

The Heritability of Personality Factors in Chimpanzees (*Pan troglodytes*)

Alexander Weiss,^{1,2} James E. King,¹ and Aurelio José Figueredo¹

Received 16 Apr. 1999—Final 4 Dec. 1999

Human personality and behavior genetic studies have resulted in a growing consensus that five heritable factors account for most variance in human personality. Prior research showed that chimpanzee personality is composed of a dominance-related factor and five human-like factors—Surgency, Dependability, Emotional Stability, Agreeableness, and Openness. Genetic, shared zoo, and nonshared environmental variance components of the six factors were estimated by regressing squared phenotypic differences of all possible pairs of chimpanzees onto $1 - R_{ij}$, where R_{ij} equals the degree of relationship and a variable indicating whether the pair was housed in the same zoo. Dominance showed significant narrow-sense heritability. Shared zoo effects accounted for only a negligible proportion of the variance for all factors.

KEY WORDS: Chimpanzee; personality; Big Five; zoo; heritability.

INTRODUCTION

One substantive finding to emerge from human personality research during the past 30 years is that human personality differences can be largely accounted for by five broad, bipolar dimensions, the “Big Five.” These dimensions include Extraversion or Surgency, Agreeableness, Conscientiousness or Dependability, Emotional Stability, and Openness to Experience (Digman, 1996; John *et al.*, 1988). Three fundamental findings suggest that these five dimensions are not applicable only to restricted human populations but instead have a biological foundation that may have preceded the emergence of modern humans. First, the five factors have been repeatedly identified across several Western and non-Western societies, showing that the factors are not specific to any particular language or culture (McCrae and Costa, 1997).

Second, King and Figueredo (1997) who obtained zoo workers’ ratings of chimpanzees on 43 adjectival

personality descriptors demonstrated generalization of the Big Five to a nonhuman hominoid, the chimpanzee. Factor analysis identified one large factor that contained 12 adjectives and was clearly related to Dominance. Each of the remaining five factors was defined by fewer than 12 adjectives and resembled somewhat narrowed versions of the human Big Five. Since the chimpanzees displayed six factors and not the human five, the factor structure was not simply an artifact of the implicit personality theories of the raters based on human personality structure. Furthermore, a review of animal personality literature by Gosling and John (1999) showed some of the Big Five factors in a wide assortment of species, ranging from octopuses to dogs.

Research on primate personality factors has been based on behavioral measures as well as subjective ratings by raters who were familiar with the animals. For primates, both methods of assessing personality have high interrater reliabilities, evidence that the resulting personality factors reflect real characteristics of the animals (Chamove *et al.*, 1972; Stevenson-Hinde *et al.*, 1980; Gold and Maple, 1994; King and Figueredo, 1997). High interrater reliability, interitem consistency, and temporal stability of individual factor scores have

¹ Department of Psychology, University of Arizona, Tucson, Arizona 85721.

² To whom correspondence should be addressed. e-mail: aweiss@u.arizona.edu.

been reported in stumptailed macaques (Figueredo *et al.*, 1995) and chimpanzees (Stevenson-Hinde *et al.*, 1980). Furthermore, some rodent (Royce *et al.*, 1973; Broadhurst, 1975), dog (Scott and Fuller, 1965), and mink (Hansen, 1996) strains have certain dispositions such as reactivity, emotionality, and social behavior that can be selectively bred. This line of work indicates that these dispositions have a genetic basis and suggests that subjectively measured personality traits in animals may be heritable.

Third, behavioral genetic research using the twin design revealed that over many samples and personality inventories, the broad-sense heritabilities of various personality measures ranged between .40 and .50 (see Nichols, 1978; Loehlin, 1992; Bouchard, 1994). Broad-sense heritability is an estimate of the proportion of phenotypic variance due to additive and nonadditive genetic effects; narrow-sense heritability is an estimate of the proportion of variance due only to additive genetic effects. Furthermore, both twin and nontwin designs have consistently shown that only a small proportion of variance in personality can be accounted for by shared environmental effects (Loehlin, 1992; Bouchard, 1994).

Studies using nontwin designs, such as family and adoption studies, produced heritability estimates that were often much lower than heritability estimates from twin studies. For instance, a family and adoption study by Ahern *et al.* (1982) showed that the upper bounds of the broad as well as the narrow-sense heritabilities of 54 personality traits were in the low .20s. This estimate was only slightly different from estimates of other adoption and family studies (Loehlin *et al.*, 1980; Scarr *et al.*, 1981).

These discrepancies between heritabilities from twin and nontwin studies probably occurred because nontwin designs can assess only the contribution of environmental and additive genetic effects. An additional problem is reflected in a review of the current literature, strongly suggesting that narrow-sense heritability estimates vary across factors and studies (Bouchard, 1994). In contrast, twin designs can also assess the contribution of nonadditive genetic effects such as dominance, epistasis, and, in extreme cases, emergence to individual differences in personality (Loehlin, 1992). Thus, the research on personality suggests that estimates of broad-sense heritabilities derived from twin designs are relatively more robust across studies, while the narrow-sense heritabilities derived from any design are more variable.

