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Assessing sources of error in comparative analyses of primate behavior: Intraspecific variation in group size and the social brain hypothesis

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ABSTRACT

Phylogenetic comparative methods have become standard for investigating evolutionary hypotheses, including in studies of human evolution. While these methods account for the non-independence of trait data due to phylogeny, they often fail to consider intraspecific variation, which may lead to biased or erroneous results. We assessed the degree to which intraspecific variation impacts the results of comparative analyses by investigating the “social brain” hypothesis, which has provided a framework for explaining complex cognition and large brains in humans. This hypothesis suggests that group life imposes a cognitive challenge, with species living in larger social groups having comparably larger neocortex ratios than those living in smaller groups. Primates, however, vary considerably in group size within species, a fact that has been ignored in previous analyses. When within-species variation in group size is high, the common practice of using a mean value to represent the species may be inappropriate. We conducted regression and resampling analyses to ascertain whether the relationship between neocortex ratio and group size across primate species persists after controlling for within-species variation in group size. We found that in a sample of 23 primates, 70% of the variation in group size was due to between-species variation. Controlling for within-species variation in group size did not affect the results of phylogenetic analyses, which continued to show a positive relationship between neocortex ratio and group size. Analyses restricted to non-monogamous primates revealed considerable intraspecific variation in group size, but the positive association between neocortex ratio and group size remained even after controlling for within-species variation in group size. Our findings suggest that the relationship between neocortex size and group size in primates is robust. In addition, our methods and associated computer code provide a way to assess and account for intraspecific variation in other comparative analyses of primate evolution.

1. Introduction

Comparative analyses have played an important role in studies of primate and human evolution (Harvey and Pagel, 1991; Nunn, 2011). These analyses examine interspecific variation between different traits to infer adaptation, using species as the units of analysis. Because species are products of the evolutionary process and share traits via common descent, however, they cannot be considered as independent data points for statistical purposes (Felsenstein, 1985). As a consequence, evolutionary biologists have developed several procedures to control for phylogenetic non-independence (Nunn, 2011; Garamszegi, 2014a). The development and adoption of these techniques have increased the impact of comparative methods, but they make several important assumptions. One relatively neglected assumption concerns intraspecific variation. Specifically, most comparative methods assume that the entire range of variation in a trait of interest can be represented by a single data point, the species

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average (Garamszegi and Møller, 2010). Thus, variation around that value—due to measurement error, differences in sample size, or biologically relevant within-species variation—is typically ignored (Garamszegi, 2014b).

Ignoring within-species variation may lead to biases and spurious results in phylogenetic comparative analyses. For example, simulations revealed that failure to account for intraspecific variation can lead to a high Type I error rate (Harmon and Losos, 2005; Felsenstein, 2008; Silvestro et al., 2015). In cases where within-species variation exceeds between-species variation, it may be inappropriate to use mean values to represent an entire species in interspecific comparisons. This is of particular importance in studies of primates, given the considerable variability exhibited within species. This has long been noted as a concern in comparative studies of primates. For example, Strier (2003: 5) stated that, "the compression of intraspecific variation in any behavioral trait into a single, species-specific value precludes interspecific comparisons…". Similarly, Struhsaker (2000: 119) warned that there is a "need to better understand interpopulational and intraspecific variation […]. Until this level of variation is understood and taken into consideration, broad interspecific comparisons and generalizations are misleading, if not counterproductive, in furthering the field of behavioral ecology".

In addition, relying on small sample sizes may lead to poor quality data for traits that show high within-species variation (Garamszegi and Møller, 2010). Attention to the quality of data is a growing concern in comparative studies (Borries et al., 2013; Patterson et al., 2014). Sample size and variability are also salient issues in the study of hominin evolution and taxonomy. A small number of specimens, often quite variable due to biases in preservation (Behrensmeyer and Kidwell, 1985), may serve as the basis for inferences for an entire population (Wood and Lonergan, 2008). It is therefore crucial to interpret the hominin fossil record with methods that account for small sample size and accurately assess variation both within- and between-species.

