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GENETIC AND ENVIRONMENTAL CONTRIBUTIONS TO
DOMINANCE AND SUBJECTIVE WELL-BEING IN
CHIMPANZEES (*Pan troglodytes*)

by
Alexander Weiss

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF PSYCHOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
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In the Graduate College
THE UNIVERSITY OF ARIZONA

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by ALEXANDER WEISS entitled GENETIC AND ENVIRONMENTAL CONTRIBUTIONS TO DOMINANCE AND SUBJECTIVE WELL-BEING IN CHIMPANZEES (PAN TROGLODYTES)

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DEDICATION

This work is dedicated to my parents, Gisela and David, whose selfish genes directly and indirectly made this possible.

TABLE OF CONTENTS

LIST OF TABLES	8
LIST OF FIGURES	9
ABSTRACT	10
CHAPTER 1. INTRODUCTION	11
1.1. Overview	11
1.2. Chimpanzees	11
1.2.1. Habitats	11
1.2.2. Social Structure	12
1.2.3. Genetic and Behavioral Affinity with Humans	14
1.3. Individual and Group Differences	15
1.3.1. Two Traditions	15
1.3.2. The Beginnings of Integration	18
1.3.3. Advantages of Using the Human Model	21
1.3.4. The Study of Individual Differences in Primates	23
1.4. Remaining Questions	25
1.4.1. The Search for the Nonshared Environment	25
1.4.2. The Search for Environmental Predictors of SWB	28
1.5. Study Description	32
1.5.1. Goals	32
1.5.2. Design	34
1.5.3. Hypotheses and Variables	36
1.5.4. Analysis Plan	38
CHAPTER 2. METHODS	41
2.1. Subjects and Measures	41
2.1.1. Zoological Parks	41
2.1.2. Subjects	41
2.1.3. Ratings	43
2.2. Environmental Analysis	47
2.2.1. Analytic Strategy	47
2.2.2. Predictor Variables	48
2.2.3. Interactions	54
2.2.4. Nested Model Comparisons	57
2.3. Genetic Analysis	58
2.3.1. Goals of the Analysis	58

TABLE OF CONTENTS—*Continued*

2.3.2. Analytic Strategy	59
2.3.3. Model Fitting	61
CHAPTER 3. RESULTS	66
3.1. Environmental Analysis	66
3.1.1. Predictors of Dominance	67
3.1.2. Predictors of Subjective Well-Being	69
3.2. Genetic Analysis	70
3.2.1. The Three Means of Comparison	72
3.2.2. Parameter Estimates	75
CHAPTER 4. DISCUSSION	80
4.1. Environmental Analysis	80
4.1.1. Overview of the Environmental Analysis	80
4.1.2. Interpretation	81
4.1.3. Conclusions from the Environmental Analysis	83
4.2. Genetic Analysis	84
4.2.1. Overview of the Genetic Analysis	84
4.2.2. Interpretation	85
4.2.3. Conclusions from the Genetic Analysis	86
4.3. General Conclusions	87
4.3.1. Proximate Causes	87
4.3.2. Ultimate Causes	90
4.3.3. Predictions	91
4.3.4. Change Over Time	93
CHAPTER 5. APPENDICES	95
5.1. Chimpanzee Personality Questionnaire	95
5.1.1. Rating Definitions	95
5.1.2. Adjectival Descriptors	95
REFERENCES	101

LIST OF TABLES

TABLE 2.1.	Relatedness of Pairs in the Same or Different Zoos	43
TABLE 2.2.	Factor Descriptions and Reliabilities	45
TABLE 2.3.	Enclosure Characteristics: Population Density and Age Structure	50
TABLE 2.4.	Mean Personality Scores in Each Zoo	53
TABLE 3.1.	Alternative Models	66
TABLE 3.2.	Nested Model Comparisons	68
TABLE 3.3.	Proportions of Variance and Covariance for the Eight Models . .	71
TABLE 3.4.	Model Comparison Via the <i>AIC</i> and <i>p</i> -Value Fit Indices	72
TABLE 3.5.	Difference Chi-Square Tests	74

LIST OF FIGURES

FIGURE 2.1.	Nested Behavior Genetic Models	60
FIGURE 3.1.	The Saturated Model	76
FIGURE 3.2.	Model 8	78
FIGURE 3.3.	Model 2	79

ABSTRACT

Zoo chimpanzees (*Pan troglodytes*) are restricted in their choice of social and physical environments. This allows for a strong test of environmental predictors of happiness including the chimpanzee-environment fit and the degree of relatedness between a chimpanzee and its enclosure mates. The interrelatedness of zoo chimpanzees permit the study of genetic and environmental contributions to Dominance and subjective well-being (SWB) and their common genetic or environmental causes.

Demographic predictors such as age and sex and environmental predictors such as density of males and females, density of male and female kin, and how similar in personality a chimpanzee was to other chimpanzees in its enclosure were tested first. A series of two-, three-, and four-way interactions was also tested. First, the effects of these predictors on Dominance were tested. Next, these effects were tested on SWB after the variance SWB shared with Dominance was removed. Eight behavioral genetic models were then tested. These models incorporated genetic and environmental variance and covariance components and any significant predictors that were discovered in the previous environmental analysis.

The relationship between age and Dominance was positive and stronger for males than females. The relationship between age and SWB was negative. The genetic model that had the best fit and most parsimony included additive genetic effects and non-shared environmental effects for Dominance and SWB. Zoo effects were negligible. Finally, the genetic correlation between Dominance and SWB was almost entirely due to shared genes.

These findings are consistent with a model positing that Dominance and SWB arise from a common temperament and are differentiated by nonshared environmental influences. They suggest that happiness in apes and humans may be a sexually selected fitness indicator.

Chapter 1

INTRODUCTION

1.1 Overview

This dissertation describes a study concerning environmental and genetic correlates of a personality factor, Dominance, and subjective well-being (SWB) in zoo chimpanzees (*Pan troglodytes*). In most instances, animal behavior researchers and differential psychologists are not familiar with each other's research. This introduction will show how both areas of research complement one another by describing a) chimpanzee natural history and the similarities between humans and chimpanzees; and b) the larger research tradition of differential psychology and, more specifically, contemporary research on human and primate personality and SWB or happiness. The case will then be made that the use of zoo chimpanzees which are more restricted with respect to their choice of environmental niches can address questions about potential environmental predictors of SWB that the human literature cannot. It will also suggest a unique prediction that chimpanzee Dominance and SWB are influenced by common genes.

1.2 Chimpanzees

1.2.1 Habitats

Chimpanzees are our closest living non-human relatives. Chimpanzees and humans shared a common ancestor between 5 and 6 million years ago (Sarich & Wilson, 1967; Waddell & Penney, 1996; Wilson & Sarich, 1969). Following the chimpanzee-hominid split, hominids migrated and settled nearly all of the major continents, whereas chimpanzees have remained in their native habitat of Africa. The major chimpanzee popu-

lations are in Bossou, Gombe, Kibale, Mahale, and Taï. These sites are isolated from one another and gene flow among sites is minimal or non-existent (Napier & Napier, 1985; Pusey, 2001). Different populations and subspecies of chimpanzees have been identified. However, a recent paper identifying a new subspecies argued that the claim that Eastern and Western populations were speciating was overstated as there is considerable gene flow between these populations (Gagneux, Gonder, Goldberg, & Morin, 2001).

1.2.2 Social Structure

There are two major ways to classify the social structures of primates. The first classification system is based on the stability of naturally occurring groups. The second is based on whether males or females disperse. These systems have consequences with respect to the composition of the groups and behavior of individuals within the groups.

Fission-Fusion Social Structure Chimpanzee social structure is unique among primates. While most nonhuman primates have groups that consist of the same individuals over lengthy periods of time, chimpanzee groups are constantly forming, splitting, and reforming over time. This social structure has come to be named fission-fusion (Pusey, 2001).

One example of this observed at the different chimpanzee sites is a sophisticated territorial defense in which groups of male chimpanzees come together to ward off or kill intruders. Evidence showing that chimpanzees in smaller territories weighed less and that females in these territories had longer interbirth intervals led Pusey (2001) to conclude that this territorial defense was primarily for food resources. Other examples have been described by researchers at various field stations. During these incidences, one group of chimpanzees splits off from the main group. Later, the males that

remained in the original group ambushed and killed nearly all of the males in the group that broke off (see Pusey, 2001, for a review).

Sex-biased Dispersal A characteristic of chimpanzee and human societies is the tendency for females, upon reaching sexual maturity, to leave their natal group. This phenomenon, female exogamy, is not common among other mammals or primates and has important consequences (Pusey, 2001).

The social structure resulting from female exogamy is one in which adult females tend to be unrelated to one another while males are related at the degree of half-brother. Kin selection theory (Hamilton, 1964) predicts that this social structure causes male chimpanzees to cooperate more than one would expect, especially during the mating season. This is consistent with the predictions of Sober and Wilson (1999) who suggested that small, interrelated groups such as these often have a greater degree of cooperation than larger groups in which the mean degree of relatedness is low. Males in such species are vertically or politically oriented because they form strategic alliances with males and females within the group. On the other hand, adult females are not likely to find other adult females who share their genes. Thus, they form circles of friends that, unlike the male alliances, are based more on reciprocal altruism and are characterized by sharing, cooperation, and reciprocity (de Waal, 2000).

These orientations may be alternative strategies that are not expected to differ within different environments. If this is the case, sex differences in orientation would not be eliminated or reversed in different social environments.

Another possibility is that these orientations reflect conditional strategies in which the potential for being vertically or horizontally oriented has been selected for and that the strategy pursued depends on environmental factors such as how many relatives are in the vicinity. This would predict that if males are removed from environments in which they are surrounded by kin then they would pursue a strategy similar to that employed by females.

These sex differences in social orientation have been observed in chimpanzees' natural habitats (Goodall, 1986) in which female exogamy exists and in captive populations (de Waal, 2000) where males and females are born in and stay in the same group their entire lives. The fact that these differences in male and female orientation are not limited to wild populations in natural habitats suggests that they are alternative strategies.

1.2.3 Genetic and Behavioral Affinity with Humans

Like other closely related species, chimpanzees and humans share genotypic and phenotypic characteristics. These similarities are particularly dramatic in that researchers have constantly been confounded in their attempt to find some single characteristic, save bipedalism, that distinguishes humans and chimpanzees.

Genetic Similarity As would be expected by the fact that we shared a common ancestor with chimpanzees some 5-6 million years ago (Sarich & Wilson, 1967; Waddell & Penney, 1996; Wilson & Sarich, 1969), chimpanzees and humans share approximately 98% of their DNA with humans (King & Wilson, 1975), more than either species share in common with gorillas (Nei & Tajima, 1985).

Behavioral Similarities There is evidence that the genetic similarity is mirrored by behavioral similarity. Chimpanzees share a number of cognitive capacities such as language (Rumbaugh & Savage-Rumbaugh, 1994), theory of mind (Byrne, 1995; Premack & Woodruff, 1978; Whiten, 1997), reciprocity (de Waal, 2000), and the beginnings of moral behavior (de Waal, 1996) that were once thought to be strictly limited to humans. Furthermore, recent evidence suggests that the structure of chimpanzee personality and its relationship to SWB also resembles that of humans (King & Landau, in press).

1.3 Individual and Group Differences

1.3.1 Two Traditions

Studies of individual and group differences represent the oldest traditions in the study of human behavior. The progenitor of this research was Charles Darwin's cousin Francis Galton. Galton founded research in different areas including character, criminality, intelligence, group differences, and behavior genetics (Degler, 1991; Galton, 1869).

The study of individual differences in primates has been neglected for some time. One possible reason is that there were not enough chimpanzees in captivity and human researchers had not yet begun observing wild chimpanzees. The different traditions within human differential psychology and animal behavior were another barrier to the study of animal personality. In the case of human differential psychology, early research was primarily correlational and focused on measuring individual differences. Early research ascribed individual differences to causes such as genetic variation and related these differences to such things as school success or work performance. While the early work on selective breeding focused on individual differences (see Gosling, 2001, for a review), animal behavior research was primarily identified with comparative psychology or ethology. In both cases the emphasis was on universal laws of learning or naturally occurring behavior, respectively, and not individual or group differences (Cronbach, 1957).

Human Personality Research Research in human personality has been concerned with the measure of personality and the unveiling of its structure. The latter has long been debated and the current consensus is that, at the level above mere descriptors, individual differences in personality can be best described by five broad dimensions: Extraversion or Surgency, Conscientiousness or Dependability, Agreeableness, Neuroticism or Emotional Stability, and Openness (Digman, 1996; John, 1990).

While some researchers argue for fewer (see Eysenck, 1967; Tellegen et al., 1988) or more than five factors (see Brand & Egan, 1989; Cattell & Cattell, 1995), personality, however defined, reflects real biological differences that have an evolutionary history (Bouchard & Loehlin, 2001).

These five dimensions have been found in many different Western and non-Western societies, a finding that indicates that these factors are neither culture or language bound (McCrae & Costa, 1997). Moreover, a review of the literature on animal personality revealed that three of the Big Five, Extraversion, Agreeableness, and Neuroticism emerged repeatedly in a wide variety of species (Gosling, 2001). On the other hand, Conscientiousness was identified only in humans and chimpanzees (Gosling & John, 1999).

