

Statistical analysis of the distribution of modern primates: a comparative approach to the spatial analysis of the Palaeolithic

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Abstract: Palaeolithic archaeology is concerned with the analysis of hominid geographical ranges (the extent of a species distribution) as they change over time. Interpretation focuses on the cultural evolution of social and technological adaptations that permitted hominids to extend those ranges, and the environmental factors that ultimately limited them. Spatial analysis of modern primate range maps provides the opportunity to characterize the behavioural traits that favour range expansion and the environmental variables that limit it in the primate order in general. A comparative study of primate distribution in relation to physical and behavioural characteristics and environmental factors was conducted using GIS and statistical techniques. This paper will cover the methodology of comparative spatial analysis, and the potential archaeological application of the results.

Key words: Biogeography, GIS, human evolution, primates, quantitative methods.

Introduction

The overall subject of my research is to investigate large-scale patterns in the distribution of early hominid species in sub-Saharan Africa. The scientific aim is to increase our understanding of the limiting factors that constrained hominid distribution in the past, and of their effects on the probabilities of speciation and extinction. The geographical distribution of hominid species is an important factor in human evolution, and analysis of spatial patterns can help us to understand evolutionary processes affecting hominids. In addition, changes in distribution may be related to changes in behaviour which are of crucial interest to students of human origins. For example, one explanation for the first expansion out of Africa by *Homo erectus* is based on an increase in brain size and associated intensification of social processes and behavioural flexibility. Thus patterns in the geographical distribution of hominid species are of great interest to archaeologists attempting to reconstruct hominid behaviour.

In order to interpret patterns in hominid distribution, we need models of the way in which distribution processes are influenced by environmental variables and species characteristics. The science of biogeography has a theoretical framework and a methodology for interpreting spatial patterns in distribution. Modern primates provide data on distribution patterns in an order of species that shares some characteristics with the hominid lineage. In this paper I will discuss the theory, method and results of a comparative analysis of primate biogeography. The aim of this analysis is to identify characteristics shared by widely distributed primate species. The relationship between variables across a range of taxa can be used to test predictions about adaptation. Thus such a comparative analysis can increase our understanding of the evolutionary and ecological processes that have shaped modern primate distribution. It is hoped that the patterns and processes identified in this analysis can be

extrapolated back in time, and evidence for or against their effects sought in the hominid fossil and archaeological record.

Discussion

Human origins and spatial distribution

Temporal variation in the geographical distribution of hominid species has implications for our understanding of evolutionary processes in human evolution. Geographical distribution has an important role in the changes leading to speciation (Foley, 1999). Geographical processes such as population dispersals and contractions, fragmentation and isolation of populations in response to the appearance of a geographical barrier, and shifting habitat boundaries result in altered selective pressures, different demographic parameters, and changes in gene flow or discontinuity (Foley, 1987). Thus the geographical distribution of early hominid species provides important evidence for the evolutionary processes that shaped human evolution.

A number of mechanisms have been proposed as driving forces in human evolution: climate change (Vrba, 1985) and variability (Potts, 1998), and competition between species (Foley, 1999). Alternatively it has been suggested that behavioural innovation may itself act as a catalyst for further evolution (Wilson, 1985). An investigation of the temporal patterns in the distribution of hominid species, and the selective pressures and adaptation associated with changes in distribution, could be used to clarify causal factors in human evolution.

There is evidence for hominid range expansion over time, possibly in the period 4-1.8 my ago among the australopithecines and early *Homo*, and certainly after 1.8 my ago with the appearance of *Homo erectus*, the first hominid species to move out of Africa. Spatial variation in hominid geographical ranges

requires explanation in terms of both external limiting factors and species' characteristics.

The human brain is uniquely large among primates, and substantial increases in brain size occurred at various stages in human evolution. Potts (1998) has suggested that increasing brain size could be a variability-selected characteristic that would increase the flexibility of responses to climate change. Variability selection is a form of natural selection that arises when a period of time is characterised by increasing fluctuations in climate and environmental change (Potts, 1998). Large brain size and behavioural flexibility in other species has been linked to colonisation success (Sol and Lefebvre, 2000). Thus we might predict a general relationship between environmental tolerance, range expansion, brain size and behavioural flexibility in hominids. Furthermore, it has been suggested that behavioural innovation may act as a selective pressure (Wilson, 1985). A change in the processes affecting human evolution might also accompany brain expansion.

