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Report

Culture and Geographic Variation in Orangutan Behavior

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Summary

Although geographic variation in an organism's traits is often seen as a consequence of selection on locally adaptive genotypes accompanied by canalized development [1], developmental plasticity may also play a role [2, 3], especially in behavior [4]. Behavioral plasticity includes both individual learning and social learning of local innovations ("culture"). Cultural plasticity is the undisputed and dominant explanation for geographic variation in human behavior. It has recently also been suggested to hold for various primates and birds [5], but this proposition has been met with widespread skepticism [6–8]. Here, we analyze parallel long-term studies documenting extensive geographic variation in behavioral ecology, social organization, and putative culture of orangutans [9] (genus *Pongo*). We show that genetic differences among orangutan populations explain only very little of the geographic variation in behavior, whereas environmental differences explain much more, highlighting the importance of developmental plasticity. Moreover, variation in putative cultural variants is explained by neither genetic nor environmental differences, corroborating the cultural interpretation. Thus, individual and cultural plasticity provide a plausible pathway toward local adaptation in long-lived organisms such as great apes and formed the evolutionary foundation upon which human culture was built.

Results

In this study, we use the predictions of a cultural plasticity model that, if confirmed, allow us to reject other developmental causes of geographic variation in behavior of orangutans (*Pongo* spp.), such as canalized development under strong genetic control or individual plasticity. We apply this approach to geographic variation in behavioral ecology (activity budgets, diet, and ranging), social organization (local density, associations, and sociosexual variables), and putative cultural behaviors observed among wild populations of orangutans in both Sumatra (*P. abelii*) and Borneo (*P. pygmaeus*) that have been the subject of long-term field studies (Figure 1).

We found that orangutan populations are genetically highly differentiated from each other. For both DNA markers used in this study, only a very small fraction of the total variance was explained by variation within populations (Table 1). Thus, there is sufficient genetic variation among populations and islands potentially to explain geographic variation in behavior.

Matrix permutation tests revealed several significant bivariate correlations between differences in behavioral ecology and genetic and environmental dissimilarities among 11 populations (Table 2). However, subsequent analyses aimed at partitioning the total observed variance into uniquely genetic and uniquely environmental components revealed that a nonsignificant 4% of the total variance in orangutan behavioral ecology was accounted for by genetic differences between sites, whereas more than 25% could be attributed to environmental differences (Table 2; Figure 2). Therefore, geographic variation in orangutan behavioral ecology appears to be much better explained by local adaptation through developmental plasticity than through genetic canalization.

The documented geographic variation in social organization among seven orangutan populations also showed several significant bivariate correlations with both genetic and environmental dissimilarities (Table 2). Subsequent estimates of the unique proportions of variance that were explained by either genetic or environmental dissimilarities showed that genetic dissimilarities consistently accounted for less than 7% of variation, regardless of which genetic marker system was used, whereas environmental factors again explained more than 25% (Table 2; Figure 2). Therefore, geographic variation in orangutan social organization also appears to result mainly from local adaptation through developmental plasticity rather than through genetic canalization.

Finally, geographic variation in behavior patterns previously suggested to be cultural [10] showed nonsignificant bivariate correlations with both genetic and environmental dissimilarities among nine populations (Table 2). Partial Mantel tests indicated that both genetic and environmental differences each accounted for a minor and nonsignificant proportion of the total variance observed (Table 2; Figure 2). These ten putative cultural variants had been selected because they were not subject to environmental influences and were among the most conspicuous and frequent ones. However, the same was found when all 24 putative cultural elements were considered: geographic variation was not significantly associated with either explanatory variable, although environmental dissimilarities approached significance (see Table S1 available online). Therefore, neither genetic canalization nor individual plasticity can account for geographic variation in putative orangutan culture.

We repeated all analyses using Spearman rank correlation matrix permutation tests for both genetic marker systems to control for undue influences of potential outliers and potential ceiling effects in our genetic dissimilarity measures. These confirmed all previous conclusions (Table S2).

