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Social fishes and single mothers: brain evolution in African cichlids

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As with any organ, differences in brain size—after adequate control of allometry—are assumed to be a response to selection. With over 200 species and an astonishing diversity in niche preferences and social organization, Tanganyikan cichlids present an excellent opportunity to study brain evolution. We used phylogenetic comparative analyses of sexed adults from 39 Tanganyikan cichlid species in a multiple regression framework to investigate the influence of ecology, sexual selection and parental care patterns on whole brain size, as well as to analyse sex-specific effects. First, using species-specific measures, we analysed the influence of diet, habitat, form of care (mouthbrooding or substrate guarding), care type (biparental or female only) and intensity of sexual selection on brain size, while controlling for body size. Then, we repeated the analyses for male and female brain size separately. Type of diet and care type were significantly correlated with whole brain size. Sex-specific analyses showed that female brain size correlated significantly with care type while male brain size was uncorrelated with care type. Our results suggest that more complex social interactions associated with diet select for larger brains and further that the burden of uniparental care exerts high cognitive demands on females.

Keywords: brain size; comparative analyses; cichlid fishes; diet; parental care; habitat

1. INTRODUCTION

It is generally assumed that changes in the size of specific structures within the brain are the result of natural selection (Harvey & Pagel 1991). Because increasing demands on cognitive ability predominantly alter the size of neural structures rather than their connectivity (Kotrschal & Junger 1988; Huber & Rylander 1992), interspecific variance in relative brain size, or the size of neural structures, should reflect differences in the cognitive challenges that have shaped brain evolution (Clark *et al.* 2001; de Winter & Oxnard 2001). Phylogenetic comparative analyses have proved a useful tool to identify the correlates of brain size across a wide range of taxa. For instance, gathering evidence for mammals suggests that social living, even more than ecological factors, may have been a key component in shaping brain evolution (Barton & Dunbar 1997; Dunbar & Bever 1998; Schultz & Dunbar 2006; Byrne & Bates 2007). In birds, larger brains have been shown to be correlated with tool use, survival, invasion success, developmental mode and song complexity (Lefebvre *et al.* 2002; Sol *et al.* 2002, 2007; Iwaniuk & Nelson 2003; Garamszegi *et al.* 2005a). Finally, although much less studied than mammals or birds, available evidence in fishes suggests an influence of habitat and diet on brain size and structure (Huber *et al.* 1997; Kotrschal *et al.* 1998; Ito *et al.* 2007; Pollen *et al.* 2007; Yopak *et al.* 2007).

Although it makes sense that a large brain reflects greater cognitive abilities, the brain has an immense range of

functions and function does not necessarily map neatly onto neural structure (Byrne & Bates 2007; Healy & Rowe 2007). As highlighted by a recent review (Healy & Rowe 2007), identification of the correlates of brain size, or of the size of a specific structure within the brain, does not equate to a test of cognitive abilities and may provide limited information on brain function. However, the aim of comparative studies is to identify the ecological factors and behavioural traits that correlate with brain size and structure. Identifying such correlates can provide a valuable guide for experiments and empirical comparative studies in determining the link between neural structure and cognitive abilities (Healy & Rowe 2007). Comparative analyses can also highlight evolutionary convergence or determine whether patterns identified at the intraspecific level or in studies involving a small number of species can be extrapolated across a broader taxonomic range (Harvey & Pagel 1991; Nishikawa 2002). Healy & Rowe (2007) also questioned whether significant changes to one, or several parts of the brain, could be detected by measuring whole brain size, when it is on the size of these separate components that natural selection probably acts. However, neural structures within the brain evolve in concert in response to specific cognitive challenges as shown by the presence of ‘cerebrotypes’ that highlight convergent response of brain architecture to specific selection pressures (Clark *et al.* 2001; de Winter & Oxnard 2001; Iwaniuk & Hurd 2005), such changes are expected to be reflected in total brain size. As an example of this, in Tanganyikan cichlids, whole brain size explained 50–76 per cent of the variation in all brain structures, except for the dorsal medulla where the variance explained was 18–32

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per cent (Pollen *et al.* 2007). Thus, the resulting correlates of brain size should point to factors that have a notable influence on one or several neural structures.