Also, extensive meta-analyses of more than two decades of twin studies on personality show that approximately 50% of the variance in these five factors is attributable to additive and non-additive genetic variance. Another finding was that the common or shared environment, those environmental conditions that should cause siblings to resemble one another, account for almost none of the variance in personality. Instead, the remaining variance is due primarily to nonshared environmental effects and error, *i.e.*, unique experiences that siblings do not share and which will make them different from one another (Bouchard & Loehlin, 2001). Recent behavior genetic studies on personality have also shown that factor analyzing genetic covariance matrices results in factor structures that are almost identical to those revealed by factor analyzing the original scales (Livesley, Jang, & Vernon, 1998; McCrae, Jang, Livesley, Riemann, & Angleitner, 2001).

Human Subjective Well-Being Research Individual differences in human SWB have also been successfully measured by human differential psychologists (see Diener, 1996; Diener, Suh, Lucas, & Smith, 1999; Diener, 2000, for reviews). These ratings have been based on consistent definitions of happiness such as the balance of positive and

negative affect and global assessments of life satisfaction (Diener et al., 1999). The amount of control the target feels over events in his or her life is another definition upon which ratings of SWB have been based (Campbell, 1981; Cantor & Sanderson, 1999).

Psychometric research in humans has shown that these measures are intercorrelated and are indicators of an underlying factor. These ratings can be made with high interrater reliability, and correlations between self- and peer-ratings on these scales are high (Diener, 1996; Diener et al., 1999).

One counterintuitive finding is that broad environmental variables such as income, social status, the country one lives in, and experiential factors only account for a small proportion of the variance in SWB (Heady & Wearing, 1989; Lykken & Tellegen, 1996). Instead, SWB is correlated with personality measures (Argyle, 1999; Diener, 1998; Diener & Lucas, 1999). The strongest correlations are with Extraversion and Neuroticism (Costa & McCrae, 1980; Emmons & Diener, 1985, 1986). Weaker correlations are with Conscientiousness and Agreeableness (Diener, 1998; McCrae & Costa, 1981). However, a recent meta-analysis showed that the difference in strength of these correlations is not robust (DeNeve & Cooper, 1998).

An individual's happiness is also stable over a lifetime and even the most traumatic or joy-inducing experiences only cause a temporary change in an individual's happiness (Costa, McCrae, & Zonderman, 1987; Costa, Zonderman, McCrae, & Cornoni-Huntley, 1987; Lykken, 1999; McCrae & Costa, 1988). The findings from behavioral genetic research on happiness have been consistent with the above findings. First, twin studies indicate that approximately 50% of the human SWB variance is due to genetic effects. This research has also revealed that, in common with personality, almost none of the SWB variance is due to shared environmental effects and that nonshared environmental effects and error account for the remaining variance (Lykken & Tellegen, 1996; Tellegen et al., 1988). However, in adults this heritability is almost exclusively due to the unique combination of genes and not additive genetic

effects, a phenomenon that Lykken terms emergence (Lykken, McGue, Tellegen, & Bouchard, 1992). Lykken and Tellegen (1996) have also shown that the heritability of the stable component of SWB is approximately 80%.

1.3.2 The Beginnings of Integration

Even within the schools of comparative psychology and ethology there was some research on individual differences. This research marked the beginning of studies of individual differences in non-human animals and can be roughly grouped into four categories. The most systematic research on individual differences in chimpanzees and other animals has been conducted on dominance. The next most studied phenomenon has been chimpanzee happiness. Cultural differences have also been extensively studied. Finally, ethologists have often described personality differences in their subjects.

State Dominance One of the oldest findings in research on chimpanzees and other nonhuman primates is the existence of dominance hierarchies (Bernstein, 1981). In the case of chimpanzees, males, whether in their natural habitat or in captivity occasionally engage in loud and active displays. The winner of these displays will later be allowed primary access to desirable resources such as food, favorite resting spots, and mating opportunities. These males also divide up resources among the group (Goodall, 1986; de Waal, 2000).

Female chimpanzees also engage in dominance displays, but not nearly to the degree of males. Winning, for females, has consequences that are related to their fitness such as having heavier infants as well as more infants that are able to survive. They also are able to solicit matings from outside their troop (Pusey, Williams, & Goodall, 1999).

These findings suggest that wild chimpanzees display a linear dominance hierarchy and that, at least in females, a chimpanzee's rank within the hierarchy is related to fitness (Pusey et al., 1999). In contrast, dominance among humans seems to be less

emphasized than in chimpanzees. This may be due to human specialization in a number of different areas and the size of modern human populations which make linear dominance hierarchies difficult to maintain.

However, while the dominance described in the non-human primate literature is rigorously measured, the construct is not like the personality traits described in human personality research which are stable over time (Allport, 1937). Instead, these measures of dominance could better be described as state-like.

Enrichment and Happiness While not as old as the study of dominance, the study of environmental enrichment and happiness in nonhuman primates has been extensive. However, because this research has mostly been dedicated to solving practical problems, it does not resemble the research on human happiness.

Part of the study of well-being in nonhuman primates is characterized by attempts to find objective measures of well-being. Proposed measures include survival and reproduction (Johnson, Petto, & Sehgal, 1991); indicators of stress or their absence such as motor stereotypy or self-injurious behavior (Baker & Aureli, 1997); and the presence of species-specific behaviors (Rosenblum, 1991).

The other part of this literature is dedicated to the evaluation of various attempts to improve the state of happiness of the captive primates by use of environmental enrichment. One class of attempts involve making environments more naturalistic (Izard, 1991; Snowdon, 1991). A second class involves increasing the amount of space per primate (Line, Markowitz, Morgan, & Strong, 1991). Finally, a third class involves increasing the environmental complexity by providing either conspecifics, toys and puzzles, or both (Reinhardt, 1991).

While attempts at environmental enrichment have been characterized by successes and failures, one cannot be certain as to whether these interventions actually make chimpanzees happier or whether they only act to eliminate or bring out different behaviors.

In other words, one cannot be certain as to whether these measures of well-being assess the same construct that humans call happiness. Indeed, many would think it strange to assess a human's happiness solely by determining how often they exhibit species-specific behaviors, how many children they have, how long they live, or the presence or absence of certain behaviors. Indeed, measures of human happiness usually do not include items assessing any of these factors. Thus, these measures of happiness in nonhuman primates may be measures of temporary states rather than long term traits.

Cultural Differences Once chimpanzees and other primates in their natural habitats became a greater source of interest to researchers, it became clear that differences in chimpanzees also existed at the group level. These cultural differences were found to exist between different populations of chimpanzees and could not be explained due to differences in the materials available in the different population sites (Whiten et al., 1999).

One example of these group differences was palm nut cracking in which the chimpanzees use tree stumps as anvils and rocks as hammers to crack palm nuts. Even though palm nuts, rocks, and tree stumps were available throughout many regions where the chimpanzees lived, only chimpanzees in the Taï forest of the Ivory Coast engaged in this behavior (Boesch, 1996).

Most researchers claim that these differences are solely cultural in origin. They emphasize that these chimpanzees are taught to engage in these behaviors at a young age (de Waal, 2001; Matsuzawa et al., 2001) and that these traditions are confined to the local populations because there is not much interchange among different groups of chimpanzees (Whiten et al., 1999). However, these findings do not rule out the possibility that genetic differences among these populations contribute to population differences in these behaviors.

Ethological Observations Animal behaviorists such as Köhler (1925/1979), Yerkes (1943), Goodall (1986), and de Waal (2000) who have studied wild or captive chimpanzees often describe individual differences in chimpanzees. These descriptions ranged from the chimpanzee's mood (happy, joyful, sad, depressed) to more long-standing traits (defiant, swaggering, nervous).

Other ethological research suggests that personality may be an important variable in chimpanzee social life. For example, ethologists have shown that to become the alpha male in a troop it is crucial for the aspiring male to build alliances with other males (de Waal, 2000; Goodall, 1986). While the relatedness between the chimpanzees is likely one important factor, another is the possible ally's reliability and trustworthiness.

Personality in chimpanzees is important as some individuals may be better suited as mediators or peacemakers. One example of this was described by de Waal (1989). Two infants were fighting and instead of directly intervening to stop the fight, the infants' mothers sought out an older dominant female as a mediator. It is hard to believe that the choice of the mediator was not made with due consideration of how patient, gentle, sympathetic, and fair-minded she was. Not taking these traits into account could have had disastrous consequences.

1.3.3 Advantages of Using the Human Model

The findings concerning chimpanzee personality in the animal behavior research tradition should be taken seriously, but they suffer from several weaknesses. These include issues such as the reliability and validity of the measures and the inability to compare species using a common scale. Both weaknesses can be surmounted by applying research methods that have been central to human personality research.

Incorporating the methods and standards of human personality research would have two advantages. First, demonstrating that independent raters are consistent

assures that ratings are not the result of anthropomorphism on the part of the raters. Second, such methods and standards enable researchers to systematically relate personality measures in chimpanzees to genetic and environmental causes and behavioral outcomes.

Validity and Reliability While the work of ethologists and primatologists strongly suggests that chimpanzees have personalities, which likely play important roles in their social lives, the value of these descriptions is limited because they cannot be examined for their construct validity or reliability.

The lack of construct validity and reliability in these measures opens descriptions of chimpanzee personality to the same criticisms that were leveled against human personality research (see Funder, 1999, for a review). That is, there is no way to tell whether these descriptions of chimpanzee personality are social constructs of the raters or whether other individuals unaware of these descriptions would give similar descriptions. Critics could claim that these descriptions are not tested against criterion measures such as behavior and that personality in chimpanzees is a social construct at best and anthropomorphism at worst.

Problems with Experimental and Quasi-Experimental Research One possible solution to the problem of subjectively assessing chimpanzee personality is, of course, to eliminate the notion of personality in chimpanzees. This solution would involve reverting back to strictly experimental research (the comparative approach) or quasi-experimental research (the ethological approach). However, while this research would be useful for understanding species-typical behaviors and capabilities, it assumes that all individual differences should be considered error variance that should either be controlled experimentally, statistically, or via other approaches such as using inbred strains.

Such approaches would not be satisfactory because personality differences would be relegated to the error term even though they may actually reflect innate behav-

ioral dispositions. Conversely, taking personality differences into account may enable researchers to understand how individual differences may moderate species-typical behaviors and capabilities by determining whether some animals are more or less likely to be affected by experimental conditions. For example, in experimental research, a bolder chimpanzee may have greater tendencies to explore the environment and, hence, more rapidly learn how to solve problems. In ethological research, the bolder chimpanzee may be more likely than others to devise some cultural innovation.

1.3.4 The Study of Individual Differences in Primates

The study of individual differences in non-human primates has come of age. Several researchers in primate behavior have measured primate personality using subjective ratings scales. This research has produced several impressive findings with respect to the validity of these ratings scales.

Stevenson-Hinde (1983) showed in macaques that a personality dimension Confidence was correlated with a macaque's actual dominance rank. Gold and Maple (1994) suggested that gorilla personality ratings may be useful tools for managing captive gorillas. Higley and Linnoila (1997) demonstrated that heritable measures of temperament in rhesus macaques were related to their alcohol intake and the number of fights they engaged in. In a later paper, Higley and Bennett (1999) showed that these measures were correlated with several neurobiological correlates such as serotonin levels and that these measures were often heritable.

Unfortunately, similar strides have not been made in the understanding of happiness in nonhuman primates. However, there have been several strong arguments made in favor of applying a human model to the study of happiness in primates (Sackett, 1991; Wemelsfelder, 1997). Moreover, some researchers have emphasized that managers of primate colonies should consider the needs of the individual animal

as opposed to attempting to find a solution that works for all of the animals in a colony (Suomi & Novak, 1991).

Modern Chimpanzee Personality Research The systematic study of chimpanzee personality in their natural habitat is limited to a single study. Buirski and Plutchik (1991) rated chimpanzees at the Gombe Stream Research Center using a modified version of the Emotions Profile Index. One chimpanzee, Passion was more aggressive, depressed, and distrustful than the other female chimpanzees. Also, she was less trustful, timid, controlled, and gregarious. A year after these ratings were made, workers at the field station noted that Passion and her daughter began stealing and eating the infants of other chimpanzees. No such behavior had previously been observed in chimpanzees.

Later research on zoo chimpanzees revealed that chimpanzee personality structure is similar to that of humans. King and Figueredo (1997) using an adjectival ratings scale based on one used in human research had zoo workers and volunteers familiar with the animals rate 100 chimpanzees. Factor analysis revealed six factors. Five factors were remarkably similar to the human Big Five and labeled Surgency, Dependability, Agreeableness, Emotional Stability, and Openness. The sixth factor was a chimpanzee-specific factor that was clearly related to dominance. Dominance was a broad factor related not only to dominance, but also to intelligence, independence, persistence, and decisiveness. The interrater reliabilities of these factors as measured by $ICC(3, k)$ (Shrout & Fleiss, 1979) ranged from .67 to .88.

The similarity of chimpanzee and human DNA led Weiss, King, and Figueredo (2000) to assess what proportion of variance in each chimpanzee personality factors was due to additive genetic effects, shared zoo effects, and nonshared environmental effects. They found that approximately 60% of the Dominance variance was heritable. They also found positive, non-significant heritability for Dependability and negligible shared zoo effects for all six factors.

Moreover, an unpublished study by King found that the personality ratings were relatively stable over time. Using a cross-sectional analysis he also found that age-related changes in human personality factors also occur with chimpanzee personality factors.