Discussion

Virtually all species show some geographic variation in their phenotypes, from morphology and physiology to behavior and life history [2–4]. This geographic variation is often thought to reflect differential local adaptation through the action of natural selection [11]. Perhaps because of the success of experimental approaches, typically focusing on invertebrates and fish [1], genetic variation accompanied by canalized

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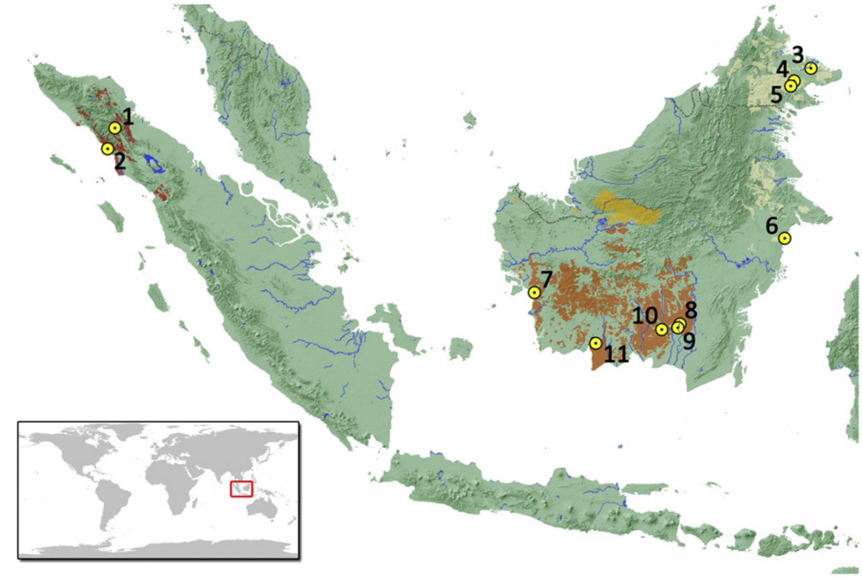

Figure 1. Geographic Locations of Sites for which Data on Orangutan Biology Were Compiled

The different colors in the map correspond to estimated distributions of the currently recognized species and subspecies (Sumatra: dark red, *P. abelii*; Borneo: beige, *P. p. morio*; orange, *P. p. pygmaeus*; dark orange, *P. p. wurmbii*). In addition, details are provided for each site on the type of information that was available (BE, behavioral ecology; SO, social organization; PC, putative culture; ENV, information on local dynamics in vegetation and climate from remotely sensed and spatially interpolated sources). The numbers of individuals for which genetic data were obtained for the particular marker system are given in the columns "HVR-I" and "mtDNA genes."

	Site	Code	Species	Island	HVR-I	mtDNA genes	BE	SO	PC	ENV
1	Ketambe	KE	*Pongo abelii*	Sumatra	17	8	+	+	+	+
2	Suaq Balimbing	SB	*P. abelii*	Sumatra	15	12	+	+	+	+
3	Lower Kinabatangan	LK	*P. pygmaeus morio*	Borneo	8	6	+	-	+	+
4	Ulu Segama	US	*P. p. morio*	Borneo	-	-	+	-	-	+
5	Danum Valley	DV	*P. p. morio*	Borneo	16	13	+	-	-	+
6	Mentoko Kutai	KU	*P. p. morio*	Borneo	4	7	+	+	+	+
7	Gunung Palung	GP	*P. p. wurmbii*	Borneo	21	9	+	+	+	+
8	Tuanan	TU	*P. p. wurmbii*	Borneo	33	4	+	+	+	+
9	Sungai Lading	SL	*P. p. wurmbii*	Borneo	26	2	+	-	+	+
10	Sabangau	SA	*P. p. wurmbii*	Borneo	29	3	+	+	+	+
11	Tanjung Puting	TP	*P. p. wurmbii*	Borneo	3	-	+	+	+	+

development is usually presented as the de facto null model to explain geographic variation in a trait [7].

A locally adaptive phenotype might also be attained through an additional pathway, namely developmental plasticity, provided that this is not too costly [3]. This pathway is especially likely if extensive gene flow or insufficient time since separation prevents local adaptations from becoming genetically fixed [12]. However, it is a plausible mechanism for behavioral traits under all conditions, because behavioral plasticity includes learning. Indeed, the ubiquity of learning, especially in birds and mammals [4, 13], suggests that individual plasticity is a common mechanism to adjust behaviorally to local conditions.

