



Does geography or ecology best explain ‘cultural’ variation among chimpanzee communities?

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ABSTRACT

Much attention has been paid to geographic variation in chimpanzee behavior, but few studies have applied quantitative techniques to explain this variation. Here, we apply methods typically utilized in macroecology to explain variation in the putative cultural traits of chimpanzees. We analyzed published data containing 39 behavioral traits from nine chimpanzee communities. We used a canonical correspondence analysis to examine the relative importance of environmental characteristics and geography, which may be a proxy for inter-community gene flow and/or social transmission, for explaining geographic variation in chimpanzee behavior. We found that geography, and longitude in particular, was the best predictor of behavioral variation. Chimpanzee communities in close longitudinal proximity to each other exhibit similar behavioral repertoires, independent of local ecological factors. No ecological variables were significantly related to behavioral variation. These results support the idea that inter-community dispersal patterns have played a major role in structuring behavioral variation. We cannot be certain whether behavioral variation has a genetic basis, is the result of innovation and diffusion, or a combination of the two.

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Introduction

The question of animal ‘culture’ has been the subject of numerous studies during the last several years (Whiten et al., 1999; van Schaik et al., 2003; Laland and Janik, 2006; Laland and Galef, 2009). Chimpanzees have been the focus of much of this research, due to their importance for understanding the evolution of human behavior (Lycett et al., 2009; Whiten et al., 2009; McGrew, 2010; Langergraber et al., 2011). Whiten et al. (2001) published a seminal paper documenting an extensive dataset of chimpanzee behaviors that varied across long-term field sites. The authors argue that much of the across-site behavioral variation exhibited by chimpanzees is cultural, because there is no clear relationship between environmental characteristics and numerous behavioral traits. They suggest that finding a relationship between behavioral and environmental characteristics may demonstrate an adaptive explanation for behavioral variation, reducing the ability to assert social learning until additional evidence is available. This

‘exclusion approach’ to invoking a cultural basis for behavioral variability has also been used in other vertebrate studies (Perry and Manson, 2003; van Schaik et al., 2003).

There are two potential weaknesses with this approach. First, as eloquently stated by Laland and Janik (2006), finding a relationship between environmental characteristics and behavioral traits does not, in and of itself, preclude these traits from having some learned basis. In fact, novel environmental conditions may generate novel behaviors that are socially learned. Second, previous attempts to draw a connection between environmental and ‘cultural’ variation in chimpanzees have been largely descriptive in nature, with a rigorous analytical approach being absent from the literature (but see Lycett et al., 2009). Most quantitative analyses have focused on the relationship between ‘culture’ and phylogeny/genetics (Lycett et al., 2007, 2009; Langergraber et al., 2011).

Lycett et al. (2007) utilized a comparative phylogenetic approach to examine whether geographic variation in chimpanzee behavior was genetically based. They compared phylogenies constructed from behavioral traits to those based on genetics using single and multiple subspecies. They found that the behavioral phylogeny using multiple subspecies did not show more structure compared with one using a single subspecies, which suggested that

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there is no genetic basis for chimpanzee behavioral variation. Therefore, the authors argued that these behaviors are culturally based. In a subsequent paper, [Lycett et al. \(2009\)](#) conducted additional phylogenetic analyses that supported their prior finding of a weak genetic effect on chimpanzee cultural diversity. They also examined whether cultural traits were adapted to the local environment. Using data from eastern and western chimpanzee communities, they found little relationship between mean rainfall and behavioral repertoires. In contrast, a recent study by [Langergraber et al. \(2011\)](#) used a non-phylogenetic approach to examine the relationship between genetics and cultural variation across chimpanzee communities. Using correlation analyses, they found a significant relationship between genetic dissimilarity and behavioral dissimilarity among chimpanzee groups in different communities. However, few individual behavioral traits were highly correlated with genetic distance. Neither of these studies simultaneously examined the potential effects of local ecology and geography on chimpanzee cultural variation.

