the variation of absolute and relative brain size across species.

TEMPO AND MODE OF EVOLUTION IN STATIC ALLOMETRIC PARAMETERS

To examine how phenotypic decoupling of brain and body sizes could have occurred, we employed a maximum-likelihood based phylogenetic comparative analysis that compares the tempo and mode of trait evolution among subsets of lineages within a phylogenetic tree (O'Meara et al. 2006; Beaulieu et al. 2012). In this analysis, we focus on patterns of evolution in static allometric parameters (i.e., slope and intercept) in relation to relative brain size. Because relative brain size in our study is a measure of deviation from the allometric relationship among species (i.e., evolutionary

Table 1. Size measurements for 40 species of Lake Tanganyika cichlid.

Species	*N*	Brain (mg) Mean$_{\pm SE}$	Body (g) Mean$_{\pm SE}$	Slope$_{\pm SE}$	Int.$_{\pm SE}$	r^2
Altolamprologus compressiceps	15	64.8$_{\pm 3.2}$	8.5$_{\pm 0.98}$	0.429$_{\pm 0.018}$	1.936$_{\pm 0.006}$	0.98
Baileychromis centropomoides	4	138.2$_{\pm 7.6}$	36.0$_{\pm 3.15}$	0.349$_{\pm 0.362}$	2.015$_{\pm 0.131}$	0.32
Batybates fasciatus	11	179.7$_{\pm 19.5}$	69.05$_{\pm 15.39}$	0.456$_{\pm 0.026}$	1.989$_{\pm 0.017}$	0.97
Batybates ferox	7	198.8$_{\pm 16.4}$	52.44$_{\pm 6.39}$	0.451$_{\pm 0.091}$	2.067$_{\pm 0.048}$	0.83
Benthochromis tricoti	12	162.6$_{\pm 3.4}$	38.99$_{\pm 1.18}$	0.498$_{\pm 0.163}$	2.014$_{\pm 0.064}$	0.48
Chalinochromis brichardi	15	53.0$_{\pm 2.3}$	10.59$_{\pm 1.03}$	0.347$_{\pm 0.067}$	1.788$_{\pm 0.017}$	0.68
Ctenochromis horei	15	132.5$_{\pm 8.7}$	14.38$_{\pm 1.86}$	0.461$_{\pm 0.043}$	2.151$_{\pm 0.010}$	0.90
Cyprochromis leptosome	13	98.5$_{\pm 3.9}$	17.04$_{\pm 1.01}$	0.550$_{\pm 0.083}$	1.976$_{\pm 0.009}$	0.80
Cyathopharynx furcifer	13	149.4$_{\pm 6.9}$	32.21$_{\pm 3.74}$	0.305$_{\pm 0.041}$	2.087$_{\pm 0.014}$	0.83
Ectodus descampsii	14	62.0$_{\pm 1.9}$	8.69$_{\pm 0.37}$	0.466$_{\pm 0.134}$	1.912$_{\pm 0.037}$	0.50
Eretmodus cyanostictus	13	60.3$_{\pm 2.0}$	7.95$_{\pm 0.53}$	0.432$_{\pm 0.071}$	1.910$_{\pm 0.023}$	0.77
Gnathochromis permaxillaris	11	108.4$_{\pm 6.7}$	41.07$_{\pm 4.23}$	0.512$_{\pm 0.071}$	1.827$_{\pm 0.030}$	0.85
Gnathochromis pfefferi	12	95.3$_{\pm 7.0}$	9.24$_{\pm 0.93}$	0.729$_{\pm 0.052}$	2.151$_{\pm 0.015}$	0.95
Haplotaxodon microlepis	14	171.0$_{\pm 8.8}$	47.21$_{\pm 5.36}$	0.463$_{\pm 0.028}$	2.020$_{\pm 0.013}$	0.96
Hemibates stenosoma	6	182.8$_{\pm 24.7}$	73.03$_{\pm 23.84}$	0.481$_{\pm 0.053}$	1.961$_{\pm 0.033}$	0.95
Julidochromis ornatus	13	41.3$_{\pm 1.6}$	4.53$_{\pm 0.37}$	0.637$_{\pm 0.060}$	1.859$_{\pm 0.034}$	0.83