A number of specific changes in behaviour associated with brain expansion could have been useful in colonization. Possibilities include risk assessment via intensification of social processes (Gamble, 1993), flexible responses to environmental variability (Potts, 1998), and the ability to maintain a broader dietary niche via more innovative foraging behaviour.

According to Gamble (1993), the key to range expansion for primate species was the investment in behaviours that would not only select and alter the environments they and their offspring inhabit, but also gather knowledge about it. At a local level this behaviour would be useful in weathering climatic variability; however such an ability to gather information would also aid successful migration (Gamble, 1993). Migration is based on an assessment of risk, which can be carried out through physiological or conscious processes. The area an individual animal can assess is finite; social life provides the framework for evaluation and dissemination of information from a wider area. By increasing a population's knowledge of the environment, social learning will therefore increase chances of making an accurate assessment (Gamble, 1993). Such social frameworks would have been particularly useful as hominids entered more seasonal environments (Gamble, 1993).

However an increase in brain size has high metabolic costs. Aiello and Wheeler (1995) have suggested that these costs were met by a corresponding reduction in gut size, requiring a change to a higher quality diet. The limited modern distribution of the great apes may be due to the high dietary requirements of large brained species (Richard, 1985). One way of improving dietary quality would have been by increasing the intake of meat. It has been suggested that hominid expansion out of Africa corresponded with the opening of a new, carnivorous dietary niche (Turner, 1992). Aspects of this change in diet and the behaviour involved could have affected *H. erectus*' dispersal ability. Prey species may have provided a crucial resource in more seasonal, colder and northern environments (Turner, 1992). Finally, increased meat eating could have added to pressures favouring range expansion. Carnivorous species tend to have a lower population density than their prey, and Walker (1996) has suggested that *H. erectus* populations may have

colonized new areas partly in order to meet this requirement.

Finally, there is considerable variation in mammal life histories, and humans are notable for their long period of maturation and adult lives (O'Connell et al., 1999). Attempts have been made to explain the evolution of life history traits with reference to climatic variability. According to K and r theory (MacArthur and Wilson, 1967), stable non-seasonal environments are predictable and therefore favour individuals that devote a lot of energy to a few offspring at a time. Such K selected individuals tend to invest in behaviour to buffer the effects of environmental pressure. By contrast, unpredictable environments favour individuals that produce large numbers of offspring early in life and have efficient dispersal mechanisms (r selection). Like their closest relatives (the Great Apes), the hominids display an extreme form of the K selected pattern. Data from brain and body size and dental eruption sequences indicates that longevity was increased and maturity delayed in *H. erectus* relative to the Great Ape and earlier hominid pattern (O'Connell et al., 1999). In general, the more long-lived and slow maturing species of primates are not the most widely distributed. This may be partly because populations with a few, slowly developing young are more vulnerable to the increased environmental variation found at higher latitudes.

There is some evidence that even at early periods hominids were not subject to the limitations on geographical distribution operating on primate species with similar life history and relative brain size characteristics (Jablonski et al., 2000). Ecological flexibility may have been of great importance in this pattern. However the existence of a demographic and social structure allowing a flexible reproductive rate would remove some of the constraints set by slow developing young. Flexibility in the rate of reproduction could be achieved by introducing an element of choice as to whether the mother or another member of the group took care of infants and young children. For example, according to the Grandmothering hypothesis, changes in the *H. erectus* life history pattern included increased survival of post-menopausal women, who would have been able to provision their daughters' children (O'Connell et al., 1999). This would have allowed a more flexible response to climatic variability, and could also have been useful in range expansion. The change in life history in *H. erectus* has been linked to an ability to expand their range, especially into arid areas where children could not successfully provision themselves (O'Connell et al., 1999).

Comparative studies

Biogeography is the science of the distribution of living things. Comparative, quantitative biogeographical studies reveal empirical patterns of interspecific variation in the sizes, shapes, boundaries, and internal structures of geographic ranges (Brown et al., 1996). The geographical range of a species is the total extent of its distribution. Analysis of these patterns contributes to an understanding of the historical and ecological processes that influence the distribution of species (Brown et al., 1996). Models of how these processes interact to produce distribution patterns could help us understand the mechanisms behind hominid distribution. The biogeographical literature is an important source of theory and methodology for this analysis.

