

No evidence for larger brains in cooperatively breeding cichlid fishes

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Abstract: The social brain hypothesis posits that frequent social interactions, characteristic of group living species, select for greater socio-cognitive abilities and the requisite neural machinery. An extension of the social brains hypothesis, known as the cooperative breeding brain hypothesis, postulates that cooperatively breeding species, which live in stable social groups and provide alloparental care, face particularly pronounced cognitive demands because they must recognize, remember, and differentially respond to multiple group members. These socio-cognitive challenges are thought to have selected for increased cognitive capacity, supported by a bigger brain. To test the prediction that cooperative breeders have larger brains, we performed a phylogenetically controlled comparison of the whole brain masses of adult fish from 16 closely related species of cooperatively and independently breeding lamprologine cichlid species from Lake Tanganyika. We collected data on brain mass from males of eight species of lamprologine cichlids and added this to brain mass data from eight more species found in the published literature. Controlling for body size and phylogeny, we found that cooperative breeding species did not have larger brains, and this was true of for both our field-collected data set and the expanded data set including published values. This study adds to a growing body of literature from other taxa that cast doubt on the cooperative breeding brain hypothesis.

Key words: brain mass, Lake Tanganyika, cooperative breeding brain hypothesis, social brain hypothesis.

Résumé : L'hypothèse du cerveau social postule que des interactions sociales fréquentes, caractéristiques des espèces vivant en groupe, entraînent la sélection de capacités sociocognitives plus grandes et de la machinerie neuronale qu'elles requièrent. Un prolongement de cette hypothèse, appelé l'hypothèse du cerveau à reproduction communautaire, postule que les espèces faisant preuve de coopération durant la reproduction, qui vivent dans des groupes sociaux stables et dont les jeunes ne sont pas élevés que par leurs parents, font face à des demandes cognitives particulièrement prononcées puisque les individus doivent reconnaître et mémoriser les différents membres du groupe et réagir différemment à ces différents membres. Ces défis sociocognitifs se seraient traduits par une sélection menant à une plus grande capacité cognitive, appuyée par un cerveau plus imposant. Pour vérifier la prédiction voulant que les espèces à reproduction communautaire aient des cerveaux plus imposants, nous avons effectué la comparaison contrôlée pour la phylogénie de la masse totale du cerveau de poissons adultes de 16 espèces étroitement reliées de cichlidés lamprologinés à reproduction communautaire ou indépendante du lac Tanganyika. Nous avons recueilli des données sur la masse du cerveau de mâles de huit espèces de cichlidés lamprologinés et les avons ajoutées aux données sur la masse du cerveau de huit autres espèces obtenues de rapports publiés. En contrôlant pour la taille du corps et la phylogénie, nous avons constaté que les cerveaux des espèces à reproduction communautaire ne sont pas plus grands que ceux des autres espèces, une constatation valide tant pour l'ensemble de données de terrain que pour l'ensemble de données plus large comprenant des données publiées. L'étude s'ajoute à un nombre croissant de rapports publiés sur d'autres taxons qui jettent un doute sur l'hypothèse du cerveau à reproduction communautaire. [Traduit par la Rédaction]

Mots-clés : masse du cerveau, lac Tanganyika, hypothèse du cerveau à reproduction communautaire, hypothèse du cerveau social.

Introduction

Neural tissue is costly to grow and maintain, therefore brains are expected to be no larger than is necessary to support survival and reproduction (Aiello and Wheeler 1995). However, larger brains, relative to body size, may arise when there is selection on cognitive capacity (Jerison 1973). For example, across primates the incidence of behavioural innovation and tool use are positively correlated with brain size (Reader and Laland 2002). In the Trinidadian

guppy (*Poecilia reticulata* Peters, 1859), fish that were artificially selected for larger brain size outperformed smaller brained fish in a learning assay, but also developed smaller guts, suggesting a trade-off between costly tissues (Kotrschal et al. 2013). The social brain hypothesis predicts that social living may be a particularly strong selective force on cognitive capacity and hence driver of increased brain size (Dunbar 1998). According to this hypothesis, group living is cognitively demanding because social animals

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must recognize, interact with, and behave appropriately towards a potentially large number of conspecifics and thus require greater neural machinery to succeed in these tasks (Dunbar 1998). However, it has been argued that not all of these socio-cognitive abilities are necessarily required in all social animals (Dunbar and Shultz 2007). In fact, many social species form large, relatively anonymous, fission–fusion societies in which complex social relationships between group members may be absent (Krause and Ruxton 2002). Therefore, it is perhaps unrealistic to expect that group living in and of itself will necessarily drive selection on increased brain size. Instead, it is possible that the depth and complexity of social relationships, in addition to grouping behaviour, are potential drivers of socio-cognitive complexity and concomitant brain size evolution (Dunbar and Shultz 2007).