Modern Chimpanzee Happiness Research To date there have been two studies of chimpanzee happiness that have used subjective measures of happiness. In the first such study, Bard and Gardner (1996) showed that infant chimpanzees reared in a nursery setting where they received extra attention displayed enhanced well-being.

More recently, King and Landau (in press) developed a scale to measure happiness in chimpanzees that was modeled after scales used to measure human SWB. Unlike other measures of happiness in nonhuman primates, there was substantial evidence that the chimpanzee SWB scales measured the same construct that the human SWB scales measured in humans. First, the interrater reliability of chimpanzee SWB scores was high ($ICC(3, k) = .83$) (Shrout & Fleiss, 1979); second, chimpanzee SWB ratings were stable over long periods of time; and third, chimpanzee SWB ratings were correlated with three factors identified in an earlier chimpanzee personality study (King & Figueredo, 1997).

Like human SWB, approximately 40% of the variance in chimpanzee SWB is heritable in the narrow-sense and almost none of the variance is due to shared zoo variance research on SWB (Weiss, King, & Enns, 1999; Lykken & Tellegen, 1996; Tellegen et al., 1988).

1.4 Remaining Questions

1.4.1 The Search for the Nonshared Environment

The most common finding in the behavior genetics of personality is that nearly all of the non-genetic variance in populations is due to nonshared environmental effects

(Bouchard & Loehlin, 2001; Plomin & Daniels, 1987). These findings indicate that when the effects of genes are taken into account, any pair of siblings will be no more similar than any two randomly selected members of a population.

Critics have argued that the failure to find shared environmental effects and the inability to isolate what the nonshared environmental effects are suggests that there are problems with the assumptions of behavior genetic research (see, Turkheimer & Waldron, 2000; Stoolmiller, 1999, for more details). While many of their methodological criticisms have been addressed (Loehlin & Horn, 2000), the lackluster results in the search for nonshared environmental effects are still a puzzle and suggest that they have been hampered, not by a lack of methodological sophistication, but by a search that is, at times, unfocused and atheoretical.

Not all research on nonshared environmental effects is unfocused and atheoretical. Scarr (1993) has been the chief proponent of the importance of gene by environment correlations and niche picking in personality developments. She argues that environmental effects are often correlated with personality because individuals with different personality dispositions choose different environments. For example, if a psychologist notices that successful adults read as children, they ascribe the individual's success to the reading. Scarr suggests that this assumption is a mistake because it does not rule out the possibility that the characteristics that cause a child to seek out books are the same characteristics that lead to their later success.

By urging developmental psychologists to consider the possibility that environments may be correlated with later outcomes due to common genetic effects, Scarr has evoked a considerable amount of ire from other developmental psychologists (Baumrind, 1993). However, she has led others to promising lines of inquiry such as the influence of peer groups (see, for example, Harris, 1998).

Peer Groups Harris (1998) proposes a theory that individuals are born with broad genetically-based dispositions. These dispositions, in turn, result in the selection of certain peer groups which, in turn, canalize the development of personality.

There is currently a dearth of research investigating peer effects on normal personality development. However, this is not the case when investigating the development of delinquency. For example, a recent study has shown that, while early-onset delinquency is more strongly influenced by genetic factors, late-onset delinquency is more strongly influenced by the onset of delinquent behavior in peers (Taylor, Iacono, & McGue, 2000). Furthermore, Rowe and Rodgers (1991a, 1991b) successfully used an epidemiological model to predict the prevalence of sexual, smoking, and drinking behavior in adolescents.

Evolutionary Hypotheses To date, most evolutionary psychology has been concerned with understanding species universals (Tooby & Cosmides, 1992). This perspective, while important, ignores individual differences. Two of the proponents of this view, Tooby and Cosmides (1990), suggest that individual differences are a by-product of evolved pathogen resistance in sexually reproducing species. That is, the need for variation in the immune systems to undermine the ability of parasitic exploitation has resulted in the genetic variability that underlies personality differences.

This view is changing. For example, MacDonald (1995) considers personality as adaptive manifestations of a broad range of fitness-enhancing traits. Figueredo and King (2001) suggest a frequency-dependent model in which competition is reduced via character displacement. Finally, there are those who see personality as being a sexually selected trait (Buss, 1990; Miller, 2000).

The evolutionary approach to personality clearly suggests several potential environmental influences on personality. These predictors include those based on kin selection (Hamilton, 1964) and reciprocal altruism (Trivers, 1971). In the case of the former, the presence or support of related individuals may result in long- or

short-term changes in behavior that would lead to different personality ratings. For example, individuals may be perceived as more agreeable when they are seen among related individuals rather than strangers because related individuals are more likely to cooperate (Segal, 1993; Segal & Hershberger, 1999). In the case of reciprocal altruism, a similar case can be made for the potential effects of being surrounded by friends or similar individuals (Trivers, 1971; Rushton, 1989).

Indirect Genetic Effects A relatively unexplored additional source of variance in personality has been in the area of indirect genetic effects. Indirect genetic effects occur when some heritable phenotype of a parent influences an offspring's phenotype (William, 1972, 1980). For example, milk quality is a heritable characteristic in cattle and it is also an important factor in the growth of calves. Hence, if a mother has a predisposition to produce low-quality milk, the growth rate of her young will be affected by this independently of any direct genetic effects. Heritable maternal effects have also been theorized to have an evolutionary origin by Dawkins (1982) who suggested that maternal effects may be a means by which the genotype of the mother drives the offspring to increase the likelihood that it survives and reproduces.

1.4.2 The Search for Environmental Predictors of SWB

Although behavior genetic research has found that environmental effects account for a small proportion of SWB variance (Lykken & Tellegen, 1996; Tellegen et al., 1988), attempts to find environmental influences on human SWB have been more successful than similar efforts in personality research (see, for example, Argyle, 1999; Myers, 1999, 2000). While a good deal of this research focuses on direct environmental influence, another portion of this research attempts to understand how environmental influences mediate the correlation between personality and SWB (see Diener & Lucas, 1999, for a review).

Social Support The major environmental factors that influence SWB all have in common the fact that they reflect greater amounts of social support (Myers, 2000). This includes positive effects of church attendance and having close friends (Myers, 2000). Another influence appears to be an authoritative parenting style on the part of the mother (Furnham & Cheng, 2000). On the other hand, possibly due to the financial consequences, divorce has been shown to be negatively correlated with SWB (Myers, 1999). These findings are consistent with predictions from evolutionary theory (see, for example, Buss, 2000). This is because kin, friends, or community support are often protective factors that can, over the long run, buffer one from circumstances that may reduce happiness (Figueredo et al., 2001).

A major problem with these findings is that these environmental influences may be reflections of heritable personality factors and are not themselves causal. That is, heritable differences in personality traits such as Extraversion, Agreeableness, and Neuroticism that are related to SWB may also be related to whether an individual is likely to attend church, have friends, or maintain a happy marriage.

Indirect Genetic Effects One possible cause of human SWB that has been almost completely ignored is the possibility of heritable maternal effects. Furnham and Cheng (2000) demonstrated independent effects of the mother's parenting style on children's SWB. While they did not rule out the possibility that this reflected a gene by environment correlation, they did not consider the possibility that these effects were indirect genetic effects. Parenting styles are heritable (see Cohen, 1999, for a review). Therefore, it is possible that Furnham and Cheng's study revealed heritable maternal effects that are independent of direct genetic effects.

Environment by Personality Interactions Another set of models of the causes of SWB are based on the fact that personality and SWB are correlated (Diener & Lucas, 1999). While the models posit that some aspect of personality interacts with the environment

to produce happiness or unhappiness, they differ in specifics such as the characterization of temperament or personality and how they interact with the environment. The two most relevant models for understanding happiness in nonhuman primates are temperament and congruence models.

Temperament models are based upon the assumption that SWB is primarily determined by biologically based temperamental dispositions such as Extraversion and Neuroticism which reflect the strength of the individual's reward and punishment system. That is, an individual's overall SWB is contingent upon how strongly the individual reacts to rewards and punishments (Gray, 1981, 1991; Heady & Wearing, 1989). In these models the causality tends to flow from genes, to temperament, to SWB. Buss and Plomin (1975) present another temperament model in which personality develops as inborn temperamental dispositions differentiate due to environmental effects. This possibility can be extended to the work on personality and SWB. *i.e.*, genes give rise to temperament, and environmental and developmental effects differentiate temperament into personality and SWB. Thus, the common variance shared between personality and SWB would be genetic in origin, whereas the unique variance would be environmental.

These models are consistent with the heritability of happiness (Lykken & Tellegen, 1996; Tellegen et al., 1988) and heritable predispositions related to happiness in children as young as 14 months (Robinson, Emde, & Corley, 2001). They postulate that the underlying causes of happiness are stable individual differences in temperament and personality. However, critics contend that the actual mechanisms by which these temperament and personality factors cause happiness have not been identified (Diener & Lucas, 1999). Also, multivariate behavior genetic models have not been used to test the theory.

Congruence models emphasize the interaction of personality and the social environment. That is, happy individuals are those that fit in well with their social environment. This is supported by evidence that individuals are happier when they are in

situations that are consistent with their personality (Moskowitz & Cotes, 1995). This evidence is consistent with findings that show that happy people have more friends (Myers, 1999, 2000). It is also consistent with behavior genetic theories of niche picking (Scarr, 1993). That is, people who attend church or who can count many people as close friends may simply be individuals that have been able to find niches that match their personalities. On the other hand, individuals who do not have any close friends, cannot fit into a community organization, or build a cohesive family may have personalities that are incompatible with most environmental niches. Hence, people who go through multiple marriages may be expressing multiple attempts to locate a niche.

Humans actively select against niches that are not congenial to them via gene by environment correlations or other mechanisms. It is therefore difficult to determine whether the correlation between personality and happiness is mediated by how well they fit into their environment. This uncertainty exists because the correlation between personality and SWB would reflect the average person-environment fit across several different contexts and situations. This occurs because niche picking insures that, in most instances, the individual does select against environments that would result in low SWB. This would be true in most circumstances except those where the number of available niches is extremely limited as in extremely impoverished countries or prisons. Consequently, most people rate themselves as being happy (Diener & Diener, 1996). For example, it is likely that some individuals may be unhappy at work because of a low person-environment fit, but they are happy with their families and friends because it is far easier selecting friends and marriage partners that lead to high SWB. As a result the mean of such an individual's SWB could be very high. However, without knowledge of all of the environments with which the individual interacts, it would be impossible to detect the contextual contributions of the environment. That is, the end effect of niche picking would be to attenuate correla-

tions between environmental variables and SWB because of the restriction of variance brought about by the selection of environments.

Genetic, Maternal, and Environmental Correlations One remaining possibility which has not been adequately tested in the human SWB literature is the possibility that SWB may be another expression of the genes that influence personality. There is evidence that this may be the case as behavior genetic studies of comorbidity of depression and anxiety show that the variance in common between these two factors is primarily due to the fact that they share common genetic and environmental causes (Kendler, 1996; Roberts & Kendler, 1999). This possibility is in marked contrast with other theories concerning the correlation between personality and SWB. Instead of suggesting that the former causes the latter either by itself or via some environmental circumstances, it suggests that the correlation is due to shared causes. If true, this would likely mean that attempts to enhance human or primate SWB by creating environments suitable for individual personalities (Suomi & Novak, 1991) would be futile. Thus, while such environments may eliminate unwanted behavioral patterns or be beneficial in other ways, they would not be able to enhance a subject's overall SWB.

1.5 Study Description

1.5.1 Goals

This study had two goals. The first was to assess the influence of demographic, environmental, genetic, and maternal effects on Dominance and SWB. The second was to attempt to better understand the source of covariance between Dominance and SWB. Pursuant to the second goal, the possibility of common genetic and environmental causes were tested.

Finding Environmental Predictors Three types of environmental influences on Dominance and SWB were examined. The first involved the demographic characteristics of sex and age. The second was the physical and social characteristics of the chimpanzees' enclosures. Physical characteristics were size and population density. Social characteristics were the age and sex of enclosure mates and kin structure. The latter is predicted by kin selection theory (Hamilton, 1964) and has never been tested as a predictor of SWB. Finally, to assess the congruence model, the personality structure of an enclosure was examined as a predictor of Dominance and SWB. That is, the possible effects of fitting or not fitting into the social environment were tested.

Finding Genetic and Maternal Predictors This study also used a behavior genetic analysis to examine several sources of variance. The first of these was the proportion of Dominance and SWB variance due to additive genetic effects - heritability in the narrow-sense. In addition, the analysis estimated the proportion of variance due to fixed zoo effects, *i.e.*, whether equally related chimpanzees in the same enclosure were more similar than equally related chimpanzees in different enclosures. These effects were identical or similar to those estimated in human behavioral genetic research. The analysis also assessed how much variance could be attributed to nonshared environmental effects and measurement error.

The proportion of variance due to heritable and non-heritable maternal effects was also estimated. Hence, the proportion of Dominance and SWB variance that is due to heritable or non-heritable behavior on the part of the mother was determined.

Finding Sources of Covariance The study assessed whether any covariance between Dominance and SWB was due to shared genetic, maternal, or nonshared environmental effects. This was assessed as part of the behavior genetic analysis. The goal was to determine the proportion of the covariance that was due to shared genetic, heritable maternal, non-heritable maternal, and nonshared environmental effects. That is, are

the same genes, maternal effects, and nonshared environmental effects that influence Dominance also influencing SWB?