Tellegen *et al.* (1988), using these techniques to examine twins reared apart and together, showed that the proportion of heritability due to additive genetic ef-

fects differed across scales of the Multidimensional Personality Questionnaire (MPQ). For example, non-additive genetic effects almost exclusively caused the heritability of Well-Being while the heritability of Stress Reaction was caused mostly by additive genetic effects (Tellegen *et al.*, 1988).

Bouchard (1994) conducted a meta-analysis synthesizing earlier studies on the heritability of personality (Nichols, 1978; Loehlin, 1992) under the framework of the five-factor model. The meta-analysis revealed some dramatic differences in narrow-sense heritability across three major studies and the five personality factors (Nichols, 1978; Loehlin, 1992; Bouchard, 1990, 1994).

These inconsistencies in the estimates of narrow sense heritabilities also occurred in different studies using the same instrument for assessing the Big Five. Bergman *et al.* (1993) assessed the heritabilities of dimensions of the NEO-PI (Costa and McCrae, 1989, cited by Bergman *et al.*, 1993) and, unlike other studies, found broad-sense heritability estimates equal to .40, .12, and .29 for Openness, Conscientiousness, and Agreeableness, respectively. Furthermore, the heritabilities of the latter two factors were due almost entirely to dominance effects.

Other investigators have also used twin designs to estimate the heritabilities of the five factors in the NEO-PI-R (Costa and McCrae, 1992, cited by Jang *et al.*, 1996). For example, Jang *et al.* (1996) showed that the heritability of Openness was attributable almost entirely to nonadditive genetic effects. A follow-up study using a Canadian and German twin sample (Jang *et al.*, 1998) showed no differences across the two samples and narrow-sense heritabilities for the five factors approaching .50. Another recent study using Costa and McCrae's instrument showed still other patterns (Riemann *et al.*, 1997).

Prior research, in both animal personality and breeding for behavioral and emotional dispositions, as well as the similarities between chimpanzees and humans, was the basis for our investigation of genetic sources of individual differences in chimpanzee personalities. However, unlike most previous behavior genetic studies in nonhuman species, our study did not demonstrate genetic correlates of personality by using different breeds or selectively bred lines. Instead, we used naturally occurring individual differences within a single breeding population to determine the heritabilities of the six chimpanzee personality traits. Because the chimpanzees in this study were distributed across different zoos, we were able to test for the influence of shared zoo environment on personality factors. The distribution of the chimpanzees across zoos offered two advantages over the use of

either inbred strains or wild populations in natural environments (including humans). First, the zoo environments were seminaturalistic to varying degrees and enabled chimpanzees to interact with conspecifics. Second, because of efforts by zoos to prevent inbreeding, related pairs of chimpanzees were housed in different as well as the same zoos. Therefore, confounding from active gene \times environment correlations was reduced since chimpanzees could not choose their home zoo, although they could choose their own social environments within each zoo. These unique within-zoo social environments would, in effect, represent a nonshared environmental effect.

Individual differences in human personality factors are caused primarily by genetic differences and nonshared environment effects, whereas the effect of the shared or common environment is usually negligible (Bouchard, 1994; Rowe, 1994). Heritability analyses allow us to answer the question of whether personality factors in chimpanzees are also heritable and whether the large disparity between the effects of shared and nonshared environments on human personality are mirrored in chimpanzee personality. The shared evolutionary history between humans and chimpanzees leads us to believe that chimpanzee personality factors may be homologous to human personality factors. This homology may be displayed not only in personality factor structure but also in the genetic and environmental sourced of individual differences. Therefore, we would expect that genetic, shared, and nonshared environmental effects should be similar in these two closely related species.

METHOD

Personality Ratings

Personality ratings were collected on 145 chimpanzees (56 males and 89 females with mean ages of 15.4 and 19.5 years, respectively) from 12 zoos in the United States and 1 zoo in Australia that participated in the ChimpanZoo Program of the Jane Goodall Institute. Raters were either zoo employees who worked at the chimpanzee habitats or observers who had extensive experience observing chimpanzees as part of the ChimpanZoo behavioral observation program. The observers had a mean of 6.5 years' experience with the chimpanzees before the ratings were made. The raters based their scoring on their overall impressions of the chimpanzees' personality attributes.