Ecological factors appear to influence brain evolution in diverse taxa, for example diet correlates with brain size in fishes, bats, primates and birds (Hutcheon *et al.* 2002; Kalisinska 2005; Dunbar & Shultz 2007; Yopak *et al.* 2007). A species' habitat also poses specific cognitive challenges related to either navigation or spatial orientation (Salas *et al.* 2003; Safi & Dechmann 2005; Pollen *et al.* 2007; Yopak *et al.* 2007). Such ecological factors are generally expected to impose similar selective pressures on both sexes (Lande 1980), although divergent pressures on males and females can result from differences in feeding habits or spatial segregation, or as a result of sexual selection leading to sexual dimorphism in neural structures and cognitive abilities (Jacobs 1996; Jones & Healy 2006; Johnson & Bouchard 2007). Factors such as parental care or sexual selection possibly impose different selection pressures on males and females leading to neural dimorphism (Gittleman 1994; Garamszegi *et al.* 2005*b*), but to be able to identify sex-specific selection pressures influencing brain evolution, analyses must necessarily involve sexually mature, sexed individuals (Healy & Rowe 2007). However, as a result of the difficulty in obtaining samples of both sexes from several species, there have been very few comparative studies analysing sex-specific influences on brain evolution, although the results of the analyses involving such datasets strongly suggest that sex-specific selection has influenced brain evolution (Gittleman 1994; Garamszegi *et al.* 2005*a,b*).

The African cichlid fishes are an excellent group for studies of brain evolution as they present a large number of closely related species, resulting from recent adaptive radiations, which exploit a wide diversity of ecological niches and present varying social organization (Meyer 1993). Two previous studies have analysed the correlates of brain size and structure in African cichlid fishes and their results suggest an influence of diet and habitat (Huber *et al.* 1997; Pollen *et al.* 2007). Interestingly, results from one study suggest a potential effect of mating pattern on telencephalon size (Pollen *et al.* 2007). However, because no adequate phylogenetic information was available for the cichlids from the three African lakes, Huber *et al.* (1997) could not account for the lack of independence of data points due to phylogeny (Harvey & Pagel 1991), while Pollen *et al.* (2007) included a limited sample from over 200 species of Lake Tanganyika, and, for the influence of mating system, only had three monogamous and four polygamous species, resulting from just two evolutionary transitions. In this study, we analysed brain evolution in 39 Tanganyikan cichlid species from six different tribes. Our sample included sexually mature, male and female individuals, thus allowing us to explore sex-specific effects. We analysed the influence of diet, habitat, form of care (substrate guarding or mouthbrooding), care type (uni- or biparental) and intensity of sexual selection on brain evolution in a multiple regression framework controlling for phylogeny, as suggested by Healy & Rowe (2007). First, we analysed the influence of these ecological and behavioural factors on mean brain size across species. Second, we reanalysed,

in an unprecedented way, the factors for each sex separately to identify potential sex-specific influences.

2. MATERIAL AND METHODS

(a) *Data*

Body weight and whole brain weight were collected from wild caught, sexually mature individuals. Fishes were anaesthetized with benzocaine. Following anaesthesia, fishes were weighed (± 0.01 g) and the head was swiftly severed and preserved in 4 per cent paraformaldehyde in a phosphate buffer for tissue fixation and preservation. Whole brain weight (± 0.001 g) was obtained from dissected brains following fixation. The number of days samples spent in paraformaldehyde prior to dissection had no effect on brain weight even when controlling for body weight ($t = -0.83$, $p = 0.41$, $n = 194$). Individuals were sexed by observing the gonads. Intraspecific sample sizes ranged from three to eight individuals, except for two species for which we only had one sample. For 33 species, we had both male and female individuals and samples per sex ranged from one to six individuals. An ANOVA with species as a factor showed that interspecific variation in brain weight was much higher than intraspecific variation ($F = 12.89$, $p = 0.0004$), thus we should have low levels of type I error (Harmon & Losos 2005). All analyses were also repeated including an estimate of intraspecific variation (see below). Weight and brain weight data were log transformed. Data on diet, habitat, form of care (mouthbrooding or substrate guarding), care type (biparental or female only) and intensity of sexual selection were collected from the literature (see the electronic supplementary material). Sexual selection was coded as either intense or moderate, based on combined information from mating system, dichromatism and sexual size dimorphism as in Gonzalez-Voyer *et al.* (2008; see the electronic supplementary material).