Biogeographers study the distribution of individual species in detail, or look for general patterns and rules through quantitative study of large numbers of species. Comparisons among species are frequently used to test hypotheses of how organisms are adapted to their environment. The comparative method is the most general technique for asking questions about common patterns of evolutionary change (Harvey and Pagel, 1991). Hypotheses of adaptation lead to predictions of correlated evolution between the presumed adaptive character and the proposed cause (Purvis and Rambaut, 1995). Comparative studies identify evolutionary trends by comparing the values of variables across a range of taxa. The comparative method is employed here in an attempt to explain the evolutionary processes shaping modern primate geographical ranges.

Size is one characteristic of a species geographical range that appears to reflect the influences of environmental limiting factors and dispersal. Within orders or families of species, range size can vary by several orders of magnitude. Recent studies have shown that this variation is associated with variation in a number of other factors. Geographical range size decreases with decreasing latitude and decreasing elevation (Brown et al., 1996). This is known as Rapoport's rule, although the degree to which it constitutes an ecological rule is under debate (Gaston et al., 1998), and orders of species vary in the extent to which they conform. For example, the geographical ranges of African primates show a latitudinal gradient south but not north of the equator (Cowlshaw and Hacker, 1997). Species richness tends to increase with decreasing latitude, and this pattern has been linked to Rapoport's rule (Stevens, 1989). There are significant correlations between range size and both body mass and some measure of average population density (Brown et al., 1996). This pattern is complicated by the relationship between body mass and abundance. A triangular relationship between body mass, population density and range size, based on niche breadth, has been demonstrated for primates (Eeley and Foley, 1999).

In addition, the geographical ranges of primate species tend to increase with climatic variability and niche breadth (Cowlshaw and Hacker, 1997, Eeley and Foley, 1999). It has been suggested that species at higher latitudes must be able to tolerate a greater range of climatic conditions in order to persist at a site (Stevens, 1989). Ecological flexibility allows these organisms to spread across a wider range of habitats, and thus expand their geographical range. Thus Rapoport's rule (and its exceptions) can be explained with reference to the selective effects of climatic variability. In hominids, niche breadth has been linked to increased independence from environmental pressure, and lowered restrictions on ranges (Vrba, 1985).

The biogeography literature highlights a number of interesting patterns in the distribution of species. However it should be noted that there is often substantial residual variation in these analyses. Some of the exceptions to these patterns can be explained by historical factors. The current distribution of species is a product of the interaction of environmental factors and the characteristics of species over time (Brown et al., 1996). This interaction is complicated by the fact that the characteristics of species undergo natural selection from their environment

(Brown et al., 1996). This observation highlights the importance of combining ecological and evolutionary perspectives on geographical distribution. Thus the combination of evolutionary and ecological theory from studies of hominid distribution and from contemporary biogeography provides a potentially comprehensive framework for the interpretation of changing hominid distribution.

Primate geographical ranges

Most non-human primates live between the Tropics of Cancer and Capricorn, and very few species occur beyond 25 degrees latitude in the north and 30 degrees latitude in the south (Foley, 1987). However primate species vary considerably in the area over which they are distributed. For example, the gelada baboon (*Theropithecus gelada*) is limited to highland Ethiopia while the vervet monkey (*Cercopithecus aethiops*) can be found throughout most of sub-Saharan Africa. Figure 1 illustrates the variation in primate distribution in Africa. The high degree of variation in distribution within the primate order requires explanation in terms of the environmental factors that limit distribution and the characteristics of species that aid dispersal.

Modern primates have often been used as a source of analogues for the behaviour of early hominid species, whether in the form of specific case studies or cross-species analysis aimed at identifying trends. As our closest relatives, primates share a number of physical and behavioural characteristics with hominid species including humans. It is likely that at least the early species of hominid had more in common with our primate relatives than with modern humans. However the period of interest in my research includes hominid species (especially *H. ergaster / erectus*) characterized by a marked increase in brain size, in tool using behaviours and use of animal resources. These adaptations could be argued to bear a closer resemblance to human behaviour. Finally, the hominids were all unique species, differing from any related species alive today. However there are a number of advantages to large scale cross species analysis as a means of investigating processes that may have been important in human evolution.