Each chimpanzee was rated on the 43 adjectival items described in King and Figueredo's (1997) study. Three items, manipulative, autistic, and clumsy, did not load on any of the factors and were dropped. Unit-weighted factor scores for the six factors were then constructed based on salient factor loadings from that study (see Table I). All chimpanzees within a zoo were rated by a common set of raters at that zoo who did not rate chimpanzees at other zoos. The number of raters at each zoo as well as the number of chimpanzees at each zoo varied. Internal consistency reliabilities based on item intercorrelations within factors were calculated using a version of Cronbach's alpha (see Nunnally and Bernstein, 1994, p. 277). These internal consistency reliabilities varied from .93 (Dominance) to .72 (Emotional Stability).

Table I. Reliabilities and Items Defining the Six Personality Factors

Factor	α		Definition
	IR	IC	
Dominance	.88	.93	+ Dominant + Independent + Decisive + Intelligent + Persistent + Bullying + Stingy - Submissive - Dependent - Fearful - Timid - Cautious
Surgency	.88	.93	+ Active + Playful + Sociable + Affectionate + Imitative + Impulsive - Solitary - Lazy - Depressed
Dependability	.78	.89	+ Predictable - Impulsive - Defiant - Reckless - Erratic - Irritable - Aggressive - Jealous - Disorganized
Agreeableness	.71	.84	+ Sympathetic + Helpful + Sensitive + Protective + Gentle
Emotional Stability	.74	.72	+ Stable + Unemotional - Excitable
Openness	.83	.87	+ Inventive + Inquisitive

Note. IR, interrater reliabilities; IC, internal consistency of the factor.

Internal consistency factor reliabilities based on data from the 45 chimpanzees most recently rated (mean = .89) were virtually identical to those from the 100 chimpanzees used in the original King and Figueredo (1997) study (.85) that were part of our sample and on which the factor compositions were determined. The high reliability of the data on the 45 additional chimpanzees is confirmatory evidence that factors reliably generalized beyond data used to determine the original factor definitions. Table I shows the interrater and the internal consistency reliabilities for all factors.

In addition, interrater reliabilities for each of the factors were calculated using formula ICC(3,k) (Shrout and Fleiss, 1979), which is also a version of Cronbach's alpha (1951). The mean square error for these formulas is ordinarily defined as the raters by subjects interaction. In our case, the interaction was generalized across zoos by using the mean square of raters by chimpanzees within zoos as the error term. These coefficients showed that interrater reliabilities of mean factor scores based on a mean of 4.1 raters for each subject ranged from .88 (Dominance and Surgency) to .71 (Agreeableness).

Quantitative Genetic Analysis

To adjust scores for small but statistically significant age and sex differences in personality scores, linear regressions of age on factor scores were performed separately for male and female chimpanzees. Residuals from the regression lines were used for the subsequent analysis.

Most techniques for estimating the proportion of phenotypic variance accounted for by genetic, shared environment, and nonshared environment effects are based on samples containing independent genetically related pairs of subjects (Plomin *et al.*, 1997). Chimpanzee populations across zoos have a complex network of familial relationships that do not lend themselves to these commonly used methods because the number of independent pairs having any particular type of genetic relationship is too small.

The problem presented by complex genealogical networks is similar to that faced by cattle breeders and researchers wishing to determine heritability of traits in wild populations of primates. A method that has been used successfully to estimate heritability in populations with complex familial structures is the symmetric differences squared (SDS) technique (Grimes and Harvey, 1980; Cheverud *et al.*, 1990a, b). Simulation and real data studies have shown that SDS is a more accurate technique than conventional methods based on analy-

sis of variance to estimate heritability of traits (Bruckner and Slinger, 1986a, b). SDS solves the familial complexity problem by incorporating phenotypic differences between all possible pairs of subjects in the sample whether related or unrelated.

SDS is based on the fact that the average squared differences of all possible pairs in a sample, where no individual is paired with itself, equals twice the sample variance. This sample variance will be biased downward relative to the population variance because observations for related animals should be positively correlated. Therefore, for correlated observations, the expected value of a squared difference between individual *i* and individual *j* equals

$$E(Y_i - Y_j)^2 = 2[\text{var}(Y) - \text{cov}(Y_i, Y_j)]$$

where $i < j$ and $\text{var}(Y) = \text{var}(Y_i) = \text{var}(Y_j)$. The estimates of the variances and covariances can be derived via a simple latent variable model (see Fig. 1) where, for any given pair of animals *i* and *j*, observations are the result of additive genetic effects (*A*), zoo effects (*Z*), and nonshared environmental effects plus error (*E*). Based on the degree of relatedness between animal *i* and animal *j*, additive genetic effects will be correlated by R_{ij} (Wright's coefficient of relationship). Zoo effects are correlated by rz_{ij} , which equals 1 if animals *i* and *j* live