Lamprologus ornatipinnis	10	28.3$_{\pm 2.4}$	2.31$_{\pm 0.25}$	0.637$_{\pm 0.090}$	1.985$_{\pm 0.079}$	0.86
Lepidiolamprologus elongatus	15	132.9$_{\pm 7.7}$	30.3$_{\pm 3.57}$	0.411$_{\pm 0.026}$	2.019$_{\pm 0.009}$	0.95
Lepidiolamprologus profundicola	15	131.6$_{\pm 7.1}$	50.76$_{\pm 5.72}$	0.471$_{\pm 0.030}$	1.889$_{\pm 0.015}$	0.95
Limnochromis staneri	10	144.8$_{\pm 10.5}$	37.37$_{\pm 4.7}$	0.408$_{\pm 0.177}$	2.008$_{\pm 0.067}$	0.40
Limnotilapia dardennii	12	177.9$_{\pm 25.0}$	41.98$_{\pm 14.11}$	0.413$_{\pm 0.023}$	2.131$_{\pm 0.011}$	0.97
Lobochilotes labiatus	15	237.1$_{\pm 18.7}$	38.41$_{\pm 7.81}$	0.443$_{\pm 0.019}$	2.228$_{\pm 0.008}$	0.98
Neolamprologus pulcher	14	35.2$_{\pm 1.3}$	5.79$_{\pm 0.32}$	0.399$_{\pm 0.122}$	1.720$_{\pm 0.056}$	0.47
Neolamprologus sexfasciatus	13	87.6$_{\pm 3.2}$	17.24$_{\pm 3.47}$	0.105$_{\pm 0.054}$	1.944$_{\pm 0.015}$	0.25
Neolamprologus tetracanthus	14	79.3$_{\pm 4.9}$	14.71$_{\pm 1.38}$	0.477$_{\pm 0.100}$	1.915$_{\pm 0.016}$	0.65
Ophthalmotilapia nasuta	18	120.5$_{\pm 2.6}$	21.07$_{\pm 1.05}$	0.274$_{\pm 0.074}$	2.054$_{\pm 0.009}$	0.46
Oreochromis tanganicae	4	346.7$_{\pm 39.5}$	458.2$_{\pm 52.72}$	0.729$_{\pm 0.521}$	1.470$_{\pm 0.760}$	0.49
Perissodus microlepis	13	83.0$_{\pm 2.7}$	11.01$_{\pm 0.73}$	0.296$_{\pm 0.141}$	1.965$_{\pm 0.026}$	0.29
Petrochromis famula	14	171.2$_{\pm 6.8}$	44.88$_{\pm 3.41}$	0.421$_{\pm 0.074}$	2.044$_{\pm 0.034}$	0.72
Petrochromis orthognathus	15	113.7$_{\pm 7.0}$	16.12$_{\pm 1.87}$	0.476$_{\pm 0.074}$	2.058$_{\pm 0.014}$	0.76
Pseudosimochromis curvifrons	12	172.9$_{\pm 8.0}$	32.61$_{\pm 2.25}$	0.565$_{\pm 0.062}$	2.061$_{\pm 0.020}$	0.89
Simochromis diagramma	15	177.4$_{\pm 7.4}$	27.63$_{\pm 2.18}$	0.472$_{\pm 0.035}$	2.138$_{\pm 0.009}$	0.93
Simochromis pleurospilus	16	97.4$_{\pm 4.3}$	11.85$_{\pm 1.39}$	0.646$_{\pm 0.117}$	2.068$_{\pm 0.019}$	0.69
Telmatochromis temporalis	15	45.4$_{\pm 1.9}$	6.56$_{\pm 0.53}$	0.486$_{\pm 0.034}$	1.847$_{\pm 0.014}$	0.94
Trematocara unimaculatum	11	61.7$_{\pm 4.5}$	19.7$_{\pm 2.68}$	0.459$_{\pm 0.097}$	1.750$_{\pm 0.017}$	0.71
Tropheus moorii	15	118.7$_{\pm 4.4}$	20.88$_{\pm 1.39}$	0.392$_{\pm 0.124}$	2.027$_{\pm 0.018}$	0.44
Tylochromis polylepis	15	113.4$_{\pm 6.0}$	12.19$_{\pm 0.99}$	0.567$_{\pm 0.097}$	2.120$_{\pm 0.017}$	0.73
Variabilichromis moorii	8	73.6$_{\pm 3.1}$	7.58$_{\pm 0.7}$	0.458$_{\pm 0.048}$	2.015$_{\pm 0.016}$	0.94
Xenotilapia flavipinnis	13	57.4$_{\pm 1.7}$	7.07$_{\pm 0.27}$	0.642$_{\pm 0.123}$	1.982$_{\pm 0.043}$	0.71
Xenotilapia melanogenys	15	89.4$_{\pm 2.9}$	14.04$_{\pm 0.75}$	0.464$_{\pm 0.109}$	1.975$_{\pm 0.011}$	0.58
Mean		119.9	35.53	0.467	1.977	0.73
SD		63.2	70.86	0.120	0.138	0.22

