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Costs of encephalization: the energy trade-off hypothesis tested on birds

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Abstract

Costs and benefits of encephalization are a major topic of debate in the study of primate and human evolution. Comparative studies provide an opportunity to test the validity of a hypothesis as a general principle, rather than it being a special case in primate or hominid evolution. If a population evolves a larger brain, the metabolic costs of doing so must be paid for by either an increased energy turnover (direct metabolic constraint) or by a trade-off with other energetically expensive costs of body maintenance, locomotion, or reproduction, here referred to as the energy trade-off hypothesis, an extension of the influential Expensive Tissue Hypothesis of Aiello and Wheeler (1995, Curr. Anthropol. 36, 199–221). In the present paper, we tested these hypotheses on birds using raw species values, family means, and independent contrasts analysis to account for phylogenetic influences. First, we tested whether basal metabolic rates are correlated with brain mass or any other variable of interest. This not being the case, we examined various trade-offs between brain mass and the mass of other expensive tissues such as gut mass, which is approximated by gut length or diet quality. Only weak support was found for this original Expensive Tissue Hypothesis in birds. However, other energy allocations such as locomotor mode and reproductive strategy may also be reduced to shunt energy to an enlarged brain. We found a significantly negative correlation between brain mass and pectoral muscle mass, which averages 18% of body mass in birds and is indicative of their relative costs of flight. Reproductive costs, on the other hand, are positively correlated with brain mass in birds. An increase in brain mass may allow birds to devote more energy to reproduction, although not through an increase in their own energy budget as in mammals, but through direct provisioning of their offspring. The trade-off between locomotor costs and brain mass in birds lets us conclude that an analogous effect could have played a role in the evolution of a larger brain in human evolution.

Keywords: Expensive Tissue Hypothesis; Brain size; Digestion; Gut size; Reproduction; Locomotion

Introduction

Ever since Darwin, anthropologists have been intrigued by the dramatic contrast in relative brain size between humans and our great ape relatives, as brain size differences are generally thought to underlie differences in cognitive performance. Because general principles have stronger explanatory value than arguments advanced to explain a special case (Cartmill, 2002), comparisons with evolutionary events in other lineages are important to evaluate theories proposed specifically to explain human peculiarities. Variation in relative brain size is increasingly documented among animals of all radiations (e.g., Towe and Mann, 1992; Kotrschal et al., 1998; Marino, 1998; Hutcheon et al., 2002; Iwaniuk et al., 2004; Kohler and Moya-Sola, 2004; Lefebvre et al., 2004) and at all taxonomic levels. For instance, in birds, a relatively very large brain evolved independently in at least six lineages: parrots, hornbills, woodpeckers, owls, pelicans, and corvids (Nealen and Ricklefs, 2001). Comparative tests of hypotheses on brain size evolution have become feasible because powerful tools to conduct comparative studies to remove influences due to a shared phylogenetic heritage of taxa (e.g., Felsenstein, 1985; Garland et al., 1992) have recently become available.

In this paper, we will use comparative data on birds to test various hypotheses for the evolution of brain size. We will now

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review a variety of hypotheses and derive predictions for testing. Unlike most recent ideas (e.g., Dunbar, 2003), these hypotheses focus on the costs of an enlarged brain, as ultimately only net benefit, i.e., benefits minus costs, will determine the selective advantage of a trait. Indeed, if benefits apply more universally across taxa, costs are likely to explain most of relative brain size variation.

An early hypothesis that stressed the energetic costs of increased brain size rather than its adaptive benefits was the direct metabolic constraints hypothesis (Armstrong, 1983; Hofman, 1983). A direct link between basal metabolic rate (BMR) and brain size was postulated based on a similarity of scaling exponents of these parameters to body size. The brain consists of energetically costly tissue (Mink et al., 1981), and thus brain size might be constrained by the total energy budget of a species. A high daily energy expenditure (DEE) is mainly generated by the skeletal muscles, which requires a high level of support by the visceral organs, and thus inevitably results in a high BMR (e.g., in shorebirds, Kersten and Piersma, 1987). Thus, BMR can be used as a predictor of DEE or field metabolic rate. However, the existence of a positive correlation between BMR and brain size, after correcting for body size, is disputed for mammals (Pagel and Harvey, 1988; McNab and Eisenberg, 1989; Martin et al., 2005). McNab and Eisenberg (1989) did not find a significant correlation, but their influential study contained a large number of rodents and a methodological error (Martin, 1998). Martin (1998) found a significantly positive correlation between brain mass and BMR in a more balanced sample of 51 mammalian species, using both raw data and independent contrasts to remove possible influences of phylogenetic non-independence. This hypothesis has not been tested so far for birds.