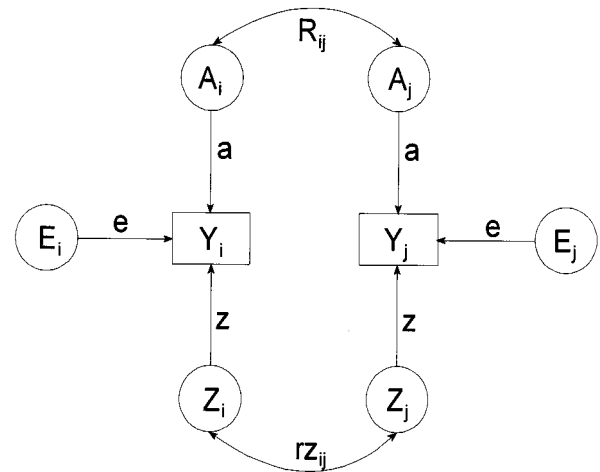


Fig. 1. The correlation in trait *Y* for any given pair of animals, *i* and *j*, is described as a function of six latent variables with variances equal to 1.0. Latent variables include additive genetic (*A*), shared zoo (*Z*), and nonshared environment plus error (*E*) effects. Paths *a*, *z*, and *e* are the effects of each variable effect on the trait of interest. Correlation R_{ij} is Wright's coefficient of relationship and rz_{ij} is a dummy-coded variable equal to 1 if a pair lives in the same zoo and 0 if it does not.

in the same zoo and 0 if they do not. Nonshared environment effects and error are not correlated in any pair. Therefore the variance and covariance between two individuals' phenotypes are given by the following two formulas:

$$\begin{aligned} \text{var}(Y) &= a^2 + z^2 + e^2 \\ \text{cov}(Y_i, Y_j) &= R_{ij}a^2 + rz_{ij}z^2 \end{aligned}$$

By means of substitution the fast equation can thus be shown to equal

$$\begin{aligned} \frac{1}{2} E(Y_i - Y_j)^2 &= \text{var}(Y) - \text{cov}(Y_i, Y_j) \\ &= e^2 + a^2(1 - R_{ij}) + z^2(1 - rz_{ij}) \\ &= b_0 + b_1x_1 + b_2x_2 \end{aligned}$$

The above formula has the form of a regression equation, where e^2 is equal to the intercept, a^2 is the unstandardized beta weight attached to $(1 - R_{ij})$, and z^2 is the unstandardized beta weight attached to $(1 - rz_{ij})$. These parameters can be estimated using ordinary least-squares regression procedure such as PROC REG (SAS Institute, 1989). The variance components can then be used to compute the proportion of variance accounted for by each potential source of variance, namely,

$$\begin{aligned} h^2 &= a^2 / (a^2 + z^2 + e^2) \\ z^2 &= z^2 / (a^2 + z^2 + e^2) \\ e^2 &= e^2 / (a^2 + z^2 + e^2) \end{aligned}$$

We first determined, for each factor, whether a restricted model that excluded z^2 , the effects of shared zoo environment, fit as well as one that included h^2 , z^2 , and e^2 . To compare the inclusive and reduced models for each factor, we used the difference R^2 F -ratio (Cohen and Cohen, 1983, p. 145):

$$F = [(R_I^2 - R_R^2) / (df_I - df_R)] / [(1 - R_I^2) / (N - k_I - 1)]$$

Here $(R_I^2 - R_R^2)$ is the difference in the total variance accounted for by the inclusive and restricted models, respectively. The term $(df_I - df_R)$ represents the difference in the degrees of freedom between the inclusive and the restricted models. The amount of variance unaccounted for by the inclusive model is represented by $(1 - R_I^2)$. N represents the total number of pairs and k_I is the number of predictor variables in the inclusive model. A nonsignificant F ratio indicates that the reduced model is not accompanied by a significant

loss in ability to account for variance. The final parameter estimates are then derived from this reduced model.

While the parameter estimates obtained from the SDS procedure are correct, the lack of statistical independence among pairs makes the standard error estimates and p values incorrect because each individual contributes to $N - 1$ squared differences. To obtain the correct p values we used a Monte Carlo simulation based on a technique described by Cheverud *et al.* (1990b). The Monte Carlo simulation incorporated 1000 iterations in which each iteration was a regression of the squared phenotypic differences onto the degree of genetic relationship and the zoo variable after the squared differences were reassigned to randomly selected pairs of chimpanzees. New values of h^2 , z^2 , and e^2 were computed and the proportion of times these values were equal to or exceeded the values obtained in the original solution was used to estimate the significance level.

RESULTS

Since none of the reduced models differed significantly from the inclusive models, shared zoo effects were eliminated from Dominance ($F = 3.13$, $p > .05$), Surgency ($F = 1.04$, $p > .05$), Dependability ($F = .00$, $p > .05$), Agreeableness ($F = .00$, $p > .05$), Emotional Stability ($F = .00$, $p > .05$), and Openness ($F = 1.04$, $p > .05$). Thus, shared zoo effects were negligible for all six personality factors, indicating that related chimpanzee pairs at the same zoo had no more similar factor scores than equally related chimpanzees at different zoos.