Sample size (*N*), body weight (g), and brain weight (mg) are presented. Allometric slope is the least squares regression of $\log_{10}$ brain weight as a function of ground mean centered $\log_{10}$ body weight. "Int." represents the intercept.

allometry), this analysis can tell us whether divergence in static allometric slope or intercept has occurred along with the evolution of brain size away from the evolutionary allometry. To estimate evolutionary parameters with information of uncertainty, it is necessary to have repeated observations (i.e., multiple species) per subset of phylogeny for each of which a unique set of evolutionary parameters are estimated (Hansen et al. 2008). It is therefore crucial that the choice of subset reflects biological question under consideration, while having repeatability within subsets. Therefore, we assigned our study species into one of three groups that

characterize how relative brain size diverged from evolutionary allometry; 13 species with the smallest values to "small relative brain size" (relative brain size; residuals from PGLS analysis of $\log_{10}$ brain weight on $\log_{10}$ body weight = −0.24 to −0.06), 13 species with the largest values to "large relative brain size" (relative brain size = 0.03–0.20) and the remaining 14 species with medium values to "medium relative brain size" (relative brain size = −0.06 to 0.03). We mapped 50 histories of transitions among these three groups differing in their relative brain size with stochastic character mapping (Huelsenbeck et al. 2003) for consensus Bayesian phylogenies using the phytools package version 0.4.56 (Revell 2012) with unequal transition rates for ancestral state estimation. Tree height (i.e., the distance from the root to the tip) was scaled to 1. We then fitted six different evolutionary models of static allometric slope or intercept evolution. These models were based either on a Brownian motion model of evolution (Felsenstein 1985) or on an Ornstein–Uhlenbeck (OU) process of evolution (Hansen 1997; Butler and King 2004). The parameter associated with BM is the rate of diffusion parameter σ^2. The OU process introduces two additional parameters, the adaptive optima θ and the strength of selection α, that collectively describe a tendency for traits to be pulled toward the optima. The two simplest models consisted of a single-rate Brownian motion model (BM1) and an OU model with single optima, diffusion rate parameter, and strength of selection parameter (OU1). The multiple-rate BM model (BMS) allowed lineages with different brain size to have different rate parameters. The multiple-optima OU model (OUM) assumed three optima for each group while keeping σ^2 and α constant. The two most complex models consisted of a multiple optima selection OU model (OUMA) and a multiple optima diffusion OU model (OUMV), which allowed lineages with different relative brain size to have different optima as well as different level of selection α (OUMA) or different rate of diffusion σ^2 (OUMV). The fit of the six alternative evolutionary models was assessed using the sample size corrected Akaike information criterion (AICc) computed in the OUwie package (Beaulieu et al. 2012). The model with the lowest AICc score represents the best fit model and support for one model over another is indicated by an ΔAICc > 4 (Burnham and Anderson 2002). Standard errors of static allometric slope and intercept were included in all cases. The reliability of the ML estimated parameters was assessed using the eigenvalues of the Hessian matrix, and only iterations with positive eigenvalues were retained to calculate global means and variances of estimated parameters.