A derived version of the social brain hypothesis, the cooperative breeding brain hypothesis, posits that cooperatively breeding species, where nonbreeding helpers-at-the-nest aid in offspring care, face particularly strong socio-cognitive challenges emerging from this complex social arrangement and therefore ought to show greater cognitive sophistication compared with their independently breeding relatives (Burkart et al. 2009; Burkart and van Schaik 2010). Cooperative breeders must recognize and respond appropriately to each group member according to their social status and their respective relationships within the group (Soares et al. 2010). Thus, cooperatively breeding species are expected to have disproportionately large brains for their body size when compared with their independently breeding relatives (Thornton and McAuliffe 2015). We are aware of only one specific test of this prediction; among the birds of the parvorder Corvida, cooperative breeders did not have larger brains than their closest relatives that breed independently (Iwaniuk and Arnold 2004). However, tests on a greater diversity of taxa are still required to understand the patterns of brain size in relation to cooperative behaviour across taxa.

The explosive radiation of cichlid fishes in the African Great Lakes has made cichlids a model system for the study of ecology and evolution (Salzburger et al. 2005). Cichlids have a remarkable diversity of behavioural and ecological specializations (Barlow 2000). Within the cichlids, the lamprologine tribe, endemic to Lake Tanganyika, shows an especially impressive diversity of social behaviour including the vast majority of all known cooperatively breeding fishes (Taborsky and Limberger 1981; Taborsky 1994; Heg and Bachar 2006). Therefore, these lamprologine cichlids represent an excellent opportunity for a test of the prediction that cooperative breeding will be associated with larger relative brain size. Here, we compare the brain mass (correcting for body mass) of adult males from four group-living and cooperatively breeding species (*Neolamprologus pulcher* (Trewavas and Poll, 1952), *Neolamprologus savoryi* (Poll, 1949), *Neolamprologus multifasciatus* (Boulenger, 1906), golden julie (*Julidochromis ornatus* Boulenger, 1898)) with four closely related nongrouping and independently breeding species (*Neolamprologus modestus* (Boulenger, 1898), fourspine cichlid (*Neolamprologus tetracanthus* (Boulenger, 1899)), *Telmatochromis temporalis* Boulenger, 1898, *Lamprologus ocellatus* (Steindachner, 1909)) of lamprologine cichlid fishes. In a follow-up analysis, we augment our investigation by expanding our sample with eight additional species using mixed-sex data drawn from the published literature (Gonzalez-Voyer et al. 2009a), resulting in a total of 16 species.

Materials and methods

Study site and field methods

All fish used were sexually mature males captured from southern Lake Tanganyika near Mpulungu, Zambia (08°46'52"S,

31°05'18"E), in February–March 2013. Individuals of eight species were located and captured using SCUBA, between depths of 6–12 m. Fish were collected using fence- and hand-nets and were brought slowly to the surface. At the surface, fish were weighed using a portable electronic balance (Scout Pro Portable Scale, Ohaus, Parsippany, New Jersey, USA) before being stunned by submersion in ice water and swiftly decapitated. Whole brains were carefully extracted and preserved in 4% phosphate-buffered paraformaldehyde for transport to McMaster University, Hamilton, Ontario, Canada, where each brain was weighed three times using an electronic analytic balance (Classic Plus AB204-S/FACT; Mettler Toledo, Mississauga, Ontario, Canada). The mean value from the three measurements was taken as the brain mass for that individual. In total, we sampled $n = 80$ sexually mature male fish, with $n = 10$ males per species. For all field-collected individual data see Supplementary Table S1.¹