Some comparative methods provide a way to incorporate intraspecific variation into analyses (Martins and Hansen, 1997; Ives et al., 2007; Felsenstein, 2008; Revell and Reynolds, 2012; Garamszegi, 2014b), but such analyses are rarely carried out in practice (Garamszegi and Møller, 2010). In many cases, data on intraspecific variation are unavailable. Even when such data are available, few studies have attempted to quantify the amounts of interspecific and intraspecific variation in traits being compared. The default procedure assumes that no within-species variation exists. The effect of ignoring intraspecific variation in comparative analyses has been studied for only a few systems, predominantly relying on simulated rather than actual data (Harmon and Losos, 2005; Ives et al., 2007; Felsenstein, 2008; Hansen and Bartoszek, 2012). Researchers have only recently begun to assess intraspecific variation in a comparative context (e.g., Kamilar and Baden, 2014; Pap et al., 2015).

Group size in primates provides an example of the issues raised above and is the focus of this paper. Group size is a commonly employed variable in comparative studies of primates and other animals, as this trait is hypothesized to play a central role in the evolution of feeding ecology (Wrangham et al., 1993; Janson and Goldsmith, 1995), social relationships (Sterck et al., 1997; Lehmann et al., 2007), parasitism (Nunn et al., 2003; Rifkin et al., 2012), predator defense (Janson and Goldsmith, 1995; Hill and Lee, 1998), and complex cognition and large brains (Deaner et al., 2000; MacLean et al., 2013). Group size features prominently in tests of the social intelligence and social brain hypotheses, which suggest that, among primates, a selective premium is placed on the cognitive abilities of individuals who must manage relationships with multiple conspecifics in large groups (Chance and Mead, 1953/1988; Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Dunbar, 1992). Support for the social brain hypothesis comes from several studies showing that neocortex size is positively correlated with group size across primate species (Sawaguchi and Kudo, 1990; Dunbar, 1992; Sawaguchi, 1992; Dunbar and Shultz, 2007). Understanding the evolution of large brains and complex cognition is a major question in the study of human evolution; thus, understanding the nuances of the analyses that underlie the social brain hypothesis is critically important for evolutionary anthropology.

The aforementioned studies used single values of group size to represent an entire species. This practice assumes that negligible variation exists in group size, yet this trait is known to vary considerably within primate species (Struhsaker, 2000; Mitani et al., 2012; Patterson et al., 2014; Strier et al., 2014). In chimpanzees, for example, communities range in size from approximately 20 to 200 individuals (e.g.,Wilson et al., 2014), yet in one widely cited paper analyzing the relationship between neocortex size and group size, this variability is collapsed into a single value, 53.5 (Dunbar, 1992). While a species mean may accurately reflect the situation in solitary and socially monogamous primates where the only source of variation in "group" size is due to offspring being born and dispersing at maturity, a species mean is likely to conceal biologically meaningful variation for primates living in larger social groups (Kamilar and Baden, 2014; Patterson et al., 2014).

In this paper, we investigated the degree to which intraspecific variation in group size influences comparative tests of the social brain hypothesis in primates. First, we examine whether between-species variation in group size exceeds the variation found within species. To do this, we estimate within-species "repeatability" in group size in terms of the amount of interspecific variability in traits being analyzed in comparative studies relative to the total amount of variation in the data (Sokal and Rohlf, 1981; Nakagawa and Schielzeth, 2010). If repeatability is high (i.e., approximates 1), then most of the variation is due to differences between species. In contrast, when repeatability is low, considerable variation exists within species. When between-species repeatability is low, controlling for intraspecific variation becomes particularly important for comparative studies (Harmon and Losos, 2005).

Next, we implemented a regression method to control for intraspecific variability in the estimates of group size when analyzing the relationship between group size and neocortex ratio (Ives et al., 2007). Using a generalized linear model, this method uses as input the means for each species and the variance or standard errors around the mean. It then estimates parameters of the linear model, taking intraspecific variation into account.

Finally, we employed a resampling procedure to assess how different estimates of group size affect the relationship between neocortex ratio and group size. For this, we treated each within-species group size value as a potentially true value, using resampled values iteratively in statistical tests analyzing the association between neocortex ratio and group size. If within-species variation has negligible effects on the results of the comparative analysis, different group size values should produce little variance in the parameter estimates of different regression models. We also compared results from this analysis to a test of phylogenetic uncertainty, or error due to different probable phylogenies, as this is another source of variation that is more commonly assessed in comparative analyses (Pagel and Lutzoni, 2002; Arnold et al., 2010).

2. Materials and methods

2.1. Data collection

We collected brain size and group size values from the published literature for the same 26 monkey and ape species included