Results

Our data showed moderate variance in static allometric parameters. The slope varied between 0.105 and 0.729, with a SD of 0.120 (Table 1). Compared to the values reported in a previous meta-analysis on static allometry (Voje et al. 2014), the variance of the brain–body static allometric slope in Lake Tanganyika cichlids is relatively small; it is closer to what has been reported for the subspecies level (SD = 0.07) than for the among-species level (SD = 0.27; Voje et al. 2014). The intercept varied between 1.472 and 2.228, with an SD of 0.138 (Table 1). This value is comparable to the parameters reported at the among-species level in Voje et al. (2014). Our assessments of the conditional variance of absolute and relative brain size in relation to body size, static allometric slope, and static allometric intercept are presented in Table 2. Note that the percentage of variance shown in this table represents the variance unexplained upon conditioning on each parameter. Thus, a higher percentage means that the conditioning parameter contributes less to the variance in brain size and vice versa. We found that the conditioning on body size left the minimum amount of unexplained variance (2.1 %), indicating a strong influence of body size in explaining the variation in brain size. Conditioning on the intercept explained 32% more of the variance than conditioning on the slope, indicating a larger contribution of intercept to variance in brain size. A visualization of the static allometric parameters between the 40 cichlid species under study, shown in Figure 2, corresponds to this finding. A similar result was found in the conditional variance of relative brain size, where conditioning on the intercept left only 0.025% variation in relative brain size unexplained, which is 87% more than conditioning on the slope. Collectively, these results provide support for the allometric constraints hypothesis; small variability of the static allometric slope may constrain brain size evolution to occur predominantly through evolution of the static allometric intercept.

By comparing the tempo and mode of evolution in static allometric parameters between species with varying relative brain size, we attempted to gain insights into how the deviations in relative brain size from the evolutionary allometric relationship could arise. The fit of six alternative evolutionary models for the evolution of static allometric slope and intercept are summarized in Table 3. Based on AICc scores, three OU models with multiple optima (OUM, OUMA, and OUMV) received support for the static allometric intercept, while four evolutionary models (BMS, OU1, OUMA, OUMV) were suggested as possible evolutionary models in explaining the evolution of the static allometric slope. However, the diffusion rate parameter σ^2 was estimated with a high uncertainty in all cases (Table S1), making it difficult to obtain biological implications from models with varying σ^2 parameters (i.e., BMS, OUMV). We therefore limit our interpretation to evolutionary models with constant σ^2 parameters. The maximum-likelihood estimated parameters for four remaining models are presented in Table 4. Two models describing the evolution of the static allometric intercept indicated that the adaptive optima were small for

Table 2. The conditional variance of brain size or relative brain size on constraining body size, static allometric intercept, or slope.

Trait	Absolute brain				Relative brain	
Constraint	Size	Intercept	Slope	Intercept and Slope	Intercept	Slope
Conditional variance	2.14%	3.99%	5.90%	3.98%	0.25%	1.85%

The numbers reflect the percentage of variance unexplained when conditioning on parameters as listed in the rows. The first four columns show conditional variance for absolute brain size and the last two columns for relative brain size.

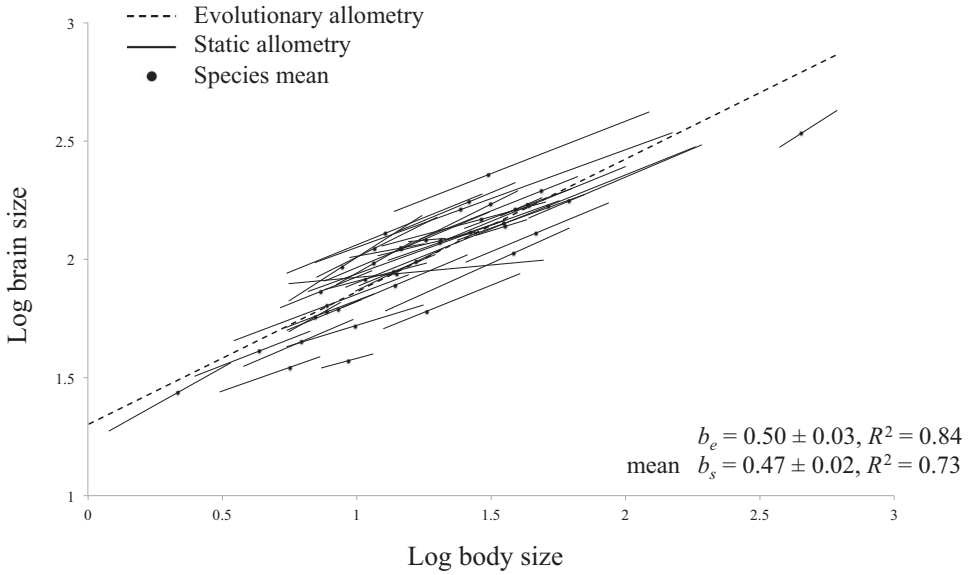

Figure 2. Evolutionary and static allometry of 40 Lake Tanganyika cichlids. The dashed line represents evolutionary allometry, solid lines represent static allometry of each species, and solid circles represent species mean body and brain size. The slope for evolutionary allometry (b_e) and the mean of static allometric slope (b_s) as well as R^2 are also given.