Only Dominance ($h^2 = .63$) was significantly heritable. Dependability showed evidence that it might be heritable, but the parameter estimates were not statistically significant ($h^2 = .21$). Two other personality traits, Agreeableness ($h^2 = .03$) and Emotional Stability ($h^2 = .08$), showed positive heritability estimates but the parameter estimates were nonsignificant and small. Openness and Surgency showed no evidence of heritability. The remaining variance was accounted for by error and nonshared environmental effects (see Table II). As in other forms of variance components analysis using least-squares estimation, negative estimates are sometimes produced due to sampling error and these are interpretable as indicating variance components with true values of virtually zero (see Figueredo *et al.*, 1995). The variance estimates for the reduced model are displayed in Table II.

Table II. Proportion of Factor Variance Accounted for by Heritability, the Shared Zoo Environment, and Error Plus the Nonshared Environment in the Inclusive and Restricted Models

Factor	h^2 (p)	z^2 (p)	e^2
Dominance	.796 (.000)	-.103 (.957)	.307
	.626 (.000)		.374
Surgency	-.386 (.926)	.024 (.369)	1.362
	-.347 (.933)		1.347
Dependability	.221 (.174)	-.008 (.547)	.786
	.209 (.145)		.791
Agreeableness	.055 (.417)	-.018 (.641)	.963
	.026 (.471)		.974
Emotional Stability	.054 (.405)	.014 (.412)	.931
	.078 (.377)		.922
Openness	-.157 (.749)	.030 (.285)	1.127
	-.108 (.676)		1.108

Note. Values of p equal to .000 indicate that none of the iterations resulted in an estimate greater than or equal to the parameter estimate and should be interpreted as $p < .001$.

DISCUSSION

The most important and striking implication of these results is their demonstration that chimpanzee personality factors share some basic properties with human personality factors. First, Dominance displayed significant heritability, *i.e.*, a significant proportion of individual differences in Dominance can be attributed to additive genetic effects. Second, the negligible between-zoo differences in chimpanzees are similar to the negligible between-family or shared environment effects in humans (Loehlin, 1992; Rowe, 1994; Bouchard, 1994). Third, the narrow-sense heritability reported for Dependability, while not significant, falls well within the range of values reported for humans. For example, in one meta-analytic review of various human studies, Bouchard (1994) found that what might be termed “measurement” or “method” effects accounted for substantial variability in the reported estimates. This method variance may account for as much as plus or minus .10 to .25 (depending on the trait) in the 95% confidence intervals for population effect size estimates of personality trait heritability in humans. Because we used a different method than was used for most human studies, this source of variability could well account for any seeming between-species discrepancies in estimates of trait heritability for some factors. Openness and Surgency may not have fallen within these confidence intervals because the Openness factor contained only two items and several items that make up Surgency or Extraversion in humans loaded on the Dominance factor in chimpanzees.

Dominance as commonly described in the primate behavior literature should be distinguished from the Dominance factor as operationalized in this experiment. An animal gaining control over a potential mate or resource is usually interpreted as an expression of the former. This sort of dominance can also be expressed by aggressive or assertive displays in the absence of any explicit resources (Bernstein, 1981). Thus, the central fact about the dominance commonly discussed in the primate literature is that it is often situation specific and may be subject to change over short periods of time, particularly after episodes of political upheaval within a primate group. The traditional dominance construct may be referred to as situational dominance.

On the other hand, dominance as described in this paper is an extremely broad personality dimension containing adjectives from all of the human Big Five factors that are related to the overall competitive prowess of the chimpanzee. This trait dominance probably remains stable over long periods of time in different social contexts. Some of the descriptors of Dominance, for example, *timid*, are similar to descriptors that define the human Extraversion factor. Others, for example, *fearful*, are descriptors that define the human factor of Emotional Stability or Neuroticism. In humans, the Extraversion and Neuroticism factors have been consistently identified not only in the Big Five factor structure but also in the two other major factor structures: Eysenck’s Big Three (Psychoticism, Extraversion, and Neuroticism) and Cattell’s 16 PF personality factor model (John *et al.*, 1988).

Primate dominance studies have typically been based on situational dominance. However, we would expect that situational and trait dominance should be positively correlated. For example, a previous study of wild chimpanzees showed a negative correlation between *timidity* on the Emotions Profile Index and situational dominance (Buirski *et al.*, 1978). Stevenson-Hinde (1983) also found a high correlation between the trait *effective* (which she defined as “gets own way; can control others”) and observations of how often rhesus monkeys displaced or avoided others. Dominance is also probably related to fitness. A recent study (Pussey *et al.*, 1997) showed that, in a natural population of chimpanzees, females displaying high situational dominance lived longer and had more infants, more surviving infants, and more rapidly maturing daughters than low-dominance females. Thus, it is likely that both trait and situational dominance are closely related to fitness.