Data from the literature

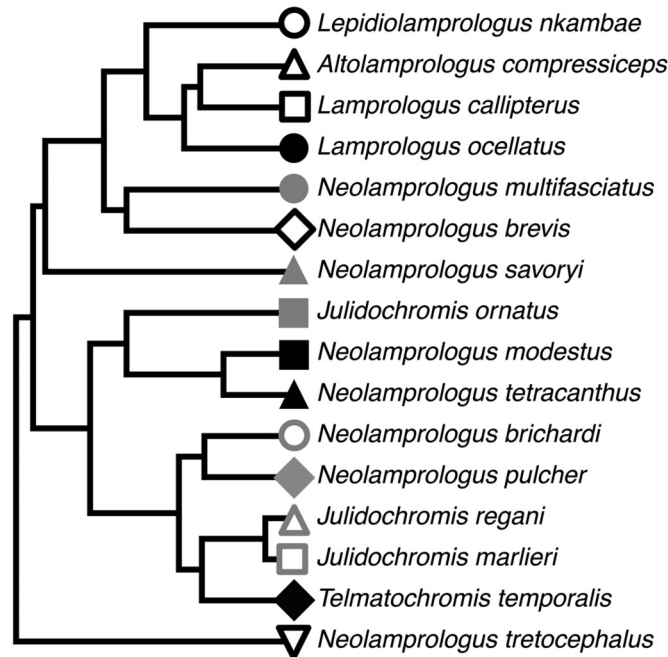
To supplement our field-collected data, we searched the literature for published accounts of lamprologine body and brain masses. We found a single source that presents mean body mass and mean brain mass for males and females of eight additional lamprologine cichlid species, including three cooperatively breeding species and five independently breeding species (Gonzalez-Voyer et al. 2009a). These data were drawn from a mixture of male and female fish collected from the field using methods similar to those used in our field collections. For the complete data set from all 16 species, including mean values from our field-collected fish and the mean values presented in Gonzalez-Voyer et al. (2009a), see Supplementary Table S2.¹

Phylogenetic tree

Nucleotide sequences for the NADH dehydrogenase subunit 2 (ND2), cytochrome *b* (*Cytb*), and mitochondrial control region for the 16 study species, as well as for four out-group species (*Asprotilapia leptura* Boulenger, 1901, *Bathybates fasciatus* Boulenger, 1901, giant cichlid (*Boulengerochromis microlepis* (Boulenger, 1899)), and yellow sand cichlid (*Xenotilapia flavipinnis* Poll, 1985)), were retrieved from the National Center for Biotechnology Information (NCBI) nucleotide data (available from <http://www.ncbi.nlm.nih.gov/nucleotide/>) (Supplementary Table S3).¹ Out-group species were selected because the divergence time for these species from the lamprologine cichlids has been previously estimated (Koblmüller et al. 2008; Sturmhuber et al. 2010). Nucleotide sequences were aligned using MUSCLE (Edgar 2004a, 2004b) and uploaded to MESQUITE (Maddison and Maddison 2011) to verify aligned sequences and trim the alignment such that only the region with overlapping sequence data for all species was retained. The resulting alignment was then used to estimate phylogenetic relationships using the software program BEAST with BEAUTi version 1.8 (Drummond and Rambaut 2007; Drummond et al. 2012) to complete 10 million runs of a Bayesian Markov chain Monte Carlo model with an uncorrelated log-normal relaxed molecular clock (Drummond et al. 2006) and HKY substitution model with gamma + invariant site heterogeneity. The model of nucleotide evolution was selected as the most appropriate using Akaike's information criterion (AIC; Posada and Buckley 2004) in the program jModelTest 2 (Guindon and Gascuel 2003; Darriba et al. 2012). The program Tracer version 1.5 (Rambaut et al. 2007) was used to analyse the output from BEAST version 1.8 and confirm estimated sample size (ESS) values >200. Within BEAST version 1.8, the program TreeAnnotator was used to find the best-supported tree, using a burnin of 10%, set with a posterior probability limit of zero, and a maximum clade credibility tree as the target tree type. The mean heights of each node were set so the