lineages with small relative brain size (OUM, $\theta_{small} = 1.83 \pm 0.06$; OUMA, $\theta_{small} = 1.85 \pm 0.04$), medium for lineages with medium relative brain size (OUM, $\theta_{medium} = 1.99 \pm 0.05$; OUMA, $\theta_{medium} = 1.98 \pm 0.05$), and large for lineages with large relative brain size (OUM, $\theta_{large} = 2.23 \pm 0.06$; OUMA, $\theta_{large} = 2.18 \pm 0.04$). The ML estimated α parameter from the OUMA model indicates that stronger selection toward different optima may have operated on the static allometric intercept for lineages with smaller and larger relative brain size compared to lineages with medium relative brain size. Two supported evolutionary models for the evolution of static allometric slope indicated that the adaptive optima overlapped with their estimated SEs, suggesting that this parameter is not associated with relative brain size (Table 4). Interestingly, according to the OUMA model, the strength of selection was almost twice as strong in lineages with relatively large ($\alpha_{large} = 8.50 \pm 0.45$) and small brain size ($\alpha_{small} = 7.40 \pm 0.49$) compared to lineages with medium relative brain size ($\alpha_{medium} = 4.44 \pm 1.28$). Finally, the ML-estimated evolutionary parameters revealed that the rate of adaptation (α) of slopes was larger than that of the intercept, despite the evolutionary stasis in the static slope.

Discussion

For decades, the tight association between brain and body sizes has inspired the idea that brain size evolution is mainly a result of correlated response to evolutionary changes in body size (Huxley 1932; Jerison 1973; Gould and Lewontin 1979; Lande 1979; Deacon 1990). Nevertheless, a range of ecological and evolutionary questions have been investigated by focusing on variation in relative brain size (Striedter 2005; Gonzalez-Voyer et al. 2009b; Maklakov et al. 2011; MacLean et al. 2014; Tsuboi et al. 2015; Abelson 2016; Benson-Amram et al. 2016; Navarrete et al. 2016). Exactly how and in what way allometry may constrain brain size evolution has, however, rarely been precisely articulated. Our comparative study on Lake Tanganyika cichlids now reveals that the intercept of brain–body static allometry is variable across species, while the evolution of the allometric slope is more constrained. We propose that brain and body sizes can present markedly different evolutionary patterns despite strong phenotypic correlation (Gonzalez-Voyer et al. 2009a; Fitzpatrick et al. 2012; Smaers et al. 2012), mainly because the static allometric intercept possesses ample evolutionary lability. Furthermore, our results provide support for the hypothesis that the small variability

Table 3. The fit of alternative evolutionary models of evolution in brain–body static allometric slope and intercept in Lake Tanganyika cichlids.

Character	Model	*N*	lnL	AICc
Intercept	BM1	50	36.06	−68.12
	BMS	50	37.99	−66.84
	OU1	50	37.91	−69.15
	OUM	50	44.89	−78.01
	OUMA	41	47.47	−77.43
	OUMV	49	46.70	−75.90
Slope	BM1	50	23.78	−43.57
	BMS	49	28.87	−48.59
	OU1	50	27.49	−48.31
	OUM	50	28.75	−45.73
	OUMA	42	33.66	−49.82
	OUMV	50	34.05	−50.60

Effective sample size (*n*), log likelihood (lnL), and AICc are presented.

of static allometric slope may act as an important constraint for brain size evolution (Gould and Lewontin 1979; Lande 1979; Deacon 1990).