The horizontal transmission of behavioral traits across sites may result from geographic variables most strongly related to behavioral variation. This is often observed in studies of human material culture, with sites in close proximity to each other exhibiting similar cultural repertoires irrespective of other factors ([Welsch et al., 1992](#); [Jordan and Shennan, 2003](#)). In orangutans, [van Schaik et al. \(2003\)](#) found a negative relationship between the geographic distance among sites and putative cultural similarity. They also tested the potential relationship between habitat type and cultural similarity, but did not find significant effect. [van Schaik et al. \(2003\)](#) argued that their findings were best explained by an innovation and diffusion process. Traits originate in a particular site and then diffuse across a region due to individuals dispersing from one locality to another. Individuals take their behavior repertoires with them to the new locality and some proportion of these traits are then learned by the existing members of the community.

Our study builds on previous research by investigating the relative importance of geography and local ecology for predicting variation in the putative cultural traits of chimpanzees at a continental scale. Examining both of these effects simultaneously is important because they are often correlated. Study sites in close proximity to each other tend to have relatively similar habitat structure ([Kamilar, 2009](#); [Kamilar and Muldoon, 2010](#)). We employed an approach typically utilized in macroecological studies to examine spatial variation in the distribution of species ([Cleary and Genner, 2006](#); [Kamilar, 2009](#)). An analogous scenario is present when examining variation in the 'cultural' repertoires of chimpanzees. Instead of being interested in explaining the abundance of species at a site, we are interested in explaining the frequency of behaviors at a site. Our paper also serves as correction to our recently retracted study ([Kamilar and Marshack, 2011](#)), which contained several coding errors in the dataset.

Material and methods

Data collection

We used the previously published putative cultural variant dataset from [Whiten et al. \(2001: Table 3\)](#). These 39 traits were quantified from eight locations, comprising nine different communities where long-term fieldwork has been done: Assirik, Bossou, Tai, Lope, Mahale M, Mahale K, Gombe, Kibale, Budongo. [Whiten et al. \(2001\)](#) created an ordinal scale for the frequency of behaviors at each site, from least to most frequent: absent, present but not-habitual or customary, habitual, and customary. We coded these frequencies from 0 to 3 for analysis (SOM). In addition, some traits, especially at Assirik and Lope, were originally designated by

[Whiten et al. \(2001\)](#) as occurring in unknown frequencies. Therefore, we conducted our analyses using two versions of the dataset to account for the possible effects of 'unknown' trait frequencies. In one analysis, we treated all of the unknowns as absent and treated all unknowns as present in a second analysis.

For each study site, we obtained data for two geographic variables, latitude and longitude, and four environmental variables: 1) maximum mean monthly temperature, 2) minimum mean monthly temperature, 3) mean annual rainfall, and 4) rainfall seasonality. Rainfall seasonality was defined as the circular statistic 'r', based on the mean vector of rainfall throughout the year ([Batschelet, 1981](#)). These data were acquired from published literature and supplemented by WorldClim GIS climate database ([Hijmans et al., 2005](#)). All environmental variables were natural log transformed before analysis.

Our environmental variables are commonly used in comparative ecology research of primates, including research examining cultural variation. Variables such as rainfall and temperature are directly related to habitat characteristics, including the diversity, abundance, and availability of food and water resources ([Rosenzweig, 1968](#); [Murphy and Lugo, 1986](#); [Bronikowski and Altmann, 1996](#); [Chapman and Chapman, 1999](#); [Andrews and O'Brien, 2000](#)), which in turn impact primate behavior and ecology ([van Schaik, 1989](#); [Sterck et al., 1997](#); [Doran et al., 2002](#); [Koenig, 2002](#)). Several behavioral ecology studies have demonstrated a relationship between quantitative proxies of habitat characteristics (i.e., rainfall and/or temperature) and behavior (*Eulemur*: [Ossi and Kamilar, 2006](#); *Baboons*: [Bronikowski and Altmann, 1996](#); *Chimpanzees*: [Doran, 1997](#); *Japanese macaques*: [Ventura et al., 2005](#)). For studies examining cultural variation in particular, [Lycett et al. \(2009\)](#) used mean annual rainfall as their only environmental variable to examine chimpanzee cultural variation. In addition, [van Schaik et al. \(2003\)](#) did not use quantitative measures of climate/ecology, but instead used gross classifications of habitat type when examining the possible connection between ecology and orangutan cultural traits. Finally, [Jordan and Shennan \(2003\)](#) quantified ecological zones (based partly on climate data) to test whether ecology influenced the geographic variation of Californian Indian material culture.

