MATRIX CORRELATION TESTS FOR MODELS OF MODERN HUMAN ORIGINS

	r	P_w	P (lower)	P (upper)
Waddle's original distances				
Regional continuity	0.259	0.060	0.018856	0.031647
Single African origin	0.409	0.010	<0.000001	0.004551
Regional continuity versus				
single African origin	−0.109	–	0.232492	0.226333
Bias-corrected distances				
Regional continuity	0.358	–	0.002905	0.004898
Single African origin	0.275	–	0.011492	0.025424
Regional continuity versus				
single African origin	0.061	–	0.356905	0.360163

The column r gives the matrix correlations and P_w gives the associated probabilities from Waddle (if available). P (lower) and P (upper) give the lower and upper tail probabilities from the complete enumeration of 479,001,060 possible permutations. Matrix correlations for regional continuity versus single African origin are given as the correlation of taxonomic distance with the difference between design matrices (after standardization). Negative correlation indicates a better fit between taxonomic distance and the single African origin model, whereas positive correlation indicates a better fit with the regional continuity model.

value of $d^2(E\{d^2\})$ is then $(n_a + n_b)/(n_a n_b)$, where n_a and n_b are the sample sizes of the two OTUs. If sample sizes are small, because Waddle's distances (d_w) were not corrected for bias, two identical OTUs would still have a non-zero squared distance. If Waddle's average taxonomic distances are replaced with bias-corrected distances (d_c), equal to $(d_w^2 - E\{d^2\})^{1/2}$, or zero if $d_w^2 < E\{d^2\}$, and using Waddle's own form of inference (that is, choosing the model which gives the highest matrix correlation and the lowest P-value), we would be forced to pick the regional continuity model as the best supported (with $r = 0.358$ and $P = 0.0049$ versus $r = 0.275$ and $P = 0.0254$ for the single African origin model). The Dow–Cheverud test shows even less support for one model of modern human origins over the other ($P=0.7171$).

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WADDLE REPLIES — Konigsberg *et al.* suggest that the one-tail permutational probabilities reported in my table are extreme for the two models of modern human origin. Although I agree with their conclusions on this point, and suggest that in future applications of this method, permutational probabilities be calculated several times to ensure that the reported values are not extreme, probabilities are not particularly informative in interpreting the results of these matrix-correlation tests, because for almost all of the models tested in this and previous work, matrix correlations are significant. As I have discussed[1], there are large portions of the single origin and regional continuity design matrices which are either identical or very similar. These areas of similarity may contribute to positive correlations and statistical significance in matrix comparisons using each of the alternative hypotheses. The ideal method for testing competing hypotheses would be one that evaluates the strength of the different models solely on the basis of the differences between them (see ref. 1).

In theory, the Dow–Cheverud test used by Konigsberg *et al.* should accomplish this goal by allowing direct comparison of two competing hypotheses. As I have discussed[1], I did not use this method because my data are clearly spatially and temporally autocorrelated. Oden and Sokal[2,3] have shown that this test results in spuriously high rejection rates when data are spatially and/or temporally autocorrelated. Konigsberg *et al.* use this method to show that neither of my basic single-origin or regional continuity models (using only one of my two sets of OTUs) provides a better explanation of my data on cranial variation. These authors have compared two of my models that have relatively low correlations relative to the other models tested, and did not address the single southwest Asian origin model, which achieved the highest correlations with the data. Therefore, their results do not change my conclusion that single-origin models provide the best explanation of cranial variation. At this time, I cannot comment on the portion of their paper discussing bias-correction for my average taxonomic distances, because the rationale behind the formula presented for the expected value of this statistic is unclear.

Finally, and most important, the approach used by Konigsberg *et al.*, in which a single set of matrix correlations is used to evaluate a hypothesis, is fundamentally flawed. The conclusions in my Letter to *Nature*[4] are based on a series of matrix correlation tests that all indicate stronger support for a single-origin model than for a continuity model. The use of such a series of tests is necessary given the amount of 'noise' present in my analysis. To be fair to both models, I used different formulations of OTUs, different formulations of geographical areas, and different weights applied to various parts of the models. The results of all my tests, demonstrating that this series consistently supported the single-origin model over regional continuity, convinced me that the single-origin model provides the better explanation of modern human origins.

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Rewards of promiscuity

SIR — Olsson *et al.*[1] described a remarkable relationship between mating behaviour of female lizards (*Lacerta agilis*) and viability of their offspring. The number of sexual partners of females was positively correlated with the hatching success of eggs, negatively correlated with the proportion of hatched young that exhibited malformations and positively correlated with survivorship of free-living juveniles. To test whether these differences in offspring viability were caused by nutrients in the ejaculates or offspring being sired by males with 'better genes', Olsson *et al.*[1] contrasted these results with those from females that mated repeatedly with the same male. The lack of significant correla-
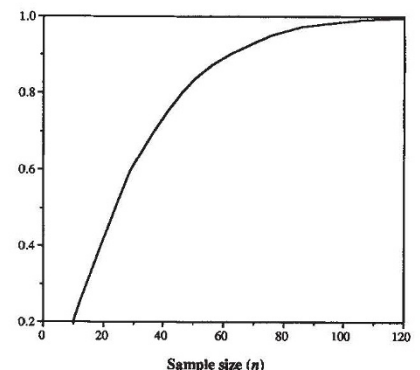
Effect of sample size on power of a correlation analysis to reject the null hypothesis of the slope = 0 when the correlation is 0.40 ($\alpha = 0.05$).

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