First, data is available for contemporary primates in more detail than for fossil species. Range boundary maps have been produced for most primate species, while hominid distribution must be estimated from a limited number of sites and from characteristics such as environmental tolerance. In addition, quantitative data is available on behavioural parameters for which there may not be direct archaeological or fossil evidence. Thus comparative analysis of modern primates allows us to expand our inferences about distribution and behaviour beyond what is visible in the archaeological record (Foley, 1992). Furthermore, the production of contemporary models can be used to document differences as well as similarities between the past and the present. By taking into account species with widely differing behaviour and ecological niches, comparative analysis identifies a range of possible primate strategies. The use of a cross-species, comparative analysis promotes the characterization of hominid species not as a sort of chimpanzee or a sort of human but as a unique form of life.

Hypotheses

There are a number of alternative hypotheses explaining greater environmental tolerance and range expansion in hominid species, as discussed above.

1. Behavioural flexibility or social learning favours range expansion, and high tolerance of climatic variability.
2. Range expansion is causally associated with increased meat eating.
3. Increased flexibility in hominid life history traits allowed range expansion beyond what would be predicted for a highly K selected primate.

The first hypothesis predicts covariation between behavioural flexibility or social learning and geographical range size and climatic tolerance in primates and hominids. The second hypothesis may be better tested using carnivore data, although some species of primate do occasionally eat meat. A further analysis will be required to address this question. Finally, the third hypothesis predicts a differing trend in hominids from the rest of the primates. According to this hypothesis, range size would be expected to increase with *r* selected life history traits in primates.

Method and analysis

A comparative study of primate distribution in relation to physical and behavioural characteristics was conducted using Geographic Information System (GIS) and statistical techniques. Geographical ranges of primates were digitized from maps, rectified and projected into equal area format. The range composition in terms of land cover and climatic variability was analysed using the statistical capabilities of GIS packages. Potential predictive variables (life history, body mass, diet, brain size) were synthesized from the literature and entered into a comprehensive database. A database of innovation frequencies was obtained from Reader (2000). Regression techniques were used to assess the relative predictive value of a comprehensive selection of variables with respect to range size and distribution. The effects of phylogenetic relationships were taken into account.

A number of questions of definition and methodology arose as part of the analysis, including the measurement of climatic variability. Climatic variation is induced by a number of climatic cycles, proceeding on different scales, from seasonal and annual up to thirty and hundred year cycles. A time series of global precipitation or temperature maps (New et al., 1999, New et al., 2000) was used as the basis for continuous measures of climatic variability within the range. This database provided monthly maps covering a thirty-year period, and the climate variability maps were based on this period in order to allow for variation caused by some of the more frequent climatic cycles.

The aim in this analysis was to measure variability at a scale that would affect individual animals. The measurements used in this analysis included spatial, seasonal and inter-annual variation. A map of mean yearly rainfall and temperature was calculated based on monthly means for 1961-90. Secondly, the temperature range for this period was used as an indicator of

seasonality. Minimum and maximum yearly temperatures were calculated from monthly values and the difference taken for the final temperature range map. Finally, a map of inter-annual variability was based on variability in mean annual rainfall, as measured by the coefficient of variation. Further processing was carried out to calculate the climatic variation within each species range. Values of spatial variability tolerated by species were calculated as the coefficient of variation of mean rainfall values within the species range. The seasonality and inter-annual variability tolerated by species was calculated as mean values within the range.

The real units of geographical ranges are the complex spatial and temporal patterns in which individual organisms are dispersed over the earth (Brown et al., 1996). Any maps of geographical ranges necessarily simplify such complexity. A map of the extent of occurrence of a species represents the limits of that species distribution. This ignores smaller scale variation such as absences within the range and variation in abundance in different areas, but was deemed appropriate to the continental scale of the analysis. Primate geographical range maps were taken from Wolfheim (1983). The data from the three main geographical areas in which primates are found (Africa, South America, and Asia) were treated as separate datasets on the grounds that unique features of the continental landmass were likely to influence distribution. The Madagascar primates were excluded from the African dataset for the same reason.

Behavioural flexibility can be defined as the capacity of a species to engage in novel behaviour. In order to carry out my analysis, it was necessary to find a measure of behavioural flexibility that could be compared across species. Species vary widely in their performance in experimental tests, and it has been suggested that behavioural innovation, or opportunistic departures from the species norm, may provide an alternative measurement (Lefebvre et al., 1998). Reader (2000) has conducted a comparative study of innovation, social learning and tool use in nonhuman primates by collecting reports of such behaviour from the primate and social learning literature. This method provides a test fair to all species and data on large numbers of species by measuring the tendency to discover or learn novel solutions to environmental or social problems relevant to the animal (Reader, 2000). The database used in this analysis was provided by Reader (2000) and all frequencies were corrected for research effort using his method.