Qualitative descriptions of diet and habitat were transformed into quantitative continuous variables reflecting a continuum of variation. Diet reflected variation in prey motility: aufwuchs and fixed algae were coded as 1; molluscs as 2; benthic prey (e.g. bottom-dwelling invertebrates and crustaceans) as 3; plankton and zooplankton as 4; invertebrates and crustaceans found in the water column as 5; and fishes as 6. Habitat reflected variation in complexity, previously shown to be correlated with brain structure (Pollen *et al.* 2007): benthic and benthopelagic habitats were coded as 1; semi-pelagic as 2; sandy or shallow vegetated habitats as 3; rocky or rubble as 4; and rock habitat as 5. Pollen *et al.* (2007) showed that sandy, rocky or rubble (intermediate) and rock habitat differ significantly in several quantitative measures of complexity, thus the categorization adequately reflects complexity. Most species do not strictly inhabit a single habitat or feed on one prey type; therefore, we used descriptive information on habitat preferences and prey to calculate an average for each species giving more weight to preferred habitats/prey based on detailed descriptions from primary publications. The results of the comparative analyses did not change if habitat was included as a categorical variable, but we could not do so for diet since the broadness of the diet of species precluded its use as a categorical variable. Form of care, care type and sexual selection were included in the analyses as dichotomous variables.

(b) *Phylogeny*

We constructed a mtDNA phylogeny for the 39 Tanganyika cichlid species (see the electronic supplementary material).

We used three mitochondrial genes, NADH 2 (1047 bp), cytochrome *b* (402 bp) and the more variable control region (369 bp), downloaded from GenBank (see the electronic supplementary material for sequence accession numbers) to reconstruct the phylogenetic relationships among species using Bayesian analysis (Huelsenbeck *et al.* 2001) in MRBAYES v. 3.1.1 (Ronquist & Huelsenbeck 2003). We used a GTR+ Γ model of sequence evolution (Salzburger *et al.* 2002) and specified *Boulengerochromis microlepis* and *Bathybates fasciatus* as the outgroup clade. Phylogeny construction followed Gonzalez-Voyer *et al.* (2008). The phylogenetic relationships in our tree are in accordance with those presented by Salzburger *et al.* (2002).

(c) Phylogenetic comparative analyses

The correlates of brain evolution were identified by means of phylogenetic generalized least-squares (PGLS) multiple regression models (Martins & Hansen 1997). Phylogenetic analyses were undertaken with APE (Paradis *et al.* 2004) in R that allows comparisons between models of evolution with either Brownian motion, Pagel's λ (Freckleton *et al.* 2002) or an Ornstein-Uhlenbeck (OU) process. The analyses were repeated with COMPARE (Martins 2004), which can incorporate error in species traits reflecting intraspecific variation; in our case variance in body size and brain weight. All analyses involved branch lengths obtained from the phylogeny reconstruction. First, we created models with species averages, combining data for both sexes. The dichotomous variables (form of care, care type and sexual selection) were entered sequentially in different models to avoid multicollinearity, since care type and mating system are correlated (Gonzalez-Voyer *et al.* 2008). Second, we repeated the analyses separately for each sex, but did not include form of care because, in the reduced dataset, the sample sizes for the two categories were unbalanced. Thus, we created seven models: the first three combined brain weight data for males and females including log body weight as a covariate (Freckleton 2002), diet and habitat as continuous independent variables and, sequentially in each model, form of care (model 1), care type (model 2) or sexual selection (model 3) as a factor. In models 4–7, we repeated the analyses for females and males separately, again including factors sequentially in the models. Our database included 33 species for which we had both male and female individuals and the phylogeny was cropped accordingly.

In §3, we present the standardized partial regression coefficients (β) for ease of comparison between models. COMPARE provides an estimate of the proportion of the variance explained by the model, and we added the predictor variables in a stepwise fashion to a null model, presenting only body weight as a predictor variable in order to be able to compare the changes in proportion of variance explained by the addition of the different variables to the model. This provides an estimate of their relative importance.