¹Supplementary tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2015-0118>

Fig. 1. The phylogenetic relationships among the 16 species of lamprologine fish included in the current study. These relationships are based on the ND2, cytochrome *b*, and mitochondrial control region sequences, and created using Bayesian Markov chain Monte Carlo analysis with *Asprotilapia leptura*, *Bathybates fasciatus*, giant cichlid (*Boulengerochromis microlepis*), and yellow sand cichlid (*Xenotilapia flavipinnis*) as the out-groups (for full details see the Materials and methods; for sequence NCBI accession numbers see Supplementary Table S3¹). Each species is represented by a unique symbol (consistent with Figs. 2A, 2B). Grey symbols represent cooperatively breeding species, whereas black symbols represent independently breeding species. Solid symbols represent species with field-collected data, whereas open symbols represent species with literature data.



final consensus tree would have the mean height at each node of all the samples (Drummond et al. 2006). Out-group species were trimmed using MESQUITE. The final tree was visualized using the package “phytools” (Revell 2012) within R version 3.1.2 (R Core Team 2015). Our phylogenetic tree (Fig. 1) was consistent with previous analysis of phylogenetic relationships among lamprologine cichlids using mitochondrial genes (Sturmbauer et al. 1994, 2010; Day et al. 2007).

Statistical analyses

We used Bayesian phylogenetically controlled statistical analyses to test for associations between brain mass and social system, including body mass, and the interaction effect between body mass and social system, as covariates. We performed two analyses. First, we performed an analysis where we used individual data for the eight species for which we had field-collected data. For this analysis, the additional species with only mean values available were trimmed from the phylogenetic tree using MESQUITE. Second, we performed an analysis on all 16 species using the mean values available in the literature for each species (Gonzalez-Voyer et al. 2009a). Using the package “MCMCglmm” (Hadfield 2010), we performed generalised linear mixed models based on a Markov chain Monte Carlo (MCMC) algorithm. Within the MCMCglmm package, the phylogenetically controlled analysis is implemented by including the phylogenetic tree as a random factor in the model (Hadfield 2010). Following examples from de Villemereuil and Nakagawa (2014), we defined our priors for the model as $V = 1$

and $\nu = 0.02$ for both the random effects and the residual variance. This corresponds to an inverse-gamma distribution with shape and scale parameters equal to 0.01, which is canonical (Gelman 2006). We ran each model for 5 million iterations, with a burnin of 1000 and a thinning interval of 50. With these priors and settings, there was no autocorrelation between successive stored iterations for any of the models (Hadfield 2015). Because Bayesian statistics are based on iterative processes, the outcomes therefore can vary slightly between runs. Therefore, we repeated the analyses three times and report mean values for the 95% highest posterior density (HPD) interval and the P_{MCMC} , which are the Bayesian equivalents of 95% confidence intervals and *P* values, respectively. Associations were considered significant when the 95% HPD excluded zero and P_{MCMC} was less than 0.05. Analyses were conducted using R version 3.2.1 (R Core Team 2015).

Ethical note

Handling time was minimized as much as possible for all of the study animals. The methods described for animal capture and euthanasia were approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol No. 10-11-71) and adhered to both Canadian and Zambian laws, as well as the guidelines of the Canadian Council on Animal Care.

Results

Individual field-collected data

Using the individual-level data for eight field-collected species (Fig. 2A), we found that brain mass was highly correlated with body mass (95% HPD interval = 0.30, 0.63; $P_{\text{MCMC}} < 0.001$). However, there was no relationship between brain mass and social system (95% HPD interval = -0.21, 0.64; $P_{\text{MCMC}} = 0.29$). The interaction effect between body mass and social system was also not significant (95% HPD interval = -0.24, 0.17; $P_{\text{MCMC}} = 0.73$).