Brain size may be used as an indirect measurement of intelligence. Brain expansion is costly, so an increase in brain size (such as occurred in human evolution) must give a strong selective advantage. This advantage is generally assumed to involve increased intelligence. Corroborative evidence for this approach comes from the correlation between a number of brain measures and innovation frequency, social learning and tool use (Reader, 2000). There are a number of competing measurements of brain size available, and the choice of measurement depends on ideas about brain evolution and brain structure (Byrne, 1995). It can be argued that absolute brain size equals processing power (Dawkins, 1976). However brain size scales with body size: allometric scaling can be used to account for this relationship. Finally, the relative size of different parts of the brain also varies, and certain parts are associated

with different functions. Thus a third type of measurement is based on the relative or absolute size of the parts of the brain associated with the behaviours of interest. In these analyses I used measurements based on each of these three approaches: absolute brain size, brain size relative to body size and the neocortex ratio.

Linear regression techniques were used to identify the best predictors of range size. Statistical analyses were also carried out using independent contrasts. As discussed above, comparison of continuous variables across a range of species can be used to identify covariation in characters and may suggest evolutionary trends. Possible covariation can be tested statistically using regression techniques. A strong relationship between range size and another variable may indicate that primate species that, for instance, have very long noses will tend to occupy large areas. This could be because long noses allow primates to smell each other over large areas and thus expand their ranges. It could also be because primate species with long noses are all related to a common ancestor that had a long nose and occupied a large area. Thus cross species analysis can identify spurious correlations.

To avoid this problem I used a package called Comparative Analysis for Independent Contrasts, provided by Purvis and Rambaut (1995). This calculates independent contrasts based on the comparison of pairs of species or higher nodes that share a common ancestor. The principle of this calculation is that the difference between these pairs will reflect only the changes that have occurred since they split from their common ancestor. The primate phylogeny used was a composite tree derived from 112 previously published phylogenies (Purvis, 1995).

Results

The principal findings of this study are that, as shown in Table 1, once phylogenetic relationships have been taken into account, innovation frequencies and relative and absolute measurements of brain size do not correlate with geographical range size in modern primate species. A number of significant results were obtained prior to using independent contrasts, and this suggests that the relationship between range size and behavioural flexibility is determined by phylogeny. These negative results are not entirely unexpected. The species most notable for high innovation and tool use frequency, the chimpanzee, also has a small and relatively habitat specific range. These results suggest that while behavioural flexibility is not a hindrance, other characteristics are necessary for successful range expansion. Other factors such as niche breadth are better predictors of range size (Eeley and Foley, 1999). This has interesting implications for the interpretation of hominid range expansion. While the primate analysis does not disprove the hypothesis that hominid range expansion was related to an increase in brain size and behavioural flexibility, it indicates that this is unlikely to have been part of a primate trend. If such factors were important in hominid range expansion, it is likely to have been on a different scale, or have involved behaviours absent in other primates that were particularly useful in encountering new environments.

However, some significant results have been obtained by

regressing innovation and tool use frequencies on measures of spatial and temporal climatic variability for African primates (see Table 2). This is consistent with the hypothesis that more intelligent or behaviourally plastic species can tolerate greater climatic variability. Given the negative results obtained for range size this suggests that, contrary to expectations, species with a high tolerance of climatic variability do not necessarily expand their ranges. This result is particularly interesting given evidence that the habitat tolerance of hominid species increased over time. Land use studies indicate a longer distance of stone tool transport, and a wider diversity of depositional settings, as well as repeated return to particular environmental features (Potts et al., 1999). This suggests that hominids became increasingly independent of environmental constraints. Further analysis will be required to ascertain whether this increased independence or tolerance was part of a primate trend related to behavioural flexibility.

In addition, there seems to be a general pattern by which the hypothesis that behavioural flexibility allows primate species to cope with greater spatial and temporal variability within their ranges is upheld for African primates but not for South American primates. This raises interesting questions regarding differences in the evolution of primate geographical ranges in the two continents. Such variation in modern distribution patterns could be the result of differences in the historical interaction of environmental factors and species' characteristics.