1.5.2 Design

Brunswik (1956) and Petrinovich (1979, 1989) argued that, to the peril of generalizability, most researchers obtain representative samples of subjects, but not of environmental stimuli. This issue is akin to that raised by Gibson (1974) who argued that behavior must be understood as the interface of the organism and environment. Thus, because experimental designs often bear little resemblance to situations encountered by the organism, the contextual interaction between the individual and the persistent characteristics of the environment is eliminated and there is little ability to generalize findings beyond the laboratory.

Shortcomings of Previous Research The prime obstacles that plague attempts to find environmental predictors of SWB are gene by environment correlations which might lead humans to select niches that lead to increased levels of SWB. These studies are characterized by their representative design and are no fault of the researchers. Some researchers have attempted to get around this problem using quasi-experimental designs (Cook, 1979). These include researchers studying humans that are institutionalized or living in other impoverished environments Other researchers have attempted to deal with this problem by actively manipulating the environment (Diener & Lucas, 1999). In all cases, there has been some success at either seeing how the environment can raise or lower SWB either alone or in conjunction with personality.

However, there are several limitations to these studies. First, none of these studies consider the possible effects of genes or the possibility of genetic correlations between personality and SWB. Second, institutionalized populations are not a random sample and may differ in a number of ways from normal populations in personality, upbringing, intelligence, and life experiences. Third, studies in impoverished countries

or studies in which experimental manipulation is involved may not provide adequate samples of the normal range of environments. Thus, results may not generalize beyond those populations since most humans are not likely adapted to these environments.

Advantages of Using Zoo Chimpanzees Humans and chimpanzees in their natural habitat engage in niche picking, a behavior that probably attenuates correlation between environmental variables and SWB. This same problem applies to attempts to test person- or chimpanzee-environment fit hypotheses.

On the other hand, captive chimpanzees, while not isolated, have a more limited set of niches to pick from. They have no choice regarding the size of the enclosure, how many other chimpanzees are in the vicinity, and other shared environment effects that may effect their happiness. Furthermore, zoos, to prevent inbreeding, trade chimpanzees. Hence, the relatedness between any target chimpanzee and its enclosure mates - one aspect of the nonshared environment - will vary across both chimpanzees and zoos.

This leads to chimpanzees having a limited number of available social niches. Hence, the ability for chimpanzees to select a niche is restricted, and this may enable detection of some aspect of the zoo's physical or social structure that affects Dominance or SWB as well as whether chimpanzees are less happy when the chimpanzee-environment fit is poor.

Zoo chimpanzees enable one to conduct a quasi-experimental study on environmental contributions to happiness. This enables one to test the effects of nonshared environment effects such as the chimpanzee-environment fit on Dominance and SWB. Unlike experiments on human prisoners there is less of a possibility that the chimpanzees differ in some way from chimpanzees in the wild. Moreover, the range of environments, especially the social environment, are more likely to reflect the normal range.

1.5.3 Hypotheses and Variables

The population of zoo chimpanzees used in this study allowed tests of several environmental hypotheses. This is because chimpanzees in zoos spend nearly their whole life within a limited space and with a relatively small social group. However, there is still the possibility that enough niches exist in the enclosure and that each population differs from general populations of chimpanzees. The latter may be due to a founders effect or the fact that the original animals were caught in the wild.

Environmental Hypotheses and Predictors One question was whether the presence of males or females as measured by their respective densities increases the frequency of behaviors related to Dominance and thus result in higher ratings of Dominance. This was predicted because dominance should be expressed more when potential competitors or receptive females are nearby (de Waal, 2000).

A second question was whether higher densities of males or females lead to reduced SWB. Frans de Waal (2000) noted that when the density of chimpanzees increases, there appears to be a greater amount of stress. This seems to be because there is less opportunity to avoid contact with others.

Another question was whether enclosures consisting primarily of older males or females contain chimpanzees that are rated higher in Dominance. This may be because the behaviors that are commonly associated with Dominance should be more evident in older males and in the presence of sexually mature females. One can also ask whether the presence of older males or females decreases SWB because of a greater incidence of health problems at later ages.

Forming coalitions is an important aspect to acquiring dominance in chimpanzee societies. For example, while competitive prowess is one factor, de Waal (2000) observed the importance of these coalitions and described how a chimpanzee becomes the alpha male involves cutting off the former alpha male from his supporters.

Kin selection predicts that relatives would be the best coalition partners (Hamilton, 1964; Pusey, 2001). Chimpanzees with more relatives in the vicinity should have an easier time forming and maintaining coalition. Hence, a question asked was whether chimpanzees with more male or female kin might be perceived as being higher in Dominance. Similarly, evolutionary psychologists (Buss, 2000) and SWB researchers (Myers, 1999, 2000) suggest that social support from family enhances SWB. Thus, another question was did having more male or female relatives, and therefore more social support, enhance SWB.

The chimpanzee-environment fit was expected to be an important predictor for Dominance and SWB. It was predicted that the similarity of other chimpanzees would serve as a proxy to how related they were or how many interests they shared in common. Such chimpanzees were expected to be similar and more likely to form the coalitions necessary for dominance. Thus, one can ask the question of whether the degree by which a chimpanzee differs from enclosure-mates in Surgency, Dependability, Agreeableness, Stability, and Openness is negatively related to Dominance.

The congruence hypothesis would predict that a good chimpanzee-environment fit should lead to high SWB because the chimpanzee is able to pick from several available niches. So, one can ask whether a low degree of fit in terms of the subject's personality and those of its enclosure mates leads to reduced SWB.

Finally, one can test a number of interaction effects to answer the question of whether any of the above predictions were moderated by enclosure characteristics or the subject's sex, age, or degree with which it fits into the environment. For example, did having several male kin in the same enclosure reduce any negative effects of stress due to a high population density?

Behavior Genetic Predictors Several behavior genetic predictors were included in the analysis. Hence, questions about the strengths of various predictors of variance and covariance for Dominance and SWB were asked.

The first question was based on the high heritability of human individual differences (Bouchard & Loehlin, 2001) and previous work on the heritability of chimpanzee personality (Weiss et al., 2000). That is, to what extent are chimpanzee Dominance and SWB heritable? A question also asked was whether the covariance can be explained by common genes.

Previous findings seem to suggest that maternal effects influence SWB (Bard & Gardner, 1996; Furnham & Cheng, 2000). These studies did not use a behavior genetic design, but it is possible that these findings revealed heritable or non-heritable maternal effects. On the other hand, it is not clear whether similar effects also influence trait Dominance, though ethological evidence suggests that they might influence dominance (Hinde & Spencer-Booth, 1971). Therefore, a question asked was to what extent do heritable or non-heritable maternal effects influence Dominance and SWB. Further asked was whether the covariance between these two traits is caused by the same heritable or non-heritable maternal effects?

Several zoo variables have already been accounted for with the environmental variables. Since the behavior genetic analysis can assess the overall proportion of variance accounted for by shared zoo effects, a question to ask is whether these two analyses show similar results or whether the behavior genetic analysis reveals that some zoo effect on Dominance or SWB is not taken into account.

Finally, while several nonshared environmental variables were previously examined, one can ask whether some nonshared environmental effects account for the variance and covariance of Dominance and SWB. This showed whether there were still effects to consider in future studies.

1.5.4 Analysis Plan

To assess the effects of the environmental predictors and the behavior genetic predictors, two analyses were required. The first assessed the environmental predictors

without considering any behavior genetics predictors using a series of general linear models (GLMs). The second analysis assessed the influence of the behavior genetics predictors and any environmental predictors of Dominance and SWB that were shown to be significant in the first analysis. This insured that environmental predictors were not confounded by genetic or maternal effects.

Environmental Analysis The common assumption is that SWB is predicted by personality factors, being that personality was the best predictor of SWB in humans and chimpanzees (see Diener et al., 1999; King & Landau, in press). One of the major goals was to find environmental effects that uniquely influence SWB. Thus, the environmental analysis consisted of two GLMs. The first had Dominance as the dependent variable, and the second had SWB as the dependent variable.

The first GLM involved predicting Dominance by environmental variables as well as a series of two-, three-, and four-way interactions. Restricted and saturated models were then compared to determine whether these additional interactions predict an additional proportion of variance over more parsimonious models.

The second GLM had SWB as its dependent variable and was identical to the previous GLM and differed only in that Dominance was entered into the model before any of the environmental variables. Because Dominance and SWB are correlated, entering Dominance first insured that only direct environmental effects on SWB were assessed (Gorsuch & Figueredo, 1991). If this step were not taken, the correlation between Dominance and SWB could lead the analysis to show that significant predictors of Dominance were also significant predictors of SWB. As before, restricted and saturated models were compared to determine whether the two-, three-, and four-way interactions accounted for more variance than would be expected based on the degrees of freedom used.

Behavior Genetic Analysis A series of multivariate behavior genetic models were examined using a multitrait derivative free restricted maximum likelihood procedure.

This procedure uses a simplex method to solve for genetic and environmental predictors of variance and covariance in multiple trait analyses (Boldman, Kriese, Van Vleck, Van Tassell, & Kachman, 1995).

The models included any significant environmental predictors of Dominance and SWB. The first was a saturated model where the variance of Dominance and SWB were predicted by additive genetic, heritable maternal, non-heritable maternal, shared zoo, and nonshared environmental effects. There were attempts to estimate genetic, heritable maternal, non-heritable maternal, and nonshared environmental correlations.

This saturated model was followed by a series of restricted models in which variance and covariance components were excluded. These models were then compared to determine whether the models which excluded parameters such as heritable or non-heritable maternal effects and correlations explained all of the variance and covariance as well as more complex models.

Chapter 2

METHODS

2.1 Subjects and Measures

2.1.1 Zoological Parks

The data were collected from 13 zoological parks (zoos). Twelve zoos are in the United States, and one is in Australia. The zoos are participants in the ChimpanZoo program of the Jane Goodall Institute.

There were more chimpanzee enclosures than zoos because one zoo, Lion Country Safari, kept its chimpanzee population on five separate islands. Each island was considered a separate enclosure; hence, the total number of enclosures was 17.

Data Collection Curators of the chimpanzee exhibits at the zoological parks were contacted by electronic mail and telephone and asked to provide the dimensions of the chimpanzee enclosures. Enclosure sizes were then converted into square meters (m^2).

Existing Data Other measures were obtained from the existing ChimpanZoo database and included the number of males and females in each enclosure, the age of males and females in each enclosure, and the genetic relationship among chimpanzees in each enclosure.

2.1.2 Subjects

Chimpanzee personality and happiness ratings were collected from a sample 128 chimpanzees (*Pan troglodytes*) in the 13 zoological parks.

Demographic Characteristics From a total sample of 128 chimpanzees, there were 49 males and 79 females with mean ages of 16.8 and 20.0 years, respectively. Age ranged from 3 to 55 years, thus including chimpanzees ranging from juveniles to old age.

Parentage Information about paternity and maternity varied considerably. This was because some chimpanzees were wild caught, and no DNA testing was used to determine paternity of chimpanzees born in zoos.

The chimpanzee population can be divided into two major groups: those born in the wild ($N = 43$) and those born in a zoo ($N = 85$). The latter group can be further subdivided into three subgroups: mother and father are known ($N = 63$), mother known ($N = 7$), and both parents unknown ($N = 15$).

Relatedness Table 2.1 shows the relatedness of all 8128 possible pairs of animals and whether they share the same enclosure. The mean degree of relatedness of chimpanzee pairs in the same enclosure ($\bar{X} = .078$) was more than twice as high as chimpanzee pairs in different enclosures ($\bar{X} = .032$). There was a significant difference between pairs that did and did not share the same enclosure ($t = -35.5; p < .0001$), but it should be kept in mind that the pairs were not independent. The fact that chimpanzee pairs in the same zoo were more related indicates that even though individual chimpanzees were moved to different zoos to prevent inbreeding, zoo keepers attempted to keep some pairs of animals together, *e.g.*, mothers and their young. It also suggests that a fixed zoo variable should be included in the final analysis because doing so would serve to unconfound any effects of the enclosure that are not captured by the environmental variables.

TABLE 2.1. Relatedness of all Possible Pairs

R_{ij} ^a	N_{same} ^b	N_{diff} ^c	N_{total}
.000	468	7430	7898
.010 – .124	33	2	35
.125 – .249	30	11	41
.250 – .374	44	26	70
.375 – .499	2	1	3
.500 – .589	56	25	81
	633	7495	8128

^a The proportion of genes, on average, that i and j have in common.

^b Number of pairs that live in the same enclosure.

^c Number of pairs that live in different enclosures.

2.1.3 Ratings

Because peer ratings are more accurate than self ratings (Gosling, 2001), the use of subjective ratings of chimpanzee personality or SWB was not problematic. It should also be noted that this means of rating subjects reflects the traditional approach to personality (Allport, 1937) and not one that assesses the way individuals behave in different situational contexts (Mischel, 1968; Mischel & Shoda, 1995).

Raters To insure the reliability of ratings, each chimpanzee was rated by several individuals. Raters were zoo employees who regularly worked in the chimpanzee enclosure or ChimpanZoo volunteers who had extensive previous experience observing chimpanzees during separate behavioral observation projects.

The raters filled out personality and SWB questionnaires at home. The raters were instructed to give their overall impressions of the chimpanzees based on all of

the time they had been in contact with them. Raters were also instructed not to discuss their ratings with other raters. When all raters at a zoo were finished, the questionnaires were sent back.