Data analyses

Previous studies examining geographic variation in the 'cultural' repertoires of chimpanzees and orangutans have used Mantel tests (e.g., [van Schaik et al., 2003](#)). This method transforms behavior and site location data into dissimilarity/distance matrices (e.g., 'cultural' dissimilarity, geographic distance). Instead of using distance matrices, a canonical correspondence analysis (CCA) using the raw data can be performed. CCA is preferred because it has greater statistical power due to the use of the raw data, as opposed to distance matrices ([Legendre, 2000](#); [Legendre et al., 2005](#)). Also, CCA provides detailed results about the relationships between each predictor variable (e.g., geography and local ecology) and the frequency of 'cultural' variants in both numeric and visual formats through biplots ([Gower and Hand, 1995](#)). These results are not available through Mantel tests. In sum, the CCA uses a set of independent variables (e.g., environment and geography) to predict a set of dependent variables (e.g., behavioral traits) while accounting for covariation within and between each dataset. This allowed us to examine the relative importance of environmental and geographic variables for explaining behavioral variation. An analytical method accounting for covariation among variables is critical because there is often some degree of covariation among environmental variables, and perhaps more importantly, between environmental and geographic variables ([Borcard et al., 1992](#);

Diniz-Filho et al., 2003). Not accounting for the relationship between ecology and geography has been a weakness of previous analyses examining geographic variation in chimpanzee behavior.

Independent variables were entered into the model in a forward stepwise fashion beginning with the variable with the lowest p value. Statistical significance was calculated by a permutation approach utilizing 999 iterations. All CCAs were conducted with CANOCO (ter Braak and Smilauer, 2002).

Results

In our initial CCA analysis, we found that only longitude approached statistical significance for predicting chimpanzee 'cultural' traits ($p = 0.057$). This was based on the dataset coding all unknowns as absent. We produced a biplot of these results to better visualize the relationships among behavioral traits, and between predictor variables and individual behavioral traits (Fig. 1) (see SOM for the behavioral codes used in the biplot). When we visually inspected the biplot, we found that one trait, Branch din (trait 39),

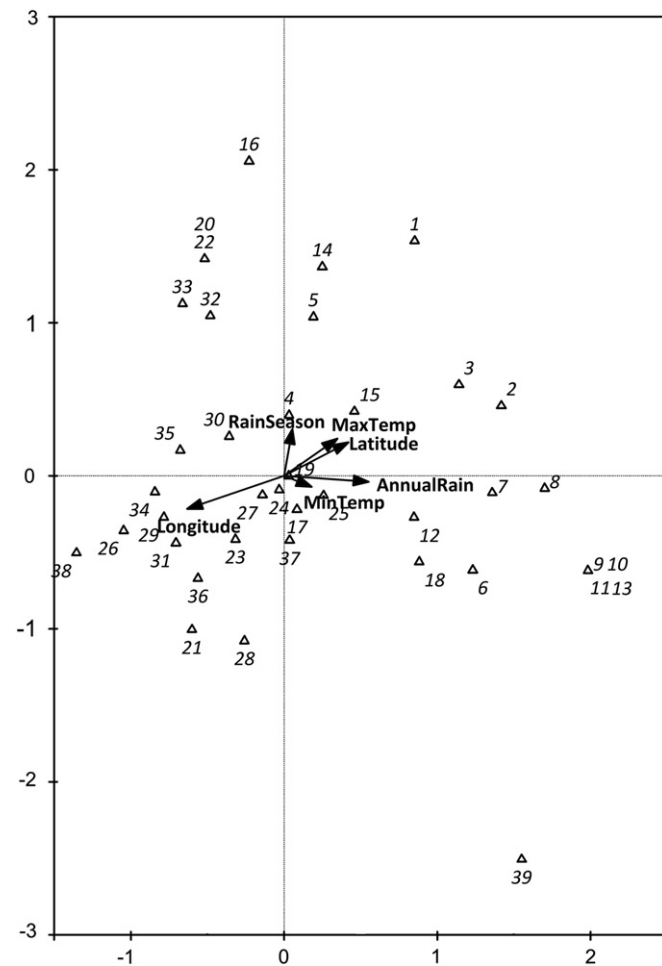


Figure 1. Biplot displaying the relationship between predictor variables and the frequency of chimpanzee 'cultural' traits. Independent variables are displayed as vectors, with the length and direction of the vector indicating the importance of the variable for predicting 'cultural' variation. Traits towards the centroid of the biplot are poorly predicted by any variable. Traits with a large magnitude (i.e., far from the centroid) and along or near the vector of an independent variable are well predicted and positively correlated with that variable. Traits that are in a perpendicular plane to an independent variable's vector are poorly predicted by those particular variables. Behaviors are designated as numbers, with codes defined in the electronic supplement. We consider trait 39 an outlier (lower right quadrant) because it is far outside the distribution of the other traits.