3. RESULTS

Multiple regression models with a λ or α parameter described trait evolution better than models with Brownian motion. We ran the analyses with an OU model of evolution (α) because analyses with COMPARE showed that this model described better the evolution of brain and body weight.

The results of the analyses combining information for males and females showed that even when controlling for body weight, there was a significant negative correlation

Table 1. Multiple regression model of brain weight (response variable) when controlling for phylogeny using PGLS. (The partial regression coefficient with standard error ($\beta \pm$ s.e.) and the standardized β - and p -values are shown. Type of care was entered in the model as a factor. Statistically significant correlations are given in italics. $n=39$ species, $\alpha=58.1$.)

	$\beta \pm$ s.e.	standardized β	p -value
log weight	0.046 \pm 0.002	0.909	< 0.0001
diet	-0.002 \pm 0.001	-0.142	0.012
habitat	0.001 \pm 0.001	0.030	0.562
care type	0.004 \pm 0.002	0.112	0.038

between brain weight and diet ($p=0.012$; table 1), which suggests that species which feed on sessile food items (e.g. aufwuchs or fixed algae) have larger brains than species which feed on motile prey (e.g. fishes). Furthermore, brain weight was significantly positively correlated with care type ($p=0.038$; table 1), thus species with female-only care have larger brains than species with biparental care. Neither habitat (table 1), form of care (standardized $\beta=0.096$, $p=0.137$) nor sexual selection (0.074, $p=0.178$) was significantly correlated with brain weight. Habitat and diet were correlated ($r=-0.42$), which could lead to multicollinearity. However, even when excluding diet from the model, brain size was not correlated with habitat (0.061, $p=0.228$). On the contrary, the significant correlation between brain size and diet remained when habitat was excluded (-0.153 , $p=0.003$). All results were the same when the analyses were repeated including intraspecific variation in COMPARE (see the electronic supplementary material). The analyses with COMPARE showed that the null model (only body weight as a predictor variable) explained 88.62 per cent of the variance, adding diet and subsequently care type resulted in an increase in the proportion of variance explained (90.81 and 92.87%, respectively). On the other hand, the addition of habitat and subsequently form of care to the null model caused only a minor increase in the variance explained (89.06 and 90.20%, respectively).

To identify possible sex-specific effects, we repeated the analyses for females and males separately. The results showed that care type was significantly positively correlated with brain weight in females ($p=0.049$) but not in males ($p=0.783$; table 2). Intensity of sexual selection was not significantly correlated with brain weight in either females (0.077, $p=0.22$) nor males (0.015, $p=0.82$). Diet was negatively correlated with brain weight in both sexes; although the correlation was not significant when the analyses were done with *R* (table 2), it was significant when the analyses were repeated with COMPARE (see the electronic supplementary material) where intraspecific variation could be accounted for. In summary, these results confirmed the species-level analyses and showed that diet selects for brain size equally in both sexes, while the larger brains in species with uniparental care are a result of larger brains in females that provide sole care for offspring when compared with females that share parental care with their partner.

4. DISCUSSION

Our results suggest that both ecological and social factors have had a major influence on Tanganyikan cichlid brain evolution. Brain size was significantly correlated with diet

Table 2. Multiple regression models of brain weight (response variable) of females and males when controlling for phylogeny using PGLS. (The partial regression coefficient with standard error ($\beta \pm \text{s.e.}$) and standardized β - and p -values are shown. Type of care was entered in the models as a factor. Statistically significant correlations are given in italics. $n=33$ species, $\alpha \text{♀} = 20.9$, $\alpha \text{♂} = 12.4$.)