Chimpanzee Personality Measure King and Figueredo (1997) and Weiss, King, and Figueredo (2000) describe the Chimpanzee Personality Measure (CPM) rating scale. The CPM contains 43 adjectives accompanied by two or three sentence definitions relating the adjectives to chimpanzees (see Chapter 5). These definitions are consistent with each adjective's dictionary definition. Most of the items came from Goldberg's (1990) taxonomy of the human Big Five. Each rater scored the 43 adjectives on a 7-point Likert scale.

King and Figueredo (1997) have shown that ratings of chimpanzee personality are highly reliable and, in some cases, more reliable than similar measures in humans. King and Figueredo conducted an exploratory factor analysis. The first factor was a chimpanzee specific factor that was clearly related to dominance. The other five factors were strikingly similar to the human Big Five: Surgency or Extraversion, Agreeableness, Dependability, Emotional Stability, and Openness.

This study used King and Figueredo's (1997) factor definitions and constructed unit-weighted factor scores for the six factors by assigning items with absolute loadings greater than .53 weights of +1 or -1 (see Table 2.2). The internal consistency alpha reliability for Dominance was .94 and the interrater reliability alpha $ICC(3, k)$ was calculated based on 61 raters with a mean of 4.3 raters per chimpanzee and equal to .89 (Shrout & Fleiss, 1979).

TABLE 2.2. Factor Descriptions, Interrater Reliabilities, and Internal Consistencies

Factor	alpha		Factor Definition		
	IR ^a	IC ^b			
Dominance	.89	.94	+ Dominant + Intelligent + Stingy - Fearful	+ Independent + Persistent - Submissive - Timid	+ Decisive + Bullying - Dependent - Cautious
Surgency	.88	.92	+ Active + Affectionate - Lazy	+ Playful + Imitative - Depressed	+ Sociable - Solitary
Dependability	.79	.90	+ Predictable - Reckless - Aggressive	- Impulsive - Erratic - Jealous	- Defiant - Irritable - Disorganized
Agreeableness	.73	.87	+ Sympathetic + Protective	+ Helpful + Gentle	+ Sensitive
Emot. Stability	.74	.73	+ Stable	+ Unemotional	- Excitable
Openness	.84	.88	+ Inventive	+ Inquisitive	
SWB	.83	.85	+ Mood + Being	+ Social	+ Goals

Note. $N = 128$

^a Internal Consistency.

^b Interrater Reliabilities of mean ratings ($ICC(3, k)$).

Subjective Well-Being Questionnaire The SWB questionnaire contained four items each related to a different facet of SWB. Raters were instructed to assign a 7 to the chimpanzee that displayed the highest amount of the trait and a 1 to the chimpanzee that displayed the lowest amount of the trait. All other chimpanzees were assigned values between 2 and 6.

This anchoring procedure was deemed desirable because it maximized individual differences in SWB and, therefore, increased the sensitivity of the SWB measure to personality differences and the environmental variables used in the study. It also reduced mean SWB differences among zoos; thus, any estimate of shared zoo environments on SWB was conservative.

The first two items in the chimpanzee SWB scale were comparable to items in human SWB scales that assess the balance of positive and negative affect (Diener, et al., 1999). Hence, the first item attempted to assess the overall happiness of each chimpanzee by asking the rater to:

Estimate the amount of time each of the chimpanzees in your zoo is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times, the chimpanzees are unhappy, bored, frightened, or otherwise in a negative mood.

The second item dealt with social relationships by asking the rater to:

Estimate, for each chimpanzee in your zoo, the extent to which social interactions with other chimpanzees are satisfying, enjoyable experiences as opposed to being sources of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience.

The third item was comparable to human SWB scales focusing on perceived personal control (Campbell, 1981; Cantor & Sanderson, 1999). It asked the rater to:

Estimate, for each chimpanzee in your zoo, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired social interactions, achieving a desired dominance status, and having access to desirable locations, devices, or materials in the enclosure.

The fourth item was unique to this study. It asked raters to assess how happy they would be if they were a particular chimpanzee. It asked them to:

Imagine that you could be one of the chimpanzees in your zoo for a week. You would be exactly like that chimpanzee. You would behave the same way as that chimpanzee, would perceive the world the same way as that chimpanzee, and would feel things the same way as that chimpanzee.

A single unit-weighted factor score was constructed based on the SWB factor described in King and Landau's (in press) study. All items had high positive loadings on the SWB factor and were assigned weights of +1 (see Table 2.2). The internal consistency alpha reliability for the SWB factor was .83. The interrater reliability alpha for mean scores was .85. This was computed using $ICC(3, k)$ (Shrout & Fleiss, 1979) and based on 51 raters with a mean of 3.6 raters per chimpanzee.

2.2 Environmental Analysis

2.2.1 Analytic Strategy

The environmental analysis addressed the question of whether the expression or perception of Dominance and SWB in chimpanzees is in part selected by environmental contingencies. The goal was to estimate the unique effects of demographic and environmental predictor variables on Dominance and SWB.

Problems of Multicollinearity The two dependent variables, Dominance and SWB, are correlated. However, the objective was to assess only the direct effects on dependent variables. Thus, the traditional canonical correlation analysis (sometimes called simultaneous canonical correlation analysis) was inappropriate. This is because simultaneous canonical correlation analysis cannot distinguish between direct and indirect effects. Hence, one cannot tell whether predictor *A* uniquely affects dependent variable *B* or whether *A* is correlated with *B* because *A* is correlated with another dependent variable *C* that is correlated with *B* (Gorsuch & Figueredo, 1991).

Assessing Unique Effects A better approach is to analyze a series of hierarchical regressions in which the predictors for one target dependent variable are entered hierarchically, but only *after* the variance from one or more previous dependent variables has been partialled out of the target dependent variable. This analysis has been called sequential canonical analysis and satisfies the goal of this analysis by yielding only the direct effects (Gorsuch & Figueredo, 1991)

Thus, the analytic strategy was to first hierarchically test for the effects of a number of predictors and their interactions on Dominance. Then, these same predictors were tested to determine whether they affect SWB, but only after the effects of Dominance were partialled out by entering it first into the model. The ordering of the two dependent variables was based on the fact that SWB is thought by most researchers to be caused, in part, by personality.

2.2.2 Predictor Variables

There were three categories of predictor variables: demographic characteristics, enclosure characteristics, and personality structure. These predictor variables and their interactions were used to test several hypotheses about the effects of different environmental contingencies, individual differences, and their interactions on Dominance and SWB.

Demographic Characteristics The first demographic variable was sex, which was coded 0 for females and 1 for males. This variable tested for any sex differences in Dominance and SWB. The second demographic variable was age in years and was used to determine age differences in Dominance and SWB.

Enclosure Characteristics There were two sub-categories of enclosure characteristics. The first sub-category described the amount of crowding within the enclosure. Because there might have been differential effects of crowding by males and crowding by females, two measures of density were used. In both cases, the target chimpanzee was not included in the measure of density.

The measure for male density was $d_m = N_m/m^2$. Here, N_m refers to the number of males in the enclosure and m^2 is the total area of the enclosure in square meters. The measure for female density was $d_f = N_f/m^2$. Here, N_f refers to the number of females in the enclosure.

The second sub-category described the age structure of a target chimpanzee's enclosure. Because there might have been differential effects of mean age of the other males and females in the enclosure, two measures, mean male age and mean female age, were used. Table 2.3 shows these predictor variables for each zoo.

TABLE 2.3. Population Density and Age Structure

Zoo ID	Zoo Name	m^2	Males		Females					
			N	density	\bar{X}_{age}	N	density	\bar{X}_{age}		
1	Dallas	165.864	1	.0060	36.00	3	.0181	23.97		
3	Oakland	296.722	3	.0101	14.40	2	.0067	13.95		
6	Los Angeles	780.360	4	.0051	15.52	7	.0090	15.00		
7	Lowry Park	306.570	3	.0098	20.10	2	.0065	11.90		
8	North Carolina	707.434	3	.0042	17.83	9	.0127	18.66		
9	Sacramento	325.150	2	.0062	38.00	2	.0062	26.30		
11	San Francisco	65.667	1	.0152	15.30	3	.0457	27.63		
12	Sedgewick County	643.332	4	.0062	10.98	4	.0062	20.60		
13	Tulsa	1040.480	1	.0010	21.30	4	.0038	23.30		
14	Sunset Zoo	627.075	1	.0016	27.70	3	.0048	21.43		
20	Cheyenne Mountain	73.577	4	.0544	10.52	4	.0054	19.52		
21	Taronga	2340.000	8	.0034	6.12	17	.0073	22.31		
	Lion Country Safari									
15	Bashful's Island	1618.690	4	.0025	16.60	2	.0012	17.80		
16	Higgy's Island	1821.030	4	.0022	15.10	6	.0033	28.43		
17	Whitey's Island	809.345	2	.0025	24.80	6	.0074	15.18		
18	Nolan's Island	1616.460	4	.0025	21.82	3	.0019	19.43		
19	Old Man's Island	1416.350	2	.0014	50.30	1	.0007	19.60		
			$\bar{X} =$	862.006	3.00	.0079	21.32	4.59	.0115	20.30
			$\sigma =$	679.067	1.77	.0126	11.27	3.82	.0152	4.74

Kin Structure Kin structure within the enclosure was a measure assessing the proportion of genes on average that the target chimpanzee shared with the other chimpanzees in the enclosure. Again, it was likely that there would be differential effects of being related to other males or females. Hence, as with the measures of density and mean age, two measures were used to indicate the mean degree of relatedness between the target chimpanzee and the other individuals within the enclosure (Figueredo et al., 2001).

Male kin density was defined as:

$$\left(\sum_{j=1}^{N_m} R_{ij} \right) / N_m$$

where R_{ij} is equal to the Wright's coefficient of relationship, the proportion of genes on average that any two individuals share; the two individuals being the target chimpanzee, i , and another male chimpanzee, j , in the enclosure; N_m was the number of males other than the target chimpanzee in the enclosure.

Female kin density was defined as:

$$\left(\sum_{j=1}^{N_f} R_{ij} \right) / N_f$$

where R_{ij} is equal to the Wright's coefficient of relationship between two chimpanzees, the target chimpanzee, i , and another female chimpanzee, j , in the enclosure; N_f was the number of females other than the target chimpanzee in the enclosure.

The mean male kin density was ($\bar{X} = .116$; $\sigma = .149$). The mean female kin density was ($\bar{X} = .107$; $\sigma = .123$). This indicates that, on average, the other males and females in an enclosure were related at approximately the degree of cousin to any given target chimpanzee.

Personality Structure These predictor variables assessed whether there was a relationship between the target chimpanzee's Dominance and SWB and a) ratings of its

other personality dimensions and b) the deviation of that chimpanzee's personality from other chimpanzees in the enclosure.

The predictors used to measure the relationships between the chimpanzee's personality and Dominance or SWB were the raw score ratings of the target chimpanzee's personality. These predictors included: Surgency, Dependability, Agreeableness, Emotional Stability, and Openness. They were also used as covariates for the next set of predictors which, as a result, indicate how much an individual deviates in personality from the other chimpanzees in its enclosure.

To assess whether there was a main effect of how much a target chimpanzee deviates in its personality from the other chimpanzees in the enclosure, the deviations of the mean factor score of the enclosure from the factor score of the target chimpanzee's enclosure were used (see Table 2.4). This was achieved by first partialling out the target chimpanzee's factor score and then entering the mean factor score for the enclosure into a regression equation.

TABLE 2.4. Mean Personality Scores in Each Zoo

ID	Name	N	Dom		Sur		Dep		Agr		Emo		Ope		SWB	
			\bar{X}	σ												
1	Dallas	4	4.4	0.8	4.1	1.3	5.4	0.7	4.0	0.3	3.4	0.8	3.5	1.6	3.8	1.3
3	Oakland	5	4.3	0.8	4.3	1.1	4.3	0.4	3.9	0.2	3.7	0.3	4.1	1.3	4.0	1.8
6	Los Angeles	11	4.0	1.0	5.4	0.5	5.5	0.6	4.7	0.9	3.5	0.6	4.2	1.2	4.0	1.3
7	Lowry Park	5	4.0	1.1	4.5	1.3	5.4	1.0	4.2	0.8	2.9	0.2	3.8	1.4	4.6	0.7
8	N Carolina	12	4.5	1.5	4.8	0.9	4.6	0.8	4.5	0.8	3.4	0.9	4.6	1.5	4.2	1.6
9	Sacramento	4	4.5	0.7	4.2	0.7	4.6	1.3	4.4	1.2	3.5	0.8	4.2	1.6	4.3	1.8
11	San Francisco	4	4.6	1.6	4.7	0.4	5.2	1.0	5.0	1.0	3.6	1.2	4.5	1.7	3.9	2.1
12	Sedgewick Cty	8	4.4	0.9	4.6	1.0	5.0	0.6	4.2	0.7	3.7	0.9	4.3	1.2	4.0	1.5
13	Tulsa	5	4.5	1.5	4.4	0.5	5.0	0.8	4.3	1.2	3.7	1.0	4.6	1.1	3.9	1.3
14	Sunset	4	4.3	0.7	4.1	1.1	4.7	0.7	3.8	0.4	3.8	0.7	4.0	1.3	4.1	1.5
20	Cheyenne Mt	8	4.3	1.2	4.8	1.3	5.5	1.0	4.1	1.1	3.5	1.2	4.9	1.7	4.0	1.7
21	Taronga Lion Country	25	4.2	0.9	4.7	1.1	5.3	0.9	4.2	0.8	4.0	0.8	4.0	1.2	4.3	0.6
15	Bashful's Island	6	4.4	0.9	4.4	0.3	4.5	0.5	3.9	0.8	3.7	0.5	3.8	0.8	4.3	1.5
16	Higgy's Island	10	4.3	0.8	4.4	1.0	4.5	0.7	4.3	0.5	3.8	0.8	4.1	0.8	4.1	1.2
17	Whitey's Island	8	4.4	0.8	4.6	0.9	4.6	0.7	4.2	0.5	3.7	0.8	4.4	1.0	4.3	1.2
18	Nolan's Island	7	4.3	0.7	4.8	0.8	4.9	0.9	4.0	0.7	3.7	0.9	4.2	1.2	3.9	0.9
19	Old Man's Island	3	4.8	1.7	4.4	1.3	4.4	0.8	3.6	1.1	3.3	0.2	4.9	1.3	4.4	2.7
		128	4.3	1.0	4.6	1.0	5.0	0.8	4.2	0.8	3.6	0.8	4.2	1.2	4.1	1.3

2.2.3 Interactions

A series of hypotheses were tested to examine whether interactions between the characteristics of the target chimpanzee and characteristics of the enclosure contributed to Dominance or SWB. Another group of interaction hypotheses that were tested concerned interactions between characteristics of the chimpanzee's enclosure.