The results for both range size and climatic variability are interesting in terms of predicted effects of higher levels of social learning. There is a conclusive lack of correlation with both range size and climatic variability, using species as data points and independent contrasts. This provides strong evidence against the hypothesis that higher frequencies of social learning will increase environmental tolerance and dispersal ability in primate species and hence lead to larger ranges. The relationship between social learning and environmental variability is theoretically complex. Social learning has advantages over learning independently at intermediate levels of environmental variation or where environmental variation is regular and predictable (Sibly, 1999). This could be why general intelligence as measured by innovation frequency is a better predictor of climatic variability than social learning frequencies.

Finally, there is some indication that *r* selected life history strategies are positively associated with larger range size. There is a significant negative relationship between geographical range size and age at first breeding (for African primates, using independent contrasts, $r = -0.522$, $n = 19$, $p < 0.05$). In addition, there is a positive relationship between range size and a measurement of reproductive rate, based on variation in other life history parameters (for African primates, using independent contrasts, $r = 0.818$, $n = 14$, $p < 0.01$). This conclusion is currently tentative and will need to be confirmed using a larger data set and more life history variables. *R* selected species are characterised by a suite of characteristics, including rapid development, frequent reproduction, shorter lifespan, and also rapid dispersal and niche breadth. Such life history traits and dispersal ability are connected to the invasion success of a species, and therefore to its range size. In addition, niche breadth covaries with

geographical range size in African primates (Eeley and Foley, 1999). However such species tend not to be those with the largest brain size and greatest evidence for innovative behaviour, tool use and social learning. K selected species are likely to disperse more slowly, but may have a selective advantage once they do reach a new area (Richard, 1985). There may be two routes by which primates expand their ranges: through high levels of behavioural flexibility, allowing species to tolerate new climatic conditions; or through the fast life history and rapid dispersal characteristic of r selected species.

Conclusions

This analysis gave a number of unexpected and thought provoking results. It has been suggested that hominid range expansion could be explained by increasing brain size and associated increases in behavioural flexibility and social learning frequencies. However the primate data contradicts the predictions of this hypothesis. If these are important factors in hominid range expansion, it is unlikely to have been as part of a primate trend. A number of predictors of primate geographical range size and tolerance of climatic variability have been identified in this analysis, and still others can be found in the biogeography literature. This suggests that there may be a number of interacting characteristics determining primate range size. One reading of the results would be to suggest two alternative primate strategies involving an increase in range size. One would include a suite of characteristics including r selected life history traits: the other a high level of behavioural flexibility. A preliminary explanation for the large increase in range size relative to the primates in human evolution could be that some hominid adaptations combined these characteristics. For instance, hominid adaptations could have included a means to increase the flexibility of their behaviour and of their life history traits. Further analysis of the evidence for hominid distribution and behaviour will be necessary to evaluate this suggestion.

This approach to hominid distribution involves a combination of theory and method that has proved very productive. Biogeography provides a theoretical framework for interpreting spatial patterns in distribution, while GIS and statistical techniques provide an efficient method for carrying out large-scale spatial analyses. This larger scale approach may aid the identification of patterns and processes invisible at the site or regional level. The use of comparative material from modern primates gave access to a detailed database of distribution patterns, and allowed me to extend inferences about behaviour beyond the information available from the hominid fossil and archaeological record. In addition, the cross species approach has proved a good solution to the problem of using comparative data to interpret hominid behaviour and ecology, without assuming similarities to particular species. A number of future research directions have been made possible by this project. This combination of approaches can be applied in a further analysis of carnivore distribution in order to test hypotheses linking range expansion to meat eating. In addition, this analysis has identified patterns in primate distribution, and I have proposed some mechanisms that could explain these patterns. It is hoped that predictions based on these processes can be

tested against the archaeological and fossil hominid data.

Acknowledgements

Many thanks to James Steele for ideas and criticism provided throughout this project, to Simon Reader who provided the database of innovation, tool use and social learning frequencies, and to both Simon Reader and Kevin Laland for their valuable comments on my research plans. I am supported during my PhD research by a NERC Research Studentship.