Table 1. Genetic Variation among Orangutan Populations

	HVR-I		mtDNA Genes	
	Variance Components	Percentage of Variation	Variance Components	Percentage of Variation
Among populations	10.30	95.84%*	32.21	98.93%*
Within populations	0.65	4.16%	0.35	1.07%
Among islands	37.06	88.92%*	48.48	79.52%*
Among populations/ within islands	3.90	9.36%*	7.81	12.81%*
Within populations	0.72	1.72%*	4.67	7.67%*

Variance components and percentage of variation explained for two analyses of molecular variance using HVR-I and mtDNA genetic data (see text), respectively, when islands are not taken into account (top) and in a data set partitioned according to islands (bottom). $^*p < 0.05$.

An additional form of behavioral plasticity is the acquisition of skills or information through social learning—cultural plasticity. Social learning ranges from learning due to proximity or attraction to the same stimuli or specific locations, to learning by directly copying goals or actions [14]. Social learning provides the standard explanation for geographic variation in human behavior, i.e. culture [15], yet similar propositions for nonhuman animals [5] remain controversial [6–8, 16].

Our analyses demonstrate that developmental plasticity plays a major role in bringing about geographic variation in orangutan behavior. If genetic differences had been responsible, we should have found covariation between genetic and behavioral variation, because populations and especially islands (Sumatra versus Borneo) were genetically highly differentiated. Nonetheless, genetic dissimilarities explained at most 7% of the behavioral variation. In contrast, environmental variation explained more than 25% of the variation in behavioral ecology and social organization, supporting a major influence of developmental plasticity.

Previous cultural interpretations of geographic variation in ape behavior have been criticized for not having incorporated the effect of environmental differences between sites [7]. Here, however, we have demonstrated that the environmental differences we measured are ecologically meaningful because they explain variation in behavioral ecology and social organization. Yet, they could not explain the variation in the putative cultural behaviors. Moreover, our reduced culture data set contains only those putative cultural elements that are unlikely to be linked to environmental factors. Because variation in putative cultural elements was correlated with neither genetic nor environmental variation, this particular category of geographic variation in behavior must have come about through local innovations, spread and maintained by social learning [10, 17].

Our findings are also supported by multiple other sources of information. First, in our data set, the contrast in social organization was the only significant predictor of dissimilarities in

Table 2. Correlates of Geographic Variation in Orangutan Behavior

		HVR-I				mtDNA Genes			
x	z	$r_{Pearson}$	95% CI	UVE	p_{Mantel}	$r_{Pearson}$	95% CI	UVE	p_{Mantel}
Δ Behavioral Ecology, 11 Populations, 55 Pairs									
φ_{ST}		0.368	0.248–0.489		0.002	0.361	0.171–0.512		0.002
Δ ENV		0.593	0.406–0.714		<0.001	0.593	0.372–0.707		<0.001
φ_{ST}	Δ ENV	0.199	0.116–0.310	3.95%	0.062	0.159	−0.045–0.311	2.53%	0.161
Δ ENV	φ_{ST}	0.529	0.309–0.631	28.00%	0.002	0.523	0.234–0.645	27.36%	0.003
Δ Social Organization, 7 Populations, 21 Pairs									
φ_{ST}		0.350	0.264–0.491		0.051	0.272	0.247–0.462		0.104
Δ ENV		0.544	0.369–0.650		0.022	0.544	0.369–0.668		0.022
φ_{ST}	Δ ENV	0.263	0.082–0.480	6.90%	0.113	0.237	0.139–0.444	5.60%	0.173
Δ ENV	φ_{ST}	0.504	0.252–0.651	25.37%	0.022	0.532	0.330–0.656	28.30%	0.022
Δ Putative Culture (Conspicuous and Frequent Elements), 9 Populations, 36 Pairs									
φ_{ST}		0.288	0.055–0.450		0.051	0.158	−0.311–0.403		0.174
Δ ENV		0.318	0.076–0.561		0.073	0.318	0.024–0.525		0.074
φ_{ST}	Δ ENV	0.223	0.042–0.344	4.98%	0.096	0.066	−0.297–0.273	4.38%	0.376
Δ ENV	φ_{ST}	0.262	0.037–0.475	6.85%	0.117	0.287	0.001–0.469	8.22%	0.116