THE BIOLOGICAL IMPLICATIONS OF EVOLUTIONARY STASIS IN BRAIN-BODY STATIC ALLOMETRIC SLOPE

There are two major lines of argument explaining the low variability of the static allometric slope. First, the developmental constraints hypothesis states that the low variance of the static allometric slope may be a manifestation of low evolvability in developmental mechanisms underpinning the proportional growth among traits (Huxley 1932; Simpson 1944; Jerison 1973; Gould and Lewontin 1979; Lande 1979; Cheverud 1982; Maynard Smith et al. 1985). This hypothesis predicts that the evolution of relative brain size should be primarily caused by evolutionary changes in the early stages of neurogenesis (Shea 1983; Atchley 1984; Riska and Atchley 1985). Indeed, coevolution of relative brain size and life-history traits related to early developmental stages is reported in Lake Tanganyika cichlids (Tsuboi et al. 2015) as well as in mammals (Isler and van Schaik 2009; Weisbecker and Goswami 2010), marsupials (Isler 2011), and birds (Iwaniuk and Nelson 2003; Isler and van Schaik 2006).

However, small variance in static allometric slope does not in itself confirm a low evolutionary lability in this parameter. An alternative hypothesis is that evolutionary stasis of the static allometric slope may be a result of external constraints imposed by selection (Pelabon et al. 2013; Voje et al. 2014). From an adaptive point of view, brain size in Lake Tanganyika cichlids is mainly driven by selection associated with the elaborate intra- and interspecific interactions observed in littoral communities of the lake (van Staaden et al. 1994; Huber et al. 1997; Pollen et al. 2007; Gonzalez-Voyer et al. 2009b; Gonzalez-Voyer and Kolm 2010). Meanwhile, the upper ceiling of brain size for a given body size and functional requirements should be under strong selection due to high energetic demand for development and maintenance of brain tissue (Tsuboi et al. 2015). Therefore, the observed stasis in brain–body static slopes might be a result of stabilizing selection to assure the exact function–energy balance across cichlids with different body sizes.

One way of disentangling the two hypotheses explained above is to compare variability in static slope and intercept (Voje et al. 2014). This can be done by comparing the rate of adaptation, α (Hansen 1997, 2012; Hansen et al. 2008). Interestingly, the static allometric slope showed a faster rate of adaptation than the intercept. According to these parameters, strong stabilizing selection, not lack of variability, may be a more plausible explanation for the evolutionary stasis of brain–body static allometric slope in Lake Tanganyika cichlids. However, our interpretations should be taken with caution, because the implementation of varying α parameters across phylogeny has only recently become available (Beaulieu et al. 2012) and the model inference framework in our study may need further development and validation (Kaliontzopoulou and Adams 2016). Refinement of the analytical capability of OU-based evolutionary models and biologically sound conceptualization of evolutionary parameters will be key to extend our understanding of allometric constraints (Hansen 2012, 2014).

THE STASIS OF BRAIN-BODY STATIC ALLOMETRIC SLOPE: COMPARISON WITH OTHER TRAITS

A growing number of studies report that most of the variation in static allometric parameters among populations or species concerns the intercept, and variation in the slope is much less common (Bonduriansky 2007; Voje and Hansen 2013; Voje et al. 2014). Variation in static allometric slopes emerges only when comparisons are made across species that diversified over time scales of millions of years (Voje and Hansen 2013; Voje et al. 2014). According to geological and molecular time calibration, the age of the Lake Tanganyika cichlids is estimated to be 7 to 12 million years (Meyer et al. 1990; Nishida 1991; Salzburger et al. 2002), while the most dramatic diversification event occurred around 2.5–5 million years ago (Nishida 1991). Based on the phylogenetic half-life of 2.5–3.25 millions of years as a benchmark for the amount of time that static allometric slopes require to evolve (Voje and Hansen 2013), the age of Lake Tanganyika cichlids is within the time scale where evolutionary stasis of static slopes would be predicted. In general, the pattern of phenotypic diversification over a macroevolutionary time scale is hypothesized to be best described by a combination of stasis over "a million of years" and a rare but substantial burst of phenotypic changes (Uyeda et al. 2011; Hansen 2012). Therefore, we propose that the brain–body

Table 4. Parameter estimates of the two best evolutionary models for static allometric intercept (OUM, OUMA) and slope (OU1, OUMA).