	females			males		
	$\beta \pm \text{s.e.}$	standardized β	p -value	$\beta \pm \text{s.e.}$	standardized β	p -value
log weight	0.043 ± 0.003	0.917	<i>< 0.0001</i>	0.047 ± 0.003	0.926	<i>< 0.0001</i>
diet	-0.001 ± 0.001	-0.107	0.107	-0.002 ± 0.001	-0.117	0.126
habitat	0.001 ± 0.001	0.051	0.377	0.001 ± 0.001	0.086	0.178
care type	0.004 ± 0.002	0.123	<i>0.049</i>	0.001 ± 0.003	0.021	0.783

and care type. The multiple regression model including diet, care type and body size as covariates, explained more than 92 per cent of the variance in brain size, which suggests these variables have had an important influence on brain evolution. Brain size was shown to decrease as the motility of prey increased, suggesting that species which feed on aufwuchs or fixed algae possess larger brains, for their body size, than species which feed on fishes. Interestingly, species with female-only care were found to possess larger brains than species with biparental care. Brain size did not correlate significantly with habitat, form of care or intensity of sexual selection. By analysing the correlates of brain size separately for males and females, we were able to show that the apparent increase in brain size in species with uniparental care actually resulted from larger female brain size in species where females provide sole parental care as opposed to species where females share the burden of parental care with their partner.

(a) *Ecological factors*

Ecological factors such as diet and habitat have been shown to be correlated with brain size in diverse taxa. Previous studies of birds and bats suggest that brains, and brain architecture, have adapted to foraging ecology (Hutcheon *et al.* 2002; Iwaniuk & Hurd 2005; Kalisinska 2005), while studies of primates and carnivores suggest that large-brained species tend to have high-quality diets (Gittleman 1986; Dunbar & Shultz 2007) in line with the elevated energetic costs of brain tissue (Isler & Van Schaik 2006). Intraspecific analyses also suggest that protein and energy content of the diet can influence both size of neural structures and cognition (Arnold *et al.* 2007; Isaacs *et al.* 2008; Ranade *et al.* 2008). Indeed, in humans, an increase in food from animal sources has been proposed as one of the factors associated with our unusually large relative brain size (Leonard *et al.* 2003). In cichlid fishes, results from a non-phylogenetic comparative analysis point to a possible influence of diet on brain architecture as piscivorous species presented larger olfactory bulbs and optic tecta than insectivores and zooplanktivores (Huber *et al.* 1997). Hence, our results suggesting that Tanganyikan species feeding on fixed algae and aufwuchs present larger brains than species feeding on fishes seem counter-intuitive. Diet is not correlated with body size (results not shown), ruling out possible confounding effects of body size. Although the data presented above make this unlikely, we cannot rule out that exploiting an abundant, although possibly low-quality, food source has allowed species to increase their relative brain size. Habitat has also been shown to influence brain size in bats

(Safi & Dechmann 2005) and, in Tanganyikan cichlids, habitat complexity was found to be associated with larger brains and larger cerebella, while the telencephalon showed a similar trend (Pollen *et al.* 2007). Habitat complexity was further shown to be correlated with the number of species and number of individuals (Pollen *et al.* 2007); however, we found that habitat and diet are correlated, but Pollen *et al.* (2007) did not include diet in their analyses, thus its influence on brain size cannot be ruled out. Our results suggest there is no significant correlation between brain size and habitat complexity.

Social complexity, resulting from intricate interspecific interactions among algae-eating littoral species, may be the key to consolidating our results with those of previous work (Huber *et al.* 1997; Pollen *et al.* 2007). The rocky littoral areas of Lake Tanganyika harbour an extremely diverse assemblage of species showing complex interspecific interactions with fine niche partitioning (Hori *et al.* 1993). Dietary preferences allowed subdivision of the species complex into 12 dietary-preference groups, composed of species sharing up to 50 per cent similarity in diet and showing prevalent commensalisms and some mutualism. Interspecific aggression increased with the degree of overlap in diet and foraging sites, and observations suggest that food is partitioned by differential foraging, achieved partly through direct interactions among competitors (Hori *et al.* 1993). Substantial evidence has accumulated, suggesting that feeding and/or breeding space is limited for many epilithic algal feeders and some benthic feeders, most of which exhibit interspecific territoriality (references in Hori *et al.* 1993). This suggests that the prevalent, complex interspecific interactions and the fine-scale niche differentiation observed in algal and benthic feeders may result in increased cognitive demands that have selected for increased brain size. If this hypothesis is correct, then dietary preferences may provide a better reflection of the cognitive challenges faced by individuals than habitat does, in accord with our results. Byrne & Bates (2007) have suggested that the advanced cognitive abilities of some coral reef fishes (Bshary *et al.* 2002) reflect selection for 'social intelligence' in a complex community of many sympatric species. Our results add to the evidence suggesting that the social brain hypothesis (Dunbar 1998) might not be limited to mammals but may also apply to fishes.