In any case, humans do not show an increased BMR compared to other primates, whereas their diet is of high energy content and easy to digest (Leonard and Robertson, 1994). A dietary shift toward meat eating in hominins is likely to have occurred roughly at the same time as the major enlargement in brain size. Aiello and Wheeler (1995) proposed the Expensive Tissue Hypothesis (ETH): An animal is able to meet the high metabolic cost of a large brain without incurring a compensatory increase in basal metabolic rate (BMR) by decreasing the amount of other metabolically expensive tissues (i.e., heart, lung, kidney, liver, and gastrointestinal tract). Among these organs, the gastrointestinal tract, being linked to diet (Chivers and Hladik, 1980), is most plastic and most amenable to evolutionary reduction (Konarzewski and Diamond, 1995; Hume and Biebach, 1996; Starck, 1999). In support of their hypothesis, Aiello and Wheeler (1995) found a significantly negative correlation of relative gut mass and relative brain mass in a small sample of anthropoid primates (Fig. 1A). Although this conclusion depends heavily on the details of analysis (Aiello et al., 2001), our re-analysis of this sample using the independent contrasts method confirmed a highly significant negative correlation ($n = 17$ contrasts, $p < 0.001$, $r^2 = 0.596$, see Fig. 1B).

Tests on non-primates are rare. Whereas there is some support in fish (Kaufman et al., 2003), a systematic analysis of bats found that relative brain mass and relative intestine length show a significantly positive correlation, rather than the negative correlation predicted by the ETH (Jones and MacLarnon, 2004). Because reliable data on gut dimensions are difficult to obtain, researchers have sometimes turned to diet quality as a better-documented proxy variable. A possible relationship between relative gut mass and relative brain mass may be reflected in a correlation between diet and brain mass (MacLarnon et al., 1986). In support of the ETH, for instance, Fish and Lockwood (2003) found a positive relationship between diet quality and brain size in 44 primate species, using an index of diet quality calculated from the percent of time spent foraging for leaves, fruit, and meat, respectively. However, a correlation between gut mass or diet quality and brain size could also be due to other factors than the ETH. Frugivory, which in primates is correlated with relatively smaller gut mass than folivory, may favor greater cognitive abilities than folivory (Clutton-Brock and Harvey, 1980; Milton, 1981; McNab and Eisenberg, 1989), or may generate social

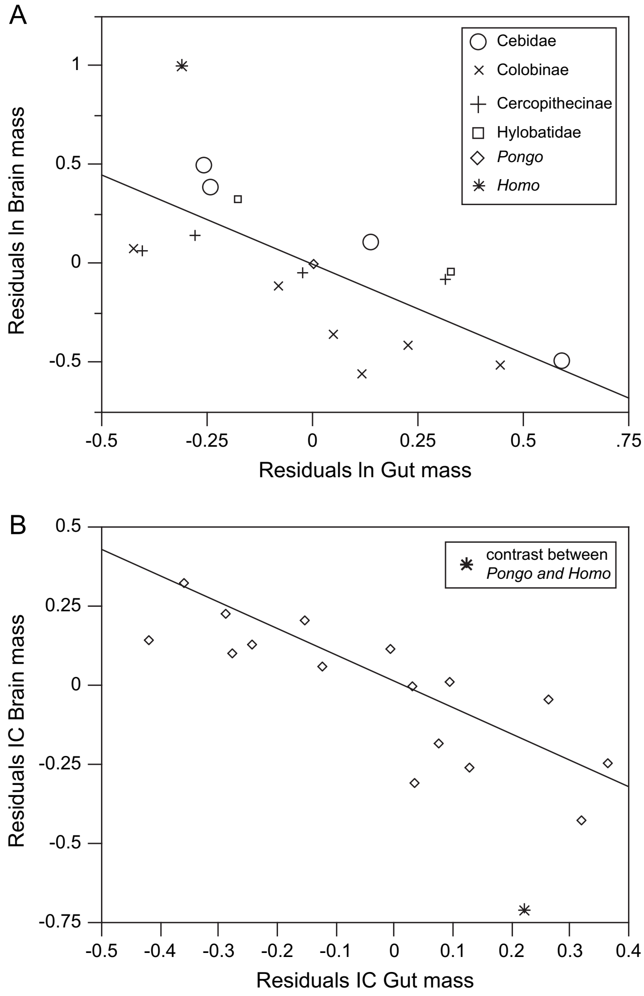

Fig. 1. Bivariate plot of the regression of the residuals of brain mass (y) vs. the residuals of gut mass (x) in anthropoids (data from Aiello et al., 2001). A) raw species values ($\ln(y) = -0.911 \ln(x)$; $n = 18$, $p = 0.002$, $r^2 = 0.476$), B) independent contrasts ($\ln(y) = -0.835 \ln(x)$; $n = 17$ contrasts, $p = 0.0003$, $r^2 = 0.596$).