The following evolutionary questions are suggested by these results. Was the five-factor personality structure of both humans and chimpanzees maintained during the approximately 5 million years in independent human and chimpanzee evolution or did it emerge independently in the two groups? If the five-factor structure was maintained, was it, or portions of it, heritable during this time? If personality dimensions in both chimpanzee and human evolution were heritable, to what extent and how did they contribute to inclusive fitness? Obviously we are not now able to give definitive answers to any of these questions.

However, we would note that Fisher's (1958) principle stating that variation in characteristics that are both fitness enhancing and heritable will diminish over time does not necessarily preclude continued variation in heritable personality traits. In fact, recent findings that measure how much genetic variability underlies a trait has found that quite often traits directly affecting fitness such as fecundity and fertility have more genetic variability than many morphological traits (Houle, 1992).

The latter point illustrates an area of contention between researchers in evolutionary psychology and researchers in behavior genetics and individual differences (for a recent review see Bailey, 1998). Some evolutionary psychologists, most notably Tooby and Cosmides (1990), claim that heritable individual differences in personality traits are not related to fitness and that these individual differences are merely random variation around a species-specific mean representing optimal fitness. On the other hand, some behavior geneticists (Bailey, 1998) and evolutionary psychologists (Buss, 1990) argue that fitness-enhancing traits can be heritable under a number of conditions. For instance, phenotypic traits that contribute to fitness in rapidly changing social and physical environments may have high heritabilities (Burger *et al.*, 1989; Wilson, 1994). This is because heritable individual differences will be maintained in a patchy environment where certain levels of a trait may enhance fitness at one point in time and space, while others enhance fitness at another point in time and space. Sexual selection may also maintain high heritabilities for fitness-enhancing traits, notably those related to pathogen resistance, because the level of a sexually selected trait that is optimal at any given time might vary indefinitely due to shifting host-parasite coevolutionary pressures (Hamilton, 1982; Hamilton and Zuk, 1982). This directionally destabilizing process

would be one manifestation of the "Red Queen" hypothesis (Ridley, 1993).

Frequency-dependent selection can also maintain individual differences in fitness-enhancing traits when the optimal level of a trait depends on the levels of the trait exhibited by other animals in the area. This theory derives the evolution of interindividual variability in innate behavioral dispositions from a frequency-dependent mechanism of disruptive selection analogous to intraspecific character displacement (Figueredo, 1995). If for a species in a given situation, an optimal norm of response exists, deviations from that norm would not be selectively neutral. Selective pressure for a species-typical mean exactly at this optimum would create a centripetal force against any substantial individuation. However, clustering of the entire population at the optimum mean might produce intense social competition in the "hump" of the distribution. Therefore, reduced social competition would occur in the "tails" of that same distribution to the extent that the random forces of mutation and recombination produced any variability at all. That would create disruptive selection for individuation as a centrifugal force perhaps partially counteracting the selective pressure pulling toward the mean. In certain circumstances, the competitive release experienced by individuals in the "tails" of the distribution could compensate for the presumed cost of deviation from the species-typical norm of response. This would, in turn, create a distribution of alternative behavioral phenotypes in the population by the progressive expansion of the "tails" of the distribution around the optimal central tendency.

For example, chimpanzees in a population with high mean trait dominance would be subject to many challenges and potentially injurious encounters. In this population, low trait dominance could be fitness enhancing since the low-trait dominance animals might spend more time in more productive activities, such as mating with females, and be less subject to being injured in a competition for situational dominance.

The heritability of at least one broad personality factor in chimpanzees is evidence that a genetic basis for personality dimensions has a fairly long evolutionary history. Thus, the expression of a personality factor such as trait dominance may have contributed to fitness in early hominid evolution. Since chimpanzee and human evolutionary lineages diverged as recently as 5 million years ago (Sarich and Wilson, 1967), the implication is that selection for the expression of these factors occurred early in hominid evolution, long before the advent of language.

ACKNOWLEDGMENTS

We would like to express our deep appreciation of Virginia Landau, Director of ChimpanZoo, and all of the zoo workers at the participating zoos who contributed the chimpanzee personality ratings. We would also like to thank Patricia Jones, James M. Cheverud, and R. Mark Enns for their invaluable assistance with the statistical portion of this paper and David Rowe, Robert McCrae, Lee Sechrest, and Samuel Gosling for their invaluable comments and suggestions.