(b) *Care type and sexual selection*

Females providing sole parental care for offspring have larger brains than females that share parental care with their partners. To our knowledge, this is the first study to identify sex-specific influences on brain evolution in fishes.

In carnivores, females caring for offspring alone were also found to have larger brains than those of biparental or communal species (Gittleman 1994). Biparental care has been found to be the ancestral state in Tanganyikan cichlids (Goodwin *et al.* 1998), with female-only care being the derived state. A previous study found that the evolutionary transition from biparental care to female-only care involved an increase in the intensity of sexual selection acting on males, leading to male abandonment (Gonzalez-Voyer *et al.* 2008). Although sexual selection was not significantly correlated with brain size, we cannot rule out that in species with uniparental care, unmeasured factors such as female choice also influence brain size (Jacobs 1996). Females providing sole parental care possibly face a higher investment in reproduction than females from biparental species, and thus may face stronger selection to control the choice of partner (Kokko *et al.* 2006), which could select for increased cognitive abilities. In the majority of fish species with parental care, the males are the sole care providers, and parental care can even be sexually selected as females preferentially mate with males that provide more or higher quality parental care (Clutton-Brock 1991; Östlund & Ahnesjö 1998). If the influence of uniparental care on brain size shown for cichlid fishes also applies to species with male-only care, then there could be increased selection for higher cognitive abilities as a result of sexual selection acting on male care.

Sexual selection did not correlate with brain size in Tanganyikan cichlids, even when analysing each sex separately, contrary to what has been found in bats and birds. In birds, more intense sexual selection was associated with brain size dimorphism, but there was no effect when analysing female and male brain size separately (Garamszegi *et al.* 2005b). However, Garamszegi *et al.* (2005b) used residuals to control for allometry, which could lead to biased parameter estimates (Freckleton 2002). Conversely, in bats, intense sexual selection was associated with a decrease in brain size, possibly due to a trade-off between brain and testis size (Pitnick *et al.* 2006); however, the lack of data on sexed individuals precluded the analysis of sex-specific effects. A previous study with Tanganyikan cichlids suggested that monogamous species had a larger telencephalon and a smaller hypothalamus (Pollen *et al.* 2007). However, there were only two independent transitions from monogamy to polygamy in the clade studied; the authors did not control for the influence of habitat complexity which they suggested was correlated, although not significantly, with telencephalon size, and their analysis—a *t*-test—did not control adequately for phylogenetic effects.

We cannot rule out that certain factors included in our analyses have subtle influences on brain structure, which are not reflected on total brain size. However, it is highly likely that diet and care type have a notable impact on one or several brain structures as shown by the high proportion of the variance in total brain size explained; the evidence suggesting that brain structures respond in concert to specific selection pressures (Clark *et al.* 2001; Iwaniuk & Hurd 2005) and the fact that previous studies analysing brain size and structure found that selection pressures influencing brain structure also generally affected total brain size (Hutcheon *et al.* 2002; Pollen *et al.* 2007).

Our results show that, in Tanganyikan cichlids, species feeding on sessile food items have larger brains than

species feeding on motile prey. We suggest that species exploiting dietary niches in the rocky habitat are faced with a complex social structure involving frequent interspecific interactions (Hori *et al.* 1993). Thus, our results in combination with those from previous studies (Huber *et al.* 1997; Bshary *et al.* 2002; Pollen *et al.* 2007) hint that the social brain hypothesis might not be limited to mammals but may also apply in fishes. Our results also showed a sex-specific influence on brain evolution. Females providing sole parental care were shown to possess larger brains than females sharing care with their partners, thus uniparental care appears to impose higher cognitive demands on females. Our use of multiple regression models and separate analyses of females and males allowed us to identify the specific influences of ecology and behaviour on brain size and demonstrate the potential for selection to cause sexual neural dimorphism (Healy & Rowe 2007).

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