Mean values from all species

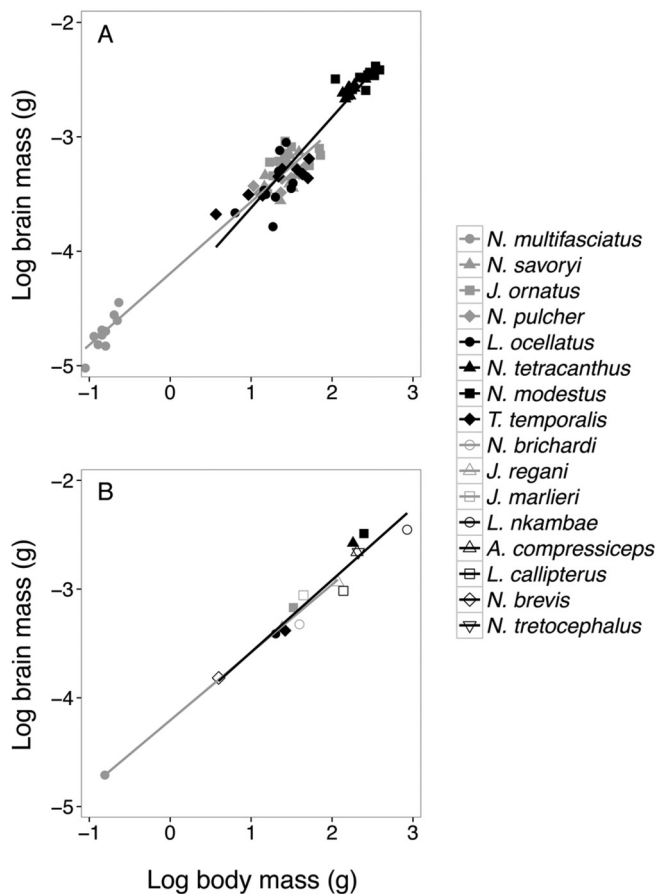
Using the mean values from all 16 species (Fig. 2B), we found that brain mass was highly correlated with body mass (95% HPD interval = 0.47, 0.76; $P_{\text{MCMC}} < 0.001$). There was no relationship between brain mass and social system (95% HPD interval = -0.40, 0.33; $P_{\text{MCMC}} = 0.87$). The interaction effect between body mass and social system was also not significant (95% HPD interval = -0.17, 0.24; $P_{\text{MCMC}} = 0.70$).

Discussion

We found no association between cooperative breeding and brain mass among lamprologine cichlid fishes either in our field-collected sample of 8 species or in our expanded sample of 16 species that included data from the published literature. Our results match those of a previous study examining the relationship between cooperative breeding and brain size in corvids, which also found no evidence of cooperative breeders having larger brains (Iwaniuk and Arnold 2004). Furthermore, among primates, cooperatively breeding species actually have some of the smallest brains for their body size (Reader 2003; Thornton and McAuliffe 2015). Although not a comparison between cooperative and independent breeders per se, a recent study examined the relationship between cooperative tendencies and brain mass in cleaner fishes, which may face similar demands to recognize and behave appropriately toward social partners, and also found no association between relative brain mass and cooperative tendency (Soares et al. 2015). Collectively, these results suggest that across taxa, cooperation is not associated with larger brain sizes.

The cooperative breeding brain size hypothesis has recently been criticized. Thornton and McAuliffe (2015) argue that many of the socio-cognitive abilities putatively associated with cooperative breeding are not unique to cooperative breeders and that cooperative breeding in and of itself is unlikely to convey

Fig. 2. The relationship between body mass and brain mass for (A) 8 species of lamprologine cichlids with field-collected data ($n = 10$ individuals per species) and (B) mean values of 16 species of lamprologine cichlids species using a combination of field-collected data and data published in [Gonzalez-Voyer et al. 2009a](#). Using a Bayesian phylogenetically controlled statistical analyses for both (A) the field-collected subset and (B) the full data set, we found a significant positive relationship between body mass and brain mass; however, neither social system nor the interaction effect between body mass and social system were significantly associated with brain mass (for full details see the Materials and methods and Results). For both panels, each species is represented by a unique symbol (consistent with Fig. 1). Grey symbols represent cooperatively breeding species, whereas black symbols represent independently breeding species. Solid symbols represent species with field-collected data, whereas open symbols represent species with literature data.



exceptional cognitive demands. For example, in their analysis, [Thornton and McAuliffe \(2015\)](#) do not find any evidence that prosociality, social learning, teaching, or social coordination are overrepresented or exceptional among cooperatively breeding species. However, we cannot exclude the possibility that cooperative breeding may be associated with brain evolution, perhaps in more subtle ways that we could not detect with our methodology. First, it is possible that a particular brain area may increase or decrease in size in association with the emergence of cooperative breeding without a corresponding change in overall brain size. In contrast to the concerted model of brain evolution, wherein developmental constraints cause the entire brain to evolve in a relatively coordinated manner ([Finlay and Darlington 1995](#)), the mosaic model proposes that brain areas can evolve at least somewhat independently ([Barton and Harvey 2000](#)). Recent work sug-