REFERENCES

- Ahern, F. M., Johnson, R. C., Wilson, J. R., McClearn, G. E., and Vandenberg, S. G. (1982). Family resemblances in personality. *Behav. Genet.* **1**:175–194.
- Bailey, J. M. (1998). Can behavior genetics contribute to evolutionary behavioral science? In Crawford, C. B., and Krebs, D. (eds.), *Handbook of Evolutionary Psychology: Ideas, Issues, and Applications*, Lawrence Erlbaum Associates, Mahwah, NJ, pp. 211–233.
- Bergeman, C. S., Chipuer, H. M., Plomin, R., Pedersen, N. L., McClearn, G. E., Nesselrode, J. R., Costa, P. T., Jr., and McCrae, R. R. (1993). Genetic and environmental effects on openness to experience, agreeableness, and conscientiousness: An adoption/twin study. *J. Person.* **61**(2):159–179.
- Bernstein, I. S. (1981). Dominance: The baby and the bathwater. *Behav. Brain Sci.* **4**:419–457.
- Bouchard, T. J., Jr. (1994). Genes, environment, and personality. *Science* **264**:1700–1701.
- Bouchard, T. J., Jr., Lykken, D. T., McGue, M., Segal, N. L., and Tellegen, A. (1990). Sources of human psychological differences: The Minnesota study of twins reared apart. *Science* **250**:223–228.
- Broadhurst, P. L. (1975). The Maudsley reactive and nonreactive strains of rats: A survey. *Behav. Genet.* **5**:299–319.
- Bruckner, C. M., and Slinger, W. D. (1986a). Symmetric differences squared and analysis of variance procedures for estimating genetic and environmental variances and covariances for beef cattle weaning weight: I. Comparison via simulation. *J. Anim. Sci.* **63**:1779–1793.
- Bruckner, C. M., and Slinger, W. D. (1986b). Symmetric differences squared and analysis of variance procedures for estimating genetic and environmental variances and covariances for beef cattle weaning weight: II. Estimates from a data set. *J. Anim. Sci.* **63**:1794–1802.
- Buirski, P., Plutchik, R., and Kellerman, H. (1978). Sex differences, dominance, and personality in the chimpanzee. *Anim. Behav.* **26**:123–129.
- Burger, R., Wagner, G. P., and Stettinger, F. (1989). How much heritable variation can be maintained in a finite population by mutation—selection? *Evolution*. **43**: 1748–1766.
- Buss, D. M. (1990). Toward a biologically informed psychology of personality. *J. Person.* **58**(1):1–16.
- Chamove, A. S., Eysenck, H. J., and Harlow, H. F. (1972). Personality in monkeys: Factor analyses of rhesus social behaviour. *Q. J. Exp. Psychol.* **24**:496–504.
- Cheverud, J. M., Falk, D., Hildebolt, C., Moore, A. J., Helmkamp R. C., and Vannier, M. (1990a). Heritability and association of cortical petalias in rhesus macaques (*Macaca mulatta*). *Brain Behav. Evol.* **35**:368–372.
- Cheverud, J. M., Falk, D., Vannier, M., Königsberg, L., Helmkamp, R. C., and Hildebolt, C. (1990b). Heritability of brain size and surface features in rhesus macaques (*Macaca mulatta*). *J. Hered.* **81**:51–57.
- Cohen, J., and Cohen, P. (1983). *Applied Multiple Regression/Correlation Analysis for the Behavior Sciences*, 2nd ed., Lawrence Erlbaum Associates, Hillsdale, NJ.
- Costa, P. T., Jr., and McCrae, R. R. (1985). *The NEO Personality Inventory Manual*, Psychological Assessment Resources, Odessa, FL.
- Costa, P. T., Jr., and McCrae, R. R. (1992). *Revised NEO Personality Inventory (NEO-PI-R) and NEO Five-Factor Inventory (NEO-FFI) Professional Manual*, Psychological Assessment Resources, Odessa, FL.
- Cronbach, L. J. (1951). Coefficient alpha and the internal structure of tests. *Psychometrika* **16**:297–334.
- Digman, J. M. (1996). The curious history of the five-factor model. In *The Five-Factor Model of Personality: Theoretical Perspectives*, Guilford Press, New York, pp. 1–20.
- Figueredo A. J. (1995). The evolution of individual differences. Paper presented at Jane Goodall Institute ChimpanZoo Annual Conference, Tucson, AZ.
- Figueredo, A. J., Cox, R. L., and Rhine, R. J. (1995). A generalizability analysis of subjective personality assessments in the stump-tail macaque and the zebra finch. *Multivar. Behav. Res.* **30**(2):67–197.
- Fisher, R. A. (1958). *The Genetical Theory of Natural Selection*, Dover, New York.
- Gold, K. C., and Maple, T. L. (1994). Personality assessment in the gorilla and its utility as a measurement tool. *Zoo Biol.* **13**:509–522 (1994).
- Gosling, S. D., and John, O. P. (1999). Personality dimensions in non-human animals: A cross-species review. *Curr. Direct. Psychol. Sci.* **8**(3):69–75.
- Grimes, L. W., and Harvey, W. R. (1980). Estimation of genetic variances and covariances using symmetric differences squared. *J. Anim. Sci.* **50**(4):634–644.
- Hamilton, W. D. (1982). Pathogens as causes of genetic diversity in their host populations. In Anderson, R. M., and May, R. M. (eds.), *Population Biology of Infectious Diseases*, Springer-Verlag, New York.
- Hamilton, W. D., and Zuk, M. (1982). Heritable true fitness and bright birds—A role for parasites. *Science* **211**:384–387.
- Hansen, S. W. (1996). Selection for behavioral traits in farm mink. *Appl. Anim. Behav. Sci.* **49**(2):137–148.
- Houle, D. (1992). Comparing evolvability and variability of quantitative traits. *Genetics*. **130**(1):195–204.
- Jang, K. L., Livesley, W. J., and Vernon, P. A. (1996). Heritability of the Big Five personality dimensions and their facets: A twin study. *J. Person.* **64**(3):577–591.
- Jang, K. L., McCrae, R. R., Angleitner, A., Riemann, R., and Livesley, W. J. (1998). Heritability of facet-level traits in a cross-cultural twin sample: Support for a hierarchical model of personality. *J. Person. Soc. Psychol.* **74**(6):1556–1565.
- John, O. P., Angleitner, A., and Ostendorf, F. (1988). The lexical approach to personality: A historical review of trait taxonomic research. *Eur. J. Person.* **2**:171–203.
- King, J. E., and Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *J. Res. Person.* **31**:257–271.
- Loehlin, J. C. (1992). *Genes and Environment in Personality Development*, Sage, Newbury Park, CA.
- Loehlin, J. C., Horn, J. M., and Willerman, L. (1981). Personality resemblance in adoptive families. *Behav. Genet.* **11**:309–330.
- McCrae, R. R., and Costa, P. T. (1997). Personality trait structure as a human universal. *Am. Psychol.* **52**(5):509–516.
- Nichols, R. C. (1978). Twin studies of ability, personality, and interests. *Homo* **29**:158–173.
- Nunnally, J. C., and Bernstein, I. H. (1994). *Psychometric Theory*, 3rd ed., McGraw-Hill, New York.
- Plomin, R., DeFries, J. C., McClearn, G. E., and Rutter, M. (1997). *Behavioral Genetics*, 3rd ed., W. H. Freeman, New York.