Character	Model	Parameter	Small brain	Medium brain	Large brain
Intercept	OUM	α	4.32 ± 0.38	4.32 ± 0.38	4.32 ± 0.38
		σ^2	0.008 ± 0.95	0.008 ± 0.95	0.008 ± 0.95
		θ	1.83 ± 0.06	1.99 ± 0.05	2.23 ± 0.06
	OUMA	α	5.03 ± 0.40	3.91 ± 0.79	4.82 ± 0.38
		σ^2	0.005 ± 1.17	0.005 ± 1.17	0.005 ± 1.17
		θ	1.85 ± 0.04	1.98 ± 0.05	2.18 ± 0.04
Slope	OU1	α	15.02 ± 1.18	15.02 ± 1.18	15.02 ± 1.18
		σ^2	0.26 ± 1.15	0.26 ± 1.15	0.26 ± 1.15
		θ	0.45 ± 0.02	0.45 ± 0.02	0.45 ± 0.02
	OUMA	α	8.50 ± 0.45	4.44 ± 1.28	7.40 ± 0.49
		σ^2	0.0003 ± 2.52	0.0003 ± 2.52	0.0003 ± 2.52
		θ	0.45 ± 0.04	0.49 ± 0.19	0.49 ± 0.05

The evolutionary diffusion parameter (σ^2), the strength of selection toward adaptive optima (α), as well as the adaptive optima (θ) for lineages with small, medium, and large relative brain size are presented. Means were calculated over the up to 50 times sampled reconstruction of trichotomized relative brain size groups for which parameters were estimated reliably (see text for details), and the approximate SEs calculated as the inverse of Hessian matrix are also presented.

static allometric slope in Lake Tanganyika cichlids is constrained, but not to any greater extent than what is predicted by available empirical data on the temporal scales of general phenotypic diversification.

THE STASIS OF BRAIN–BODY STATIC ALLOMETRIC SLOPE: TAXONOMIC COMPARISONS

A persistent interest in studies of brain–body allometry lies in explaining the striking similarity of allometric slopes across lineages with vastly diverse ecological backgrounds and evolutionary histories (Striedter 2005). In mammals, the static allometric slopes typically fall in the range 0.2–0.4 (Jerison 1973; Pilbeam and Gould 1974; Shea 1983). Interestingly, the brain–body static allometric slopes of Lake Tanganyika cichlids were on average slightly higher than the range reported in mammals (i.e., mean $b_s = 0.47 \pm 0.02$). We propose two possible explanations for this difference. First, assuming that the static allometric slope represents the rate of proportional growth at later stages of life (Huxley 1932), the continuing brain proliferation in adult fish (Zupanc 2006) might have resulted in the higher brain–body static allometry than in mammals, in which neurogenesis is mostly completed at birth (Count 1947; Kobayashi 1963). Second, from the perspective that the exponent of brain–body allometry indicates underlying energetic constraints (e.g., Kleiber's law, Kleiber 1947; Capellini et al. 2010), our found discrepancy may have stemmed from the external thermoregulation in fish, which presumably results in highly different patterns of metabolism from endothermic mammals (Bennett and Ruben 1979; but see Mink et al. 1981). Future efforts to include wider taxonomic ranges covering both endo- and ectothermic animals in research of brain–body allometry will be necessary to confirm, and to further investigate the apparent mammalian–fish dichotomy in static allometric slopes.

CONCLUSION: BRAIN SIZE EVOLUTION AND ALLOMETRIC CONSTRAINTS

Originally developed by Dutch naturalist Eugéne Dubois and French physiologist Louis Lapicque, the study of brain–body allometry has a long history (Strauss 1993; Gayon 2000). The subject was further elaborated by Stephen Jay Gould, who placed allometry in the center of arguments against the dominance of functionalism within the neo-Darwinian paradigm (Gould 1966; Gould and Lewontin 1979). However, recent research trends have shifted from viewing allometry as a simple constraint toward viewing allometry as an evolutionary dynamic entity (Eberhard and Gutierrez 1991; Emlen and Nijhout 2000; Bonduriansky 2007), even though the evidence supporting the latter standpoint still remains equivocal (Voje and Hansen 2013; Pelabon et al. 2014; Voje et al. 2014). Our study solves at least a part of this controversy by showing that brain size can evolve independent of body size through evolution of the static allometric intercept, while the allometric slope appears to be more constrained toward evolutionary change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Molecular phylogeny of 40 Lake Tanganyika cichlids.
Table S1. Maximum likelihood (ML) estimates of all considered evolutionary models (BM1, BMS, OU1, OUM, OUMA, OUMV) in our study.