Matrix Pearson correlation coefficients (Mantel and partial Mantel tests) for two different genetic marker systems of behavioral dissimilarity matrices with genetic (φ_{ST}; HVR-I and mtDNA genes) and environmental (Δ ENV) dissimilarities. The top two rows in each subsection of the table denote bivariate correlations; the bottom two denote partial correlations (explanatory variables are indicated with x; variables that were partialled out are indicated with z). The following abbreviations are used: CI, bootstrapped confidence interval; UVE, unique proportion of variance explained.

conspicuous and frequent putative cultural behaviors (Table S3), which is consistent with site-specific sociability being a good predictor of the local repertoire size of putative cultural variants [10]. Second, wild immature orangutans show selective visual attention to exactly those behaviors thought to be most difficult to acquire independently [18], nearby populations exhibit differences in diet composition and call repertoires consistent with innovation and social learning [19], and orangutans are proficient social learners in captivity [20]. Finally, similar work on other species, especially chimpanzees [21], supports this conclusion. Thus, our study provides the strongest support to date in the ever-growing chain of evidence substantiating a cultural interpretation of geographic variation in certain elements of nonhuman primate behavior [10, 17].

Although historically it has been good scientific practice to assume canalized development as the null model, we might now have to question its adequacy for long-lived animals that rely on extensive external inputs, including social ones, during development. First, long-lived animals are likely to be confronted with variation over time in environmental conditions, and being usually large-bodied also tend to roam so widely that they may encounter many different conditions. Second, these animals may not have the demographic potential to respond rapidly to selection for local adaptation, forcing them to rely more on plasticity to maintain locally adaptive phenotypes [22]. The indications for extensive social learning and cultural variation in other long-lived organisms such as dolphins [23], whales [24], elephants [25], monkeys [26], and some birds [27] support the idea that cultural plasticity is an important pathway to local adaptation. The fact that culture is found in great apes moreover gives us a much better basis for developing a theoretical framework for cultural evolution, within which to address the question of the elaboration of this ability in humans [15].

Our results are entirely consistent with the cultural interpretation, by demonstrating that the proportion of geographic variation in putative cultural behaviors explained by genetic or environmental differences among populations is very low, but also highlight the importance of phenotypic plasticity, of which culture is just one aspect, in long-lived animals more generally.

Experimental Procedures

The Cultural Plasticity Model

In the cultural plasticity model, plasticity (individual or cultural) is implicated if there is no correlation between genetic and behavioral variation across populations. Note that this does not mean that the behavior itself has no genetic basis, but merely that geographic variation in its manifestation is primarily due to developmental plasticity. Because the expression of virtually all behavioral traits is caused by polygenic loci, identification of the genes potentially responsible for the geographic variation in complex behaviors is virtually impossible [28]. Therefore, the only feasible approach in wild animal populations is to use neutral genetic markers, followed by estimating the extent of genetic divergence as an index for the differences between populations in the genes causally involved in the behaviors, as done previously [29].

The use of this measure can be criticized if local selection subsequent to divergence of two populations has favored differences among particular coding genes, which therefore became disassociated from the overall genetic dissimilarity across sites. However, selection on the polygenic traits most likely responsible for behavioral variation will be attenuated over multiple loci, so that each locus behaves as if it evolved nearly neutrally [30]. Moreover, simulations showed that genetic differentiation measures calculated from quantitative trait loci are almost identical to those derived from neutral markers, regardless of the selective regime imposed on the selective trait [31]. This fact justifies the use of overall genetic similarity measures even in the potential presence of selection on behavior patterns.