- Pussey, A., Williams, J., and Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science* **277**:828–831.
- Ridley, M. (1993). *The Red Queen: Sex and the Evolution of Human Nature*, Penguin Books, New York.
- Riemann, R., Angleitner, A., and Strelau, J. (1997). Genetic and environmental influences on personality: A study of twins reared together using the self- and peer report NEO-FFI scales. *J. Person.* **65**(3):449–475.
- Rowe, D. C. (1994). *The Limits of Family Influence*, Guilford Press, New York.
- Royce, J. R., Poley, W., and Yeudall, Y. T. (1973). Behavior genetic analysis of mouse emotionality: I. factor analysis. *J. Comp. Physiol. Psychol.* **83**:36–47.
- Sarich, V. M., and Wilson, A. C. (1967). Immunological time scale for hominid evolution. *Science* **158**:1200–1203.
- SAS Institute (1989). *SAS/STAT User's Guide, Version 6, Vol. 2*, 4th ed., SAS Institute, Cary, NC.
- Scarr, S., Webber, P. L., Weinberg, R. A., and Wittig, M. A. (1981). Personality resemblance among adolescents and their parents in biologically related and adoptive families. *J. Person. Soc. Psychol.* **40**:885–898.
- Scott, J. P., and Fuller, J. L. (1965). *Genetics of the Social Behavior of the Dog*, University of Chicago Press, Chicago.
- Shrout, P. E., and Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychol. Bull.* **86**:420–428.
- Stevenson-Hinde, J. (1983). Individual characteristics and the social situation. In Hinde, R. A. (ed.), *Primate Social Relationships: An Integrated Approach*, Sinauer Associates, Sunderland, MA, pp. 28–35.
- Stevenson-Hinde, J., Stillwell-Barnes, R., and Zunz, M. (1980). Subjective assessment of rhesus monkeys over four successive years. *Primates* **21**:66–82.
- Tellegen, A., Lykken, D. T., Bouchard, T. J., Jr., Wilcox, K. J., Segal, N. L., and Rich, S. (1988). Personality similarity in twins reared apart and together. *J. Person. Soc. Psychol.* **54**:1031–1039.
- Tooby, J., and Cosmides, L. (1990). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *J. Person.* **58**:17–67.
- Wilson, D. S. (1994). Adaptive genetic variation and human evolutionary psychology. *Ethol. Sociobiol.* **6**:219–236.

Edited by Michael Miller