appeared to be an outlier. Re-analyzing the data without this trait yielded a statistically significant effect of longitude ($p = 0.031$), independent of ecology, on behavioral variation. In addition, neither latitude, nor any ecological variables were strong predictors of chimpanzee behavioral traits (Table 1). These results demonstrate that chimpanzee communities in close longitudinal proximity to each other share more behavioral traits in common with each other compared with distant communities, and this is independent of local ecological effects. We found qualitatively similar results in our second set of analyses using a dataset with unknowns coded as present. Longitude was the only statistically significant predictor variable in an initial analysis ($p = 0.043$), as well as a subsequent analysis with one outlier removed ($p = 0.041$). We only present the details of our first set of analyses for brevity.

Interestingly, longitude was not related to a specific class of behaviors. Some behaviors that were closely linked to longitude are related to processing food resources, such as the more frequently observed Nut-hammer, stone hammer on stone anvil and Ant-dip single behaviors in western communities. Yet, many other behaviors that are linked to food acquisition/processing are not related to longitude, such as Food-pound onto wood or Termite-fish using leaf midrib. Other traits that are correlated to longitude are less easily categorized, such as Leaf-groom and Leaf-inspect.

Discussion

We found that geographic variation in the behavioral repertoires of chimpanzee communities is best explained by longitude, not local ecology. Communities that are in closer longitudinal proximity to each other are most behaviorally similar, with behavioral similarity decreasing with increasing longitudinal distance. At the broadest scale, longitudinal variation corresponds with different chimpanzee subspecies. Yet this pattern likely occurs within subspecies as well, considering our dataset contains several communities within a single subspecies.

Our results demonstrate a pattern of 'cultural' variation in a geographic context that is likely due to individuals dispersing from one community to another through time. Inter-community dispersal may be relatively easy on a small spatial scale and within an individual's lifetime, but may also occur at greater spatial scales in deeper time. For instance, there are genetic signatures of long-range gene flow distances in excess of 900 km (Morin et al., 1994). It is not difficult to imagine that large dispersal distances are possible through evolutionary time. Chimpanzees are distributed along a greater longitudinal extent (from approximately 31.1 to -15.5° longitude) compared with a latitudinal one (from approximately 13.1 to -8.7° latitude) (Jones et al., 2009). This distribution likely has been relatively consistent in the past considering that the three most commonly recognized chimpanzee subspecies, *Pan troglodytes verus*, *Pan troglodytes schweinfurthii*, and *Pan troglodytes troglodytes* are found in non-overlapping longitudinal ranges. Therefore, the path that cultural and/or genetic

Table 1

Results from the canonical correspondence analysis predicting behavioral variation across chimpanzee communities.^{a,b}

Predictor variable	F Ratio	p value
Longitude	1.480	0.031
Latitude	1.140	0.366
Mean annual rainfall	0.890	0.449
Rainfall seasonality	1.090	0.370
Mean minimum temp.	1.250	0.295
Mean maximum temp.	1.100	0.378

^a 999 permutations were used to assess statistical significance.

^b Results are presented without the outlier trait, Branch din.

diffusion occurs is mostly along a longitudinal direction. Although individual dispersal patterns may be responsible for a geographic distance effect, we cannot be sure of the specific mechanism driving geographic variation in behavior.