Provided genetic and behavioral variation are uncorrelated, the plasticity interpretation is confirmed if environmental variation explains a considerable proportion of the behavioral variation. In this case, we can further distinguish between individual and cultural plasticity because only cultural plasticity can produce geographic variation in behavior in the absence of environmental differences. In sum, if we find for those behavior patterns previously hypothesized to be cultural that their geographic variation is predicted by neither genetic nor ecological differences, whereas that in other behaviors is, we must accept a cultural interpretation for those behavior patterns. Admittedly, the ability to distinguish between genetic and plasticity explanations comes at a price: cultural variants with a strong environmental imprint, and thus presumably the most adaptive ones may go undetected. We therefore assume that showing the presence of culture unrelated to environmental variation implies the presence of environmentally adaptive culture.

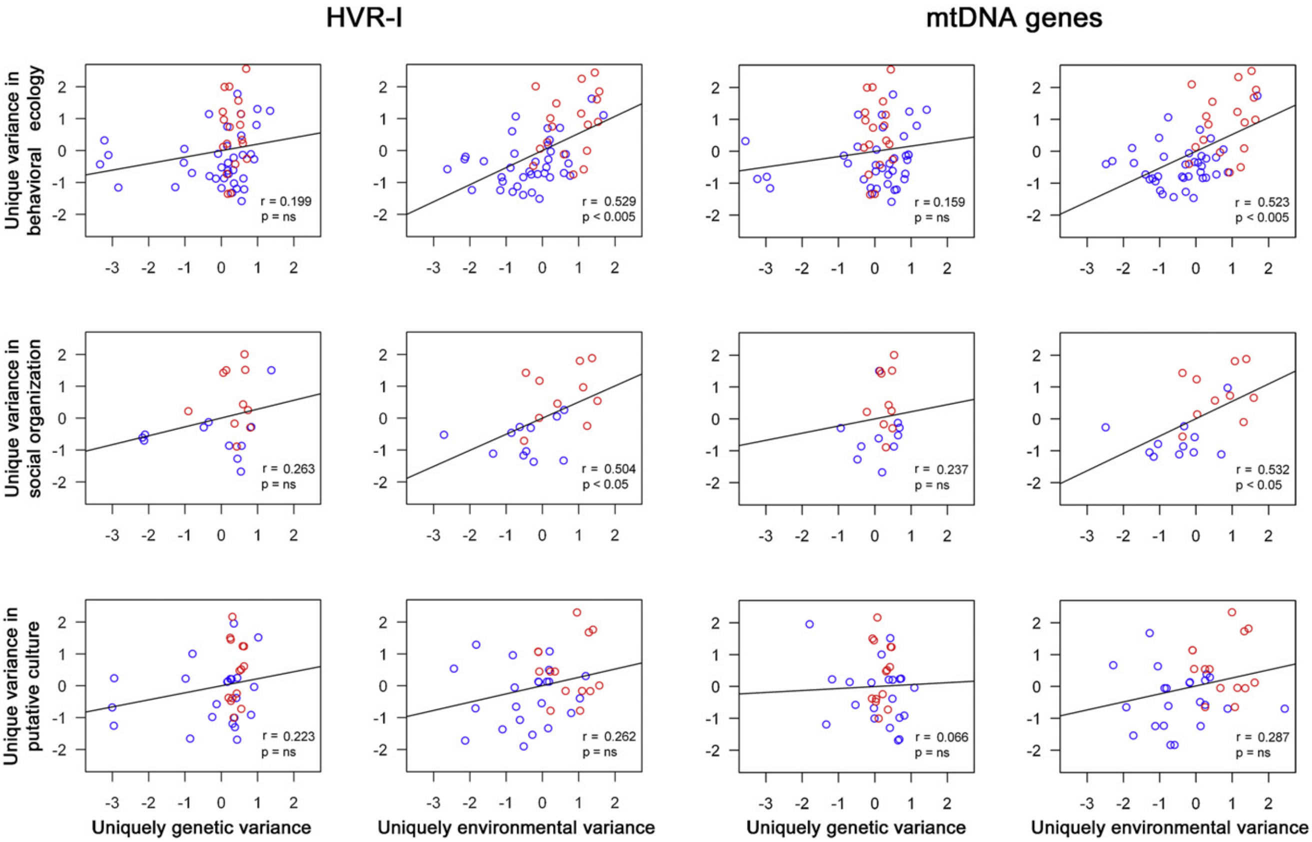

Figure 2. Uniquely Genetic and Environmental Contributions to Behavioral Variation among Orangutans

Residual plots of genetic and ecological dissimilarity as a function of dissimilarities in behavioral ecology, social organization, and putative culture for two different genetic marker systems. Each dot represents a pairwise difference between sites. Blue dots denote comparisons within islands; red dots denote comparisons between islands.