Two-Way Interactions The first interaction was age by sex. It was entered into the model after the main effects of age and sex were to test whether age effects were different for males and females.

The first set of two-way interactions were between the target chimpanzee's demographic characteristics (age or sex) and the population characteristics of an enclosure (male density, female density, mean male age, and mean female age). This answered the question of whether ratings of individuals in an enclosure were conditional upon demographic characteristics of the individual and characteristics of the enclosure in which chimpanzees were placed.

The second set of two-way interactions were between the target chimpanzee's demographic characteristics and the kin structure of its enclosure (male and female kin density). This tested a series of predictions derived from the kin selection theory. For example, are chimpanzees with more copies of their genes in an enclosure likely to be more dominant or happy as a result of the better support that would be predicted to come from relatives?

Finally, the third set of interactions were between different characteristics of the zoo enclosure. These included the four possible interactions between the male and female density, and the mean male and female age. These interactions answered four questions about the effects on Dominance and SWB of different compositions of age and sex within an enclosure. First, was there any positive or negative effect of male density and the age of males on Dominance or SWB of the chimpanzees in the enclosure? Second, was there any positive or negative effect of female density and

the age of females on Dominance or SWB? Third, was there any positive or negative effect of the male density and the age of females on Dominance or SWB? Finally, was there any positive or negative effect of female density and the age of males on Dominance or SWB?

Three-Way Interactions The first set of three-way interactions tested hypotheses concerning joint effects of age and sex of a target chimpanzee and the four population characteristics of their enclosure (male density, female density, mean male age, and mean female age). These showed whether age by sex interactions were moderated by the social crowding or age structure of an enclosure.

The second set of three-way interactions concerned joint effects among age, male or female density, and male or female kin density variables. These predictors tested the hypotheses that age or sex effects on Dominance or SWB may be moderated by how related a particular chimpanzee is to the males or females in the enclosure.

The third set of three-way interactions concerned whether a chimpanzee's Dominance or SWB was related to that chimpanzee's other personality dimensions, male or female density, and male or female kin density. These interactions tested whether Dominance or SWB was, in part, related to the joint effects of the target chimpanzee's personality, social crowding, and the degree of support from related individuals.

The fourth set of three-way interactions were identical to the third set except that they also included the joint effects of the density variables, kin structure variables, and the mean personality of the enclosure. Hence, these predictors assessed the effects of the degree by which a chimpanzee deviated from others in its enclosure in terms of Surgency, Dependability, Agreeableness, or Emotional Stability. The predictor mean Openness score was dropped from the study because it could not be estimated due to a linear dependency with the previous variables.

Four-Way Interactions Eight four-way interactions having the sex variable in common were entered into the analysis. These interactions tested whether the effects

of sharing genes with other males or females were moderated by joint effects of the target chimpanzee's sex, male or female density, and the mean male or mean female age.

The first of these interactions tested whether Dominance or SWB was predicted by the joint effects of sex, male density, male kin density, and mean male age. This interaction tested whether males in zoos that contain a lot of older males were more dominant or happy if they were related to these males.

Similarly, the second interaction tested whether Dominance or SWB of a target chimpanzee was predicted by the joint effects of sex, male density, female kin density, and mean male age. This interaction tested whether males in zoos that contain a lot of older males were more dominant or happy if they were related to the females within the zoo enclosure.

The third interaction tested was whether the Dominance or SWB of a target chimpanzee could be predicted by its sex, male density, female kin density, and mean female age. This interaction tested whether the predicted increase in the ability of males to have access to females, as a result of having male relatives present would result in the perception that they were more dominant or happy.

The fourth interaction tested is whether a target chimpanzee's Dominance or SWB could be predicted by sex, male density, female kin density, and mean female age. This tested whether males in enclosures with a high density of males show increased Dominance or SWB because they share genes in common with older females. Hence, the target chimpanzees that have a lot of older female relatives may gain their support politically or perhaps gain in dominance and happiness by granting access to these females.

The four final interactions were identical to the first four except that, instead of being predictors in which sex and male density were present in all the interactions, sex and female density were shared in common.

The first four-way interaction tested whether males in zoos with a large number of females were rated as being higher in Dominance or SWB. Hence, chimpanzees that share genes in common with older males in a zoo enclosure with high female density may benefit because they are granted access to the females.

The second of these four-way interactions tested whether males in zoos with older males and a high female density benefit if they share genes in common with the females. That is, it asked the question of whether male chimpanzees showed higher Dominance or SWB ratings by being able to grant access to the females or by having females as allies.

The third of these four-way interactions tested whether males in enclosures with a high density of older females received higher Dominance or SWB ratings if they also shared a large proportion of genes with other males in the enclosure. This tested to see whether being granted sexual access by other males to females resulted in either higher ratings of Dominance or SWB.

The fourth and final four-way interaction tested whether males were rated as having higher Dominance or SWB if they were in an enclosure with a high density of older females with whom they share genes in common. This prediction stems from observations suggesting that, to be dominant, males need the backing of females.

2.2.4 Nested Model Comparisons

A series of three hierarchically nested model comparisons were used to assess the best model for Dominance and SWB. This involved comparing successively more complex models to the prior model to determine whether the inclusion of sets of more complex predictor terms was warranted.

Comparisons were made by computing an F -Ratio for the differences in R^2 s between these different models. A non-significant F -Ratio would mean that the increase in model complexity, as measured by a reduction in error degrees of freedom (df_e),

does not result in a better-fitting model. A significant F -Ratio would mean that the increase in model complexity significantly improves model fit.

Restricted Model 1 The first restricted model was identical to the inclusive model except that it did not contain four-way interactions. This restricted model was more parsimonious than the inclusive model because it had eight more error degrees of freedom and no four-way interactions.

Restricted Model 2 The second restricted model was identical to the first restricted model except that it did not include the 46 three-way interactions. This restricted model was more parsimonious than the first restricted model because it had 46 more error degrees of freedom and no four- or three-way interactions.

Restricted Model 3 The third restricted model was identical to the second restricted model except that it contained only main effects and the sex by age interaction. This model was the most parsimonious model in that it had 20 more error degrees of freedom than the previous model.

2.3 Genetic Analysis

2.3.1 Goals of the Analysis

These analyses determined the extent to which additive genetic, heritable maternal, non-heritable maternal, and nonshared environmental effects contributed to chimpanzee Dominance and SWB.

The genetic analysis estimated genetic and environmental parameters from the pedigree records. It also controlled for effects from the environmental analysis by setting them as covariates.

2.3.2 Analytic Strategy

Eight nested models incorporating different sources of variance and covariance were compared (see Figure 2.1). All eight models included fixed zoo effects for Dominance and SWB. These models also included covariates for Dominance and SWB based on the results of the sequential canonical analysis. Thus, sex, age, and the age by sex interaction were covariates for Dominance, and age was a covariate for SWB.

Model 1 was an inclusive model estimating additive genetic (A), heritable maternal (M), non-heritable maternal (C), and nonshared environment and error variance (E) for Dominance and SWB. This model also estimated source of covariance between Dominance and SWB. Hence, it assessed genetic (r_g), heritable maternal (r_m), non-heritable maternal (r_c), and nonshared environmental (r_e) correlations.

Model 2 was nested within Model 1. Model 2 differed from Model 1 in that non-heritable maternal effects on Dominance and non-heritable maternal correlations were fixed to zero. That is, it tested whether there was a difference in model fit between a model that did and did not include the variance and covariance due to non-heritable maternal effects.

Models 3 and 4 were nested within Model 2. Model 3 differed from Model 2 in that the covariance among heritable maternal effects was set equal to zero. Model 4 differed from Model 2 in that the covariance among the additive genetic effects was set equal to zero.

The difference between Models 5 and 3 was that in Model 5 heritable maternal contributions to Dominance variance were set equal to zero. Models 6, 7, and 8 were nested within Model 5. The difference between Models 6 and 5 was that the heritable maternal contribution to SWB was set equal to zero. The difference between Models 7 and 5 was that the non-heritable maternal contribution to SWB was set equal to zero. Model 8 was the most restricted of these models. The two differences between

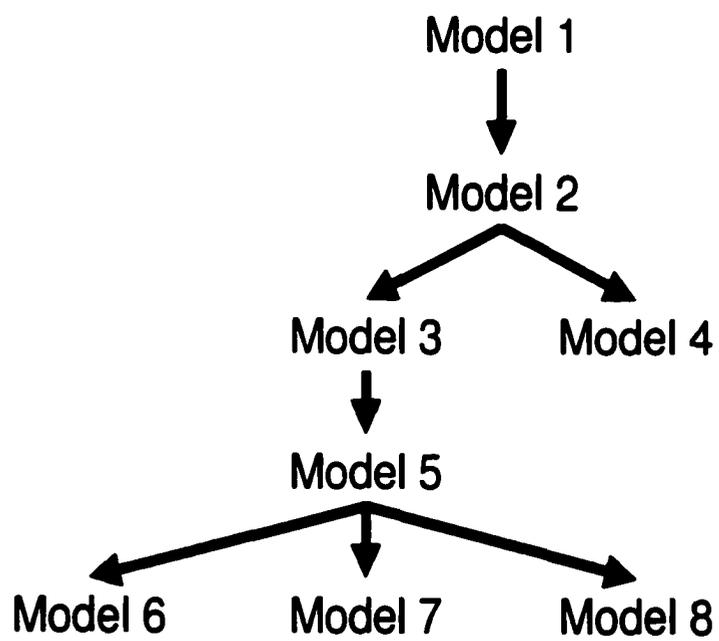


FIGURE 2.1. Nested Behavior Genetic Models

Models 8 and 5 were that in Model 8 heritable and non-heritable contributions to SWB were set equal to zero.

2.3.3 Model Fitting

Behavior geneticists that study humans typically test models using independent pairs of differently related individuals. However, chimpanzee populations are characterized by a promiscuous mating system (Pusey, 2001). This makes the identification of enough unique pairs difficult and rules out most techniques that are used in human behavioral genetic research. Thus, it was necessary to turn to analytic techniques developed by animal breeders. These techniques use the relationships between all possible pairs of animals to partition the phenotypic variance and covariance into various genetic and environmental effects. Because these techniques use all possible relationships among animals, they have the advantage of having more statistical power, especially when working with smaller samples.

MTDFREML Model fitting and parameter estimation were performed with the Multi-trait Derivative Free Restricted Maximum Likelihood (MTDFREML) package (Boldman et al., 1995). Derivative free restricted maximum likelihood (DFREML) is a parameter estimation technique developed by Meyer (1989, 1991) to solve one or more animal model equations (Henderson, 1975). The animal model is a linear equation in which an individual's phenotype is predicted by a number of fixed and random effects. Thus, for each individual:

$$y_i = \beta_i + a_i + m_i + c_i + e_i$$

where y_i is an individual animal's phenotype score on either Dominance or SWB; and β_i is a fixed effect indicating how much the individual deviates from the grand mean because of the zoo it is in. Random effects include a_i , the amount an individual deviates from the zoo mean attributable to additive genes; m_i , the amount an individual

deviates from the zoo mean attributable to heritable characteristics of its mother; c_i , the amount an individual deviates from the zoo mean attributable to non-heritable characteristics of its mother; and e_i , the residual.

In the case where there are several animals, it is necessary to relate each of these effects to an individual. This can be done via the following equation:

$$\mathbf{y} = \mathbf{X}(\boldsymbol{\beta}) + \mathbf{Z}_a(\mathbf{a}) + \mathbf{Z}_m(\mathbf{m}) + \mathbf{Z}_c(\mathbf{c}) + \mathbf{e}$$

where \mathbf{y} is a vector of phenotype scores; $\boldsymbol{\beta}$ is a vector of fixed effects; and \mathbf{X} is a known incidence matrix relating these fixed effects to the phenotype scores, \mathbf{y} of all individuals. The vectors of additive genetic, heritable maternal, and non-heritable maternal effects for all individuals are \mathbf{a} , \mathbf{m} , and \mathbf{c} , respectively. The three known incidence matrices \mathbf{Z}_a , \mathbf{Z}_m , and \mathbf{Z}_c relate the random additive genetic, heritable maternal, and non-heritable maternal effects, respectively, to each individual's phenotype in the \mathbf{y} vector. Thus, the products of the effects vectors and incidence matrices indicate how much each individual deviates from the zoo mean due to additive genetic, heritable maternal, and non-heritable maternal effects. Finally, \mathbf{e} is the vector of random nonshared environmental effects and error.