gests that the mosaic model is a better fit than the concerted evolution model for explaining the diversification of neuroanatomy in Tanganyikan cichlids ([Gonzalez-Voyer et al. 2009b, 2009c; Gonzalez-Voyer and Kolm 2010](#)). Specifically, overall brain size explains only 86% of the variation in the size of various gross brain structures in Tanganyikan cichlids, a substantially lower proportion than in other taxa ([Gonzalez-Voyer and Kolm 2010](#)). This suggests that brain areas are somewhat free to change size independently through evolution, thereby potentially obscuring or abolishing any effect on overall brain size. A recent study on one of the cooperatively breeding lamprologine cichlid fishes included in our sample, *N. pulcher*, provides support for the mosaic model in this species at least on a developmental time scale ([Fischer et al. 2015](#)). The treatment of brains as uniform structures is one of several criticisms that have been levelled against studies comparing brain size across species ([Healy and Rowe 2007](#)). Admittedly, our study suffers from this limitation, but as a preliminary investigation, our results do suggest that neuroanatomical differences between cooperatively and independently breeding lamprologine cichlids, if present, are subtle and may be specific to certain brain areas.

In addition, other ecological or life-history differences between the species that we examined may have a larger effect on brain mass than cooperative breeding per se. Factors including diet, parental care patterns, depth, habitat complexity, and territory size are known to affect various aspects of brain morphology, including whole brain size, in Tanganyikan cichlid fishes ([Gonzalez-Voyer et al. 2009a, 2009b, 2009c; Gonzalez-Voyer and Kolm 2010; Tsuboi et al. 2015](#)). Therefore, alternative ecological or life-history variables may have confounded or obscured any differences between the cooperatively and the independently breeding species in our sample. However, the lack of variation in relative brain size among our sampled species argues against this alternative.

Previous work has shown that sex may be an important factor in determining relative brain size in cichlid fishes ([Gonzalez-Voyer et al. 2009a; Kotrschal et al. 2012, 2015; Samuk et al. 2014](#)). However, our field-collected data included only males and the literature values that we found were not split by sex, precluding any investigation of potential sex-specific patterns of brain size in relation to social system. Future work is now needed to address the relationship among sex, social system, and brain size in the lamprologine cichlids.

Finally, the lack of pattern that we observed between cooperatively and independently breeding Tanganyikan cichlids could simply result from small sample sizes at the species level, the individual level, or both. Indeed, we had only 8 species in our field-collected sample and 16 species in our total sample, both of which are substantially fewer than the number used in the previous study on birds ([Iwaniuk and Arnold 2004](#)). However, our total sample does cover 35% of the known cooperatively breeding cichlids in Lake Tanganyika, which together account for the vast majority of all known cooperatively breeding fish species ([Taborsky 1994; Heg and Bachar 2006](#)). At the individual sample level, our field-collected sample size ($n = 10$ individuals per species) is greater than the sample sizes used in most other studies (e.g., [Iwaniuk and Arnold 2004; Gonzalez-Voyer et al. 2009a, 2009b, 2009c; Gonzalez-Voyer and Kolm 2010](#)). While it is possible that subtle brain size differences do exist between cooperative and independently breeding lamprologines, this would require large sample sizes to detect and the highly consistent relative brain mass that we found among our sampled species suggests that this is unlikely.

Future work should measure the brains of the remaining cooperatively breeding lamprologine fishes along with a larger sample of closely related independent breeders. It would also be interesting to examine group-living species that are not cooperative (e.g., *Neolamprologus caudopunctatus* ([Poll, 1978](#)); [Schaedelin et al. 2015](#)) to

disentangle the effect of group living from cooperative breeding per se. Future studies should endeavour to sample females in addition to males, as sex differences in brain size may interact with social system. Finally, exploring how the different brain areas vary in size, complexity, and connectivity between cooperative and independent breeders would also be a natural avenue for future investigation. Specifically, looking at the relative volumes of particular brain areas as a test of the mosaic model of brain evolution would be a worthwhile future direction. The preliminary results that we report here add to the evidence suggesting that cooperative breeding in and of itself may not select for larger brains and supports a skeptical appraisal of the cooperative breeding brain size hypothesis.

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