Separating individual from cultural plasticity is possible in principle through transplantation and social isolation experiments [32]. However, these experiments are often impossible for logistic, ethical, and legal reasons, especially for primates, forcing us to resort to a parsimony approach by selecting the most consilient explanation for all relevant observations. Thus, in the case of great apes, the cultural interpretation of geographic variation in some behavior patterns [15] is consistent with captive experiments showing reliable social transmission of novel skills [20] and observations suggesting selective visual attention for novel and especially difficult behavioral skills [18]. However, none of these studies directly addresses geographic variation as observed in the wild.

General Methodological Approach

Data on orangutan behavior were compiled from 11 study populations, with well over 100,000 hours of total observational effort [9] over 40 years. We included data on orangutan behavioral ecology and social organization and also considered behavioral variants that had previously been interpreted as cultural [10, 33], in two forms: (1) a set of ten conspicuous and frequent behaviors without obvious environmental correlates, thus eliminating the role of possible observer bias, differential observation intensity, or environmental differences among sites, and (2) the total published set [33]. We assessed the level of genetic dissimilarities between all populations using two mitochondrial DNA marker systems. The first marker system, “HVR-I,” comprises 323 base pairs of the hypervariable region I (HVR-I) of the mitochondrial DNA; the second marker system, “mtDNA genes,” comprises 1,355 base pairs of three concatenated parts of coding mtDNA genes (16S rDNA, cytochrome *b*, and NADH-ubiquinone oxidoreductase chain 3). Both marker systems differ in their mutation rates and therefore provide better dissimilarity estimates at shorter or longer periods since separation from a common ancestor, respectively. We quantified environmental differences between sites by constructing a data matrix consisting of ten variables to capture local dynamics in vegetation and climate. We used matrix permutation correlation tests [34] to investigate potential associations between the three behavioral dissimilarity matrices and genetic and environmental dissimilarity matrices. To estimate the proportions of the total variance in orangutan behavior attributable to either uniquely genetic or ecological differences between sites, we calculated squared partial matrix correlation coefficients, presented as unique variation explained. Details are given in the Supplemental Experimental Procedures.

Statistical Analysis

All collated data on orangutan biology (behavior, genetics, and ecology) at the various study sites were transformed into pairwise dissimilarity matrices. For each of the three behavioral as well as the environmental data sets, pairwise distances were expressed by Gower dissimilarity matrices, calculated in the “ecodist” package [35] for R 2.10.1 [36]. The Gower dissimilarity metric [37] was chosen for its ability to deal with mixed variable types and its robustness against missing values [34, 38]. Genetic dissimilarity between populations was parameterized by φ_{ST} values for mtDNA markers.

Matrix analyses were conducted using the Mantel permutation test implemented in the “ecodist” package for R 2.10.1. Pearson correlation coefficients and associated bootstrapped 95% confidence intervals ($n_{bootstraps} = 1{,}000$) were calculated and assessed for statistical significance ($n_{permutations} = 10{,}000$). To estimate the unique proportions of the total variance in orangutan behavior attributable to either uniquely genetic or ecological differences between sites, we calculated squared partial matrix correlation coefficients, presented as unique variation explained independently by each of the two main variables, as suggested previously [39]. This approach is valid only if collinearity between the two explanatory variables is sufficiently low. This condition was met, because the correlation between environmental dissimilarity and both genetic dissimilarity measures was low ($r_{Pearson} = 0.25$ and 0.31 for HVR-I and mtDNA genes, respectively).

To account for the possibility that outliers may have exerted an undue influence on our analyses, we additionally calculated Spearman rank correlation coefficients and assessed these for statistical significance through Mantel matrix permutations.

Supplemental Information

Supplemental Information includes five tables and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.09.017.

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