In the case of related individuals, some effects would covary with one another because related individuals are more likely to share these effects than unrelated individuals. Thus, the more related individuals are, the more similar will be their deviations due to genetic effects. Heritable maternal effects are similar except that the similarity of the degree to which individuals deviate from the mean will be conditional upon how related their *mothers* are. Finally, individuals who share the same mother, whether related or not, should have similar deviations from the mean due to non-heritable maternal effects. Finally, by definition, nonshared environment effects are independent among individuals. This can be expressed:

$$\sigma_y^2 = \mathbf{A}\sigma_a^2 + \mathbf{A}\sigma_m^2 + \mathbf{I}\sigma_c^2 + \mathbf{I}\sigma_e^2$$

Here, σ_y^2 refers to the total phenotypic variance, σ_a^2 refers to the additive genetic variance, σ_m^2 refers to the heritable maternal variance, σ_c^2 refers to the non-heritable maternal variance, and σ_e^2 refers to the amount of nonshared environmental variance. Because additive genetic and heritable maternal variances are related to the degrees of relatedness among individuals and mothers, respectively, these variances are weighted by **A**, the numerator relationship matrix (Searle, 1966). This is the matrix indicating what Wright's coefficient of relatedness is for every possible pair of animals in the sample. Thus, it indicates for any given pair what proportion of genes on average they share in common. In the study, this was computed using information from the Chimpanzee Species Survival Plan (Fulk, 1999).

Because both non-heritable maternal effects and nonshared environmental effects do not covary among either related mothers or related individuals, respectively, these variance components are weighted by **I**, an identity matrix which holds that these effects are independent. As both the **A** and **I** are known, the variance components can be solved using a restricted maximum likelihood procedure.

Single Trait Models Restricted maximum likelihood procedures can solve for fixed and random effects by using various iterative procedures to assess the proportion of variance accounted for by each effect. The iterative procedure used for DFREML assigns different proportions of variance to the effects; estimates the inverse log likelihood ($-2\log\lambda$), a measure of congruence between the predicted (\hat{y}) and observed (y) scores; and repeats this procedure until the congruence between predicted and actual phenotype scores meeting a predefined criterion (converges on a solution). When DFREML converges on a solution, the $-2\log\lambda$ is at a minimum and any change in variance estimates will cause it to be greater.

Multitrait Models This procedure can be generalized to multiple traits. Because the variance between phenotypes and effects can covary when there are multiple traits, it is possible to estimate variances and covariances in a manner similar to estimating

variance components in the univariate model. In the study, there were two correlated phenotypes, Dominance and SWB. Hence, DFREML needed to simultaneously solve for both phenotypes. The animal model for such a problem is:

$$\begin{bmatrix} \mathbf{y}_d \\ \mathbf{y}_s \end{bmatrix} = \begin{bmatrix} \mathbf{X}_d & 0 \\ 0 & \mathbf{X}_s \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_d \\ \boldsymbol{\beta}_s \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a_d} & 0 \\ 0 & \mathbf{Z}_{a_s} \end{bmatrix} \begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_s \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{m_d} & 0 \\ 0 & \mathbf{Z}_{m_s} \end{bmatrix} \begin{bmatrix} \mathbf{m}_d \\ \mathbf{m}_s \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{c_d} & 0 \\ 0 & \mathbf{Z}_{c_s} \end{bmatrix} \begin{bmatrix} \mathbf{c}_d \\ \mathbf{c}_s \end{bmatrix} + \begin{bmatrix} \mathbf{e}_d \\ \mathbf{e}_s \end{bmatrix}$$

where \mathbf{y}_d and \mathbf{y}_s are vectors for the phenotype scores for Dominance and SWB, respectively. \mathbf{X}_d and \mathbf{X}_s are known incidence matrices relating the fixed zoo effects, $\boldsymbol{\beta}_d$ and $\boldsymbol{\beta}_s$, to the Dominance and SWB vectors, respectively. \mathbf{Z}_{a_d} and \mathbf{Z}_{a_s} are known incidence matrices relating the additive genetic effects \mathbf{a}_d and \mathbf{a}_s to the Dominance and SWB vectors, respectively. \mathbf{Z}_{m_d} and \mathbf{Z}_{m_s} are known incidence matrices relating the heritable maternal effects \mathbf{m}_d and \mathbf{m}_s to the Dominance and SWB vectors, respectively. \mathbf{Z}_{c_d} and \mathbf{Z}_{c_s} are known incidence matrices relating the non-heritable maternal effects \mathbf{c}_d and \mathbf{c}_s to the Dominance and SWB vectors, respectively. Finally, \mathbf{e}_d and \mathbf{e}_s are random nonshared environment and error vectors for Dominance and SWB, respectively.

As in the previous example, DFREML uses an iterative procedure to solve these equations. However, if there are multiple correlated traits, DFREML also needs to take into account covariances among traits and effects. By weighting the covariances as well as the variances by the \mathbf{A} or \mathbf{I} matrices, the variances and covariances can be partitioned into genetic and non-genetic effects. In the case of this study, the variances of the random effects equaled:

$$\text{var} \begin{bmatrix} a_d \\ a_s \\ m_d \\ m_s \\ c_d \\ c_s \\ e_d \\ e_s \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{a_d}^2 & \mathbf{A}\sigma_{a_d a_s} & \mathbf{A}\sigma_{a_d m_d} & \mathbf{A}\sigma_{a_d m_s} & 0 & 0 & 0 & 0 \\ \mathbf{A}\sigma_{a_d a_s} & \mathbf{A}\sigma_{a_s}^2 & \mathbf{A}\sigma_{a_s m_d} & \mathbf{A}\sigma_{a_s m_s} & 0 & 0 & 0 & 0 \\ \mathbf{A}\sigma_{a_d m_d} & \mathbf{A}\sigma_{a_s m_d} & \mathbf{A}\sigma_{m_d}^2 & \mathbf{A}\sigma_{m_d m_s} & 0 & 0 & 0 & 0 \\ \mathbf{A}\sigma_{a_d m_s} & \mathbf{A}\sigma_{a_s m_s} & \mathbf{A}\sigma_{m_d m_s} & \mathbf{A}\sigma_{m_s}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}\sigma_{c_d}^2 & \mathbf{I}\sigma_{c_d c_s} & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}\sigma_{c_d c_s} & \mathbf{I}\sigma_{c_s}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{I}\sigma_{e_d}^2 & \mathbf{I}\sigma_{e_d e_s} \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{I}\sigma_{e_d e_s} & \mathbf{I}\sigma_{e_s}^2 \end{bmatrix}$$

Here, the diagonal consists of the variance components including: additive genetic (σ_a^2), heritable maternal (σ_m^2), non-heritable maternal (σ_c^2), and nonshared environment and error (σ_e^2). In each case the subscript indicates whether the variance component belongs to Dominance (*d*) or SWB (*s*).

The off-diagonal elements of the matrix important to the study are those that partition the Dominance and SWB covariance. These include the genetic ($\sigma_{a_d a_s}$), heritable maternal ($\sigma_{m_d m_s}$), non-heritable maternal ($\sigma_{c_d c_s}$), and nonshared environmental variance ($\sigma_{e_d e_s}$). Covariances between two different effects on the same phenotype such as $\sigma_{a_s m_s}$ as well as covariances between two different effects on two different phenotypes such as $\sigma_{a_d m_s}$ are usually small and were fixed to zero in the current study.

Chapter 3

RESULTS

3.1 Environmental Analysis

Hierarchical partitioning of variance was accomplished by analyzing the inclusive and restricted models for Dominance and SWB using SAS's general linear model procedure (PROC GLM) (SAS Institute, 1989). Table 3.1 shows the proportions of Dominance and SWB variance accounted for in the inclusive and restricted models.

TABLE 3.1. Alternative Models Predicting Dominance and SWB

Number	Model	R^2	df_m^a	df_e^b	F	p
Dominance						
D1	M ^c	.585	19	108	8.01	< .0001
D2	M+2W ^d	.661	39	88	4.41	< .0001
D3	M+2W+3W	.831	85	42	2.44	= .0010
D4	M+2W+3W+4W	.859	93	34	2.24	= .0047
Subjective Well-Being						
S1	M	.478	20	107	4.89	< .0001
S2	M+2W	.557	40	87	2.74	< .0001
S3	M+2W+3W	.760	86	41	1.51	= .0717
S4	M+2W+3W+4W	.855	94	33	2.07	= .0101

Note. $N = 128$

^a Model degrees of freedom.

^b Error degrees of freedom.

^c Main effects and the age by sex interaction.

^d nW indicates n -way interaction terms.

Standardized regression coefficients (β s) were calculated using the regression procedure (PROC REG) (SAS Institute, 1989). To increase the efficiency of parameter estimation, only significant predictors and any main effects that were part of significant interactions were included in the models.

3.1.1 Predictors of Dominance

Omnibus Null Tests Table 3.2 shows the results of conducting hierarchically nested model comparisons of the three restricted models. It shows that the inclusion of two-way interactions did not significantly improve model fit enough to offset the loss in model parsimony; the inclusion of three-way interactions did not improve the fit over a model containing main effects and two-way interactions; and the inclusion of four-way interactions did not improve the fit of the model containing main effects and both two- and three-way interactions. Finally, model fit did not improve by including all of the two-, three-, and four-way interactions to the model that consisted of main effects and the age by sex interaction.

The model with the most explanatory power and the greatest parsimony only included main effects and the age by sex interaction. This model accounted for a significant proportion of Dominance variance ($R^2 = .585$; $F(19, 108) = 8.01$; $p < .0001$).

TABLE 3.2. Nested Model Comparisons for Dominance and SWB

Number	Comparison ^a	R_{Δ}^2 ^b	df_{Δ} ^c	df_e	F	p
Dominance						
1	D4-D3	.028	8	34	0.84	= .5713
2	D3-D2	.170	46	42	0.92	= .6128
3	D2-D1	.076	20	88	0.99	= .4865
4	D4-D1	.274	74	34	0.89	= .6639
Subjective Well-Being						
1	S4-S3	.095	8	33	2.70	= .0208
2	S3-S2	.203	46	41	0.75	= .8241
3	S2-S1	.079	20	87	0.78	= .7344
4	S4-S1	.377	74	33	1.16	= .3264

Note. $N = 128$

^a This refers to the notations used in Table 3.1.

^b The difference in explanatory power between the compared models.

^c The difference in model degrees of freedom between the compared models.

Significant Predictors Two demographic predictors were significant. The first was a positive effect of age on Dominance ($\beta = .331$; $F(1, 108) = 31.36$; $p < .0001$) indicating that Dominance increased as a function of age. There was also a significant age by sex interaction ($\beta = .333$; $F(1, 108) = 10.03$; $p = .0020$) indicating that the age effects on Dominance were greater for males than for females.

Four personality predictors were significantly correlated with Dominance. There were positive effects of Surgency ($\beta = .137$; $F(1, 108) = 13.01$; $p = .0005$) and Openness ($\beta = .244$; $F(1, 108) = 8.90$; $p = .0035$). There were negative effects of Dependability ($\beta = -.438$; $F(1, 108) = 35.25$; $p < .0001$) and Emotional Stability

($\beta = -.357$; $F(1, 108) = 35.82$; $p < .0001$). However, these significant effects were most likely an artifact of using unit-weighting to create the factor scores as they were not the original weights used to find an orthogonal solution.

3.1.2 Predictors of Subjective Well-Being

Omnibus Null Tests Table 3.2 shows the results of the hierarchically nested model comparisons of the three restricted models. The inclusion of two-way interactions did not significantly improve model fit enough to offset the loss in model parsimony, and adding three-way interactions did not improve the fit over a model containing main effects and two-way interactions. However, including four-way interactions improved the fit of the model containing main effects and both two- and three-way interactions.

Results were ambiguous with respect to whether the four-way interactions were significant or whether the significance was due to alpha slippage. The decision to reject the model containing the four-way interactions was predicated on a more conservative test of interactions. This test compared the model containing main effects and the age by sex interaction to the inclusive model and found that the two models did not differ in fit.

Two four-way interactions were statistically significant. They accounted for approximately 7% of the variance and were one to two orders of magnitude larger in effect size than the other four-way interactions. While the final model selected did not include these effects, it is possible that they are real.

Significant Predictors Dominance was a positive predictor of SWB accounting for approximately 27% of the variance ($\beta = .629$; $F(1, 107) = 55.11$; $p < .0001$). Age was negatively related to SWB ($\beta = -.057$; $F(1, 107) = 4.77$; $p = .0312$). There were also positive effects on SWB of Surgency ($\beta = .276$; $F(1, 107) = 17.08$; $p < .0001$) and Dependability ($\beta = .292$; $F(1, 107) = 14.56$; $p = .0002$).

The two *potentially* significant four-way interactions were constructed as directional, single degree of freedom hypotheses for multiple regression. Thus, they were more readily interpretable than multiple degree of freedom interactions typically tested in analysis of variance. Significant interactions indicated that the effect was conditional on all four conditions being present.