One explanation for this pattern is the innovation and diffusion of behavioral traits across the geographic range of chimpanzee communities. Numerous studies in captivity and in the wild have documented the importance of local innovation and social transmission within and across chimpanzee groups. For example, in the wild, Lonsdorf (2006) showed that a chimpanzee's termite-fishing proficiency is dependent on learning from their mother. A study by Humle (2010) found a similar pattern in ant-dipping behavior at Bossou. Detailed studies of captive chimpanzees have demonstrated that social knowledge can be accurately transmitted across several individuals (Horner and De Waal, 2009) or across different groups (Whiten et al., 2007). Horner and De Waal (2009) conducted a study that taught one individual per group an alternative method of obtaining food from an experimental apparatus. When these 'innovators' returned to their respective group, other group members more frequently adopted their group-specific method compared with the alternative one. Their study demonstrated that behavioral innovation and diffusion within a group may lead to behavioral repertoire differences among groups. This same phenomenon may also produce a homogenizing effect across the behavioral repertoires of groups. Whiten et al. (2007) found that alternative foraging behaviors that originated in separate groups eventually spread within, and then in a serial fashion across groups with a high degree of accuracy. Considering these studies, it is reasonable to believe that the importance of innovation and diffusion may also affect behavioral variation at greater spatial scales, provided enough time has elapsed.

At large spatial scales, similar patterns have been demonstrated in studies focusing on human material culture. Jordan and Shennan (2003) found that geographic variation in material culture of Californian Indians was best predicted by geography, with little ecological effect using a similar analytical approach to our current paper. In addition, the importance of geography has also been observed in an earlier study of orangutan behavioral variation (van Schaik et al., 2003). The importance of social learning for generating the observed geographic patterning of 'cultural' variation may be a shared characteristic of great apes and humans.

We cannot completely dismiss the idea that the horizontal transmission of behavioral traits may have a genetic basis. Langergraber et al. (2011) showed a relationship between genetic distance and 'cultural' distance across chimpanzee study sites. Although, Langergraber et al. (2011) did not specifically investigate the effect of geography, there is a good concordance between geographic and genetic distance among chimpanzee populations (Becquet et al., 2007). The difficulty of disentangling this relationship is the basis for one of the main criticisms of Langergraber et al. (2011), recently published in Lycett et al. (2011) and Whiten (2011). In addition, it is important to note that previous studies of orangutans and chimpanzees did not account for the potential confounding effects of geography and ecology.

An earlier study that only investigated the effect of mean annual rainfall on the putative cultural variation across chimpanzee communities (Lycett et al., 2009) supports our more detailed analysis. Although we did not find a strong ecological effect on chimpanzee behavior, our measures of climate, and consequently habitat, have been found to influence several aspects of behavior and biology in other primate studies (van Schaik et al., 2005; Ossi and Kamilar, 2006; Kamilar, 2009). For chimpanzees in particular, previous researchers have suggested that communities with decreased sociality and increased rates of infanticide may be the result of increased fruit availability seasonality, which is driven by

increased rain seasonality (Doran et al., 2002). Of course, we do not dismiss the possibility that analyzing additional ecological characteristics may provide different results to ours. For example, Schöning et al. (2008) found that geographic variation in some tool construction and foraging style behaviors were linked to differences in the biology of ant prey species. In addition, the interaction between micro-ecological variation and social learning was demonstrated by Humle et al. (2009). The acquisition and proficiency of ant-dipping by immature chimpanzees at the Bossou community was influenced by the number of learning opportunities from their mother. In turn, mothers with infants ant-dipped at trails more frequently than at ant nests, which reduced the risk of injury from the biting ants. The somewhat discordant findings between our research and these fine-scaled studies nicely illustrate that behavioral and ecological patterns may vary at different scales of analysis. Additional research integrating a variety of datasets is needed to better understand the mechanisms generating behavioral diversity.

In terms of better understanding the comparative behavior of chimpanzees, we feel that there are interesting avenues of research that can be explored in the future. The currently published dataset for chimpanzee putative culture is extensive, yet far from exhaustive. Increasing the size of the dataset, both in terms of sampling more study sites and recording additional behaviors will enhance our ability to conduct rigorous quantitative analyses with high statistical power. Recent studies of chimpanzees in the wild have already provided new insights into their behavioral diversity (Sanz and Morgan, 2007). An important analysis that would be more feasible with a larger dataset is a detailed investigation of the factors associated with variation in specific types of behavior, e.g., food acquisition and processing versus communication. It would be a logical expectation that different behavior types are related to ecological and geographic factors in different ways. For example, behaviors related to food acquisition and processing may be closely tied to micro-habitat structure and the availability (or unavailability) of local dietary resources.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jhevol.2011.11.008.

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