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Tables

	Innovation frequency	Tool use frequency	Social learning	Absolute brain size	Relative brain size	Neocortex ratio
Africa	$r = 0.141$ $n = 24$ $p > 0.1$	$r = -0.161$ $n = 24$ $p > 0.1$	$r = 0.233$ $n = 24$ $p > 0.1$	$r = 0.059$ $n = 33$ $p > 0.1$	$r = 0.063$ $n = 33$ $p > 0.1$	$r = 0.030$ $n = 12$ $p > 0.1$
South America	$r = 0.397$ $n = 23$ $0.1 > p > 0.05$	$r = 0.142$ $n = 23$ $p > 0.1$	$r = -0.087$ $n = 23$ $p > 0.1$	$r = -0.060$ $n = 23$ $p > 0.1$	$r = -0.255$ $n = 23$ $p > 0.1$	$r = 0.395$ $n = 10$ $p > 0.1$
Asia	$r = -0.390$ $n = 22$ $0.1 > p > 0.05$	$r = -0.390$ $n = 22$ $0.1 > p > 0.05$	$r = -0.017$ $n = 22$ $p > 0.1$	$r = 0.000$ $n = 24$ $p > 0.1$	$r = -0.387$ $n = 24$ $0.1 > p > 0.05$	Insufficient data.

Table 1. Results of regression of innovation, tool use and social learning frequencies, and measures of brain size, on total geographical range size, using phylogenetically independent contrasts.

Dependent variable	Location	Innovation frequency	Tool use frequency	Social learning frequency
Spatial variability	Africa ($n = 24$)	$r = 0.505$ $p < 0.01$	$r = 0.633$ $p < 0.01$	$r = 0.069$ $p > 0.1$
	South America ($n = 23$)	$r = -0.192$ $p > 0.1$	$r = -0.124$ $p > 0.1$	$r = -0.210$ $p > 0.1$
Seasonal variability	Africa	$r = 0.396$ $p = 0.05$	$r = 0.305$ $p > 0.1$	$r = 0.329$ $p > 0.1$
	South America	$r = -0.152$ $p > 0.1$	$r = 0.022$ $p > 0.1$	$r = -0.147$ $p > 0.1$
Interannual variability	Africa	$r = 0.376$ $0.1 > p > 0.05$	$r = 0.447$ $p < 0.05$	$r = -0.026$ $p > 0.1$
	South America	$r = -0.312$ $p > 0.1$	$r = -0.123$ $p > 0.1$	$r = -0.147$ $p > 0.1$

Table 2. Results of regression of innovation, tool use and social learning frequencies on measures of climatic variability, using phylogenetically independent contrasts.

Figures

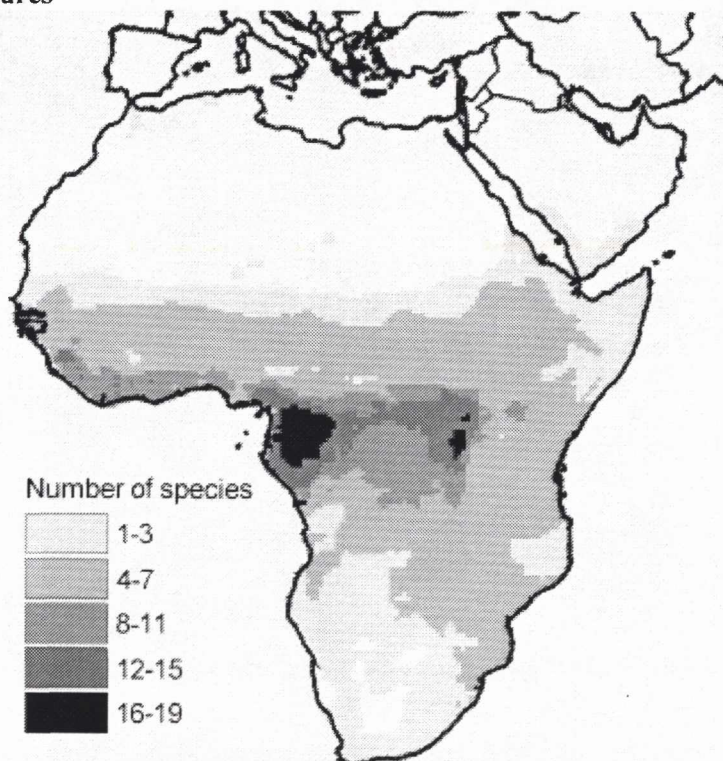


Figure 1. Primate species richness in Africa, from Wolfheim (1983).