The first interaction was positive ($\beta = 16.274$; $F(1, 33) = 7.69$; $p = .0091$) indicating that males are happier in enclosures where there are more males per square meter, older males, and related females are happier. The second interaction was also positive ($\beta = 23.511$; $F(1, 33) = 7.77$; $p = .0088$) indicating that males are happier in enclosures where there are more males per square meter, older females, and related females are happier.

3.2 Genetic Analysis

Table 3.3 shows the parameter estimates for each of the eight models in the study. It also shows which parameters were fixed to zero in the various restricted models.

In any covariance structure analysis, different models that include different parameter estimates must be compared to one another to determine which model best fits the data. These comparisons need to consider how well the model fits and the number of parameters that are free to vary in the model.

TABLE 3.3. Proportions of Variance and Covariance

Model	Subjective well-being					Dominance					Correlations ^a			
	h^2	m^2	c^2	z^2	e^2	h^2	m^2	c^2	z^2	e^2	r_g	r_m	r_c	r_e
1	.26	.31	.07	.03	.32	.60	.04	.01	.02	.31	1.00	0.32	1.00	0.00
2	.27	.33	<.01	.03	.37	.64	.03	F	.02	.29	1.00	1.00	F	0.04
3	.35	.19	<.01	.04	.42	.65	<.01	F	.02	.31	1.00	F	F	0.12
4	<.01	.22	<.01	.04	.74	.33	.02	F	.02	.61	F	1.00	F	0.59
5	.34	.19	<.01	.04	.44	.65	F	F	.02	.31	1.00	F	F	0.13
6	.41	F	.11	.04	.45	.63	F	F	.02	.32	0.93	F	F	0.14
7	.36	.19	F	.03	.42	.65	F	F	.02	.31	1.00	F	F	0.11
8	.40	F	F	.03	.56	.63	F	F	.02	.32	0.88	F	F	0.19

Note. F indicates that the parameter was fixed to 0.00. h^2 is the proportion of variance due to additive genetic effects; m^2 is the proportion of variance due to heritable maternal effects; c^2 is the proportion of variance due to non-heritable maternal effects; z^2 is the proportion of variance due to fixed zoo effects; and e^2 is the proportion of variance due to nonshared environmental effects and error. Each age (a^2), sex (s^2), and age by sex interaction (i^2) effect was 0.01 or less.

^a Correlations among additive genetic (r_g), heritable maternal (r_m), non-heritable maternal (r_c), and nonshared environmental (r_e) effects.

3.2.1 The Three Means of Comparison

Akaike's Information Criterion, p -values, and difference Chi-square tests were used to compare the eight nested covariance structure models. These model fit comparisons were based on the fact that the log likelihood ratios ($-2\log\lambda$) are distributed as Chi-squares.

Akaike's Information Criterion One way to compare several covariance structure models is to use Akaike's Information Criterion (*AIC*) (Akaike, 1987). The *AIC* index adjusts the model fit statistic by twice the number of parameters estimated. Hence, it corrects model fit for the degree of parsimony. Typically, *AIC* equals $\chi^2 + 2k$ where χ^2 is the measure of model fit and $2k$ is twice the number of parameters that were estimated. However, because the log likelihood ratios are distributed as Chi-square, *AIC* also equals $-2\log\lambda + 2k$ where $-2\log\lambda$ indicates model fit and $2k$ is the correction for the number of parameters estimated. In both cases, the lowest number indicates the model that best balances model fit and parsimony.

A comparison of *AIC* scores (see Table 3.4) indicates that the best model in terms of fit and parsimony was Model 8 and that the worst was Model 4, which did not include a genetic correlation.

TABLE 3.4. Model Comparison Via the Fit Indices

Model	$-2\log\lambda$	df_e	Δdf	$\Delta\chi^2$	p	k	<i>AIC</i> ^a
1	2642.414	0				12	2666.414
2	2642.419	2	2	0.005	1.000	10	2662.419
3	2644.105	3	3	1.691	0.639	9	2662.105
4	2648.725	3	3	6.311	0.097	9	2666.725
5	2644.105	4	4	1.691	0.792	8	2660.105
6	2645.569	5	5	3.155	0.676	7	2659.569
7	2644.110	5	5	1.696	0.889	7	2658.110
8	2645.988	6	6	3.574	0.734	6	2657.988

Note. All differences are between the model of a given row and Model 1.

^a Akaike's Information Criterion

p-Values A second way to compare model fit is by computing the *p*-value for the difference Chi-square tests between each restricted model and the saturated model (Model 1). Cohen (1990) criticized the use of *p*-values for null hypothesis testing. However, others have argued that within a single study *p*-values can be meaningfully compared in the same way as the more traditional fit indices are (Abelson, 1997). In this instance higher *p*-values indicate a closer correspondence between the restricted model and the saturated model when the comparison is adjusted for the number of parameters that are fixed.

A comparison of *p*-values (see Table 3.4) to assess which model best balanced fit and parsimony revealed that the *p*-value for the difference between Model 1 and Model 2 was the highest indicating that Model 2 was the model that was closest to Model 1 in fit when parsimony was considered. However, it should be noted that two of the parameters included in Model 2 were non-heritable maternal effects on SWB and heritable maternal effects on Dominance were almost equal to zero. Furthermore, the heritability estimates for the heritability of SWB ($h^2 = .40$) and Dominance ($h^2 = .63$) in Model 8 were closer to what were found in previous univariate analyses of these traits (Weiss et al., 1999). Thus, while the *p*-value indicated that Model 2 was the best, all other indicators suggested that the increase in model fit may have been due to the fact that the inclusion of the additional parameters was significant by chance alone.

Nested Model Comparisons A third way to find the best model is by comparing the difference in log likelihood ratios between two models in which one model is nested in the other. The difference in log likelihood between two nested models is distributed like a Chi-Square with the degrees of freedom equal to difference in the number of fixed parameters. If this difference is significant, then one should accept the model with the additional parameters. If it is not significant, then these parameters do

not increase model fit above the loss in parsimony, and the simpler model should be accepted.

Table 3.5 shows the results from comparing each set of nested models in the study. The only significant difference is between Model 4 and Model 2. These models differ only in that the genetic correlation was eliminated in Model 4.

Of the three models that were nested within Model 5, Model 7 shows the least change in Chi-Square. However, while the comparison between Model 5 and Model 8 has a larger Chi-Square value, this difference is not significant, yet it is more parsimonious by virtue of having one more degree of freedom. Thus, Model 8 appears to be the best model in terms of explanatory power and parsimony. It includes additive genetic, shared zoo, and nonshared environmental contributions to SWB and Dominance, as well as contributions of age, sex, and the age by sex interaction as predictors of Dominance and age as a predictor of SWB. Excluded from Model 8 were all maternal effects as contributors to SWB and Dominance.

Model 8 included a high genetic correlation between SWB and Dominance and a low nonshared environmental correlation. These findings indicate that the same genes influenced both traits and that nonshared environmental contributions independently influenced Dominance and SWB.

TABLE 3.5. Difference Chi-Square Tests

Comparison	$\Delta\chi^2$	Δdf	<i>p</i>
Model 2 – 1	0.005	2	1.000
Model 3 – 2	1.687	1	0.194
Model 4 – 2	6.306	1	0.012
Model 5 – 3	0.000	1	1.000
Model 6 – 5	1.464	1	0.226
Model 7 – 5	0.005	1	0.944
Model 8 – 5	1.883	2	0.390

3.2.2 Parameter Estimates

Parameter estimates for the saturated model (Model 1), the best fitting model according to the difference Chi-square test and the *AIC* (Model 8), and the best fitting model using the *p*-value criterion (Model 2) were calculated. These models contained some notable consistencies. In all three models, the evidence for the heritability of Dominance and SWB as well as the genetic correlation was strong, while evidence for non-heritable maternal and shared zoo effects for Dominance and SWB was weak. Evidence for heritable maternal effects on Dominance was also weak.

The evidence for heritable maternal effects on SWB was somewhat ambiguous. Models 1 and 2 seemed to suggest that this effect existed but was moderate in strength. However, Model 8, which eliminated it, was the best model in terms of the *AIC*, but not the *p*-value.

Model 1 In Model 1, the saturated model (see Figure 3.1), SWB was influenced by additive genetic ($h^2 = .26$), heritable maternal ($m^2 = .31$), non-heritable maternal ($c^2 = .07$), nonshared environmental ($e^2 = .32$), shared zoo ($z^2 = .03$), and age effects ($a^2 < .01$).

Similarly, Dominance was influenced by additive genetic ($h^2 = .60$), heritable maternal ($m^2 = .04$), non-heritable maternal ($c^2 = .01$), nonshared environmental ($e^2 = .31$), shared zoo ($z^2 = .02$), age ($a^2 = .01$), sex ($s^2 < .01$), and age by sex interaction effects ($i^2 = .01$).

The additive genetic effects were correlated ($r_g = 1.00$) as were the heritable maternal effects ($r_m = .32$) and non-heritable maternal effects ($r_c = 1.00$). The correlation among nonshared environmental effects suggested that they were independent ($r_e = .00$).

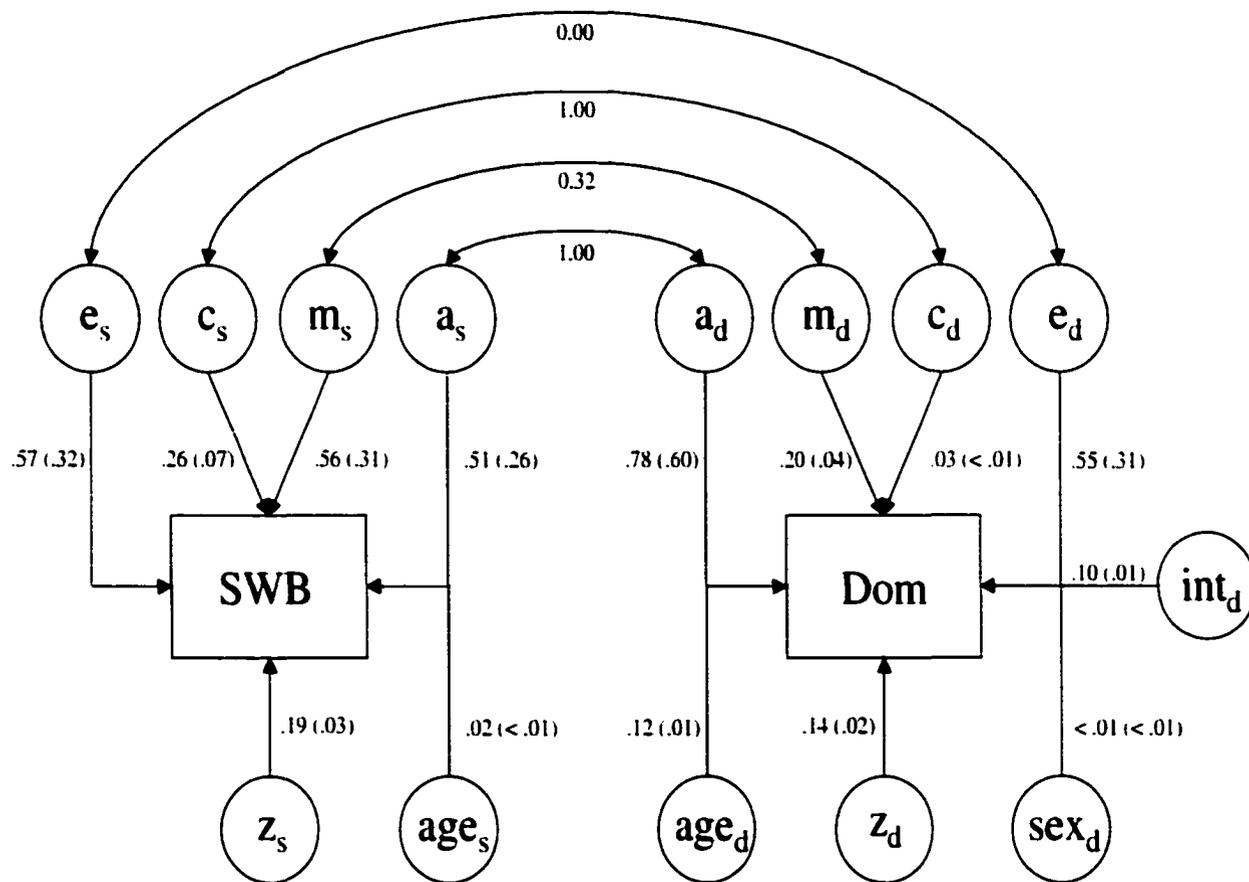


FIGURE 3.1. Model 1: The Saturated Model

Model 8 In Model 8, the model chosen as having the best fit and most parsimony (see Figure 3.2), SWB was influenced by additive genetic ($h^2 = .40$), nonshared environmental ($e^2 = .56$), shared zoo ($z^2 = .03$), and age effects ($a^2 < .01$).

Dominance in this model was influenced by additive genetic ($h^2 = .60$), nonshared environmental ($e^2 = .32$), shared zoo ($z^2 = .02$), age ($a^2 = .01$), sex ($s^2 < .01$), and age by sex interaction effects ($i^2 = .01$).

Additive genetic ($r_g = .88$) and nonshared environmental effects ($r_e = .19$) were correlated. Because the MTDFREML algorithm required the presence of the nonshared environmental effects, this parameter could not be tested for significance.

Model 2 In Model 2, the model that had the best fit according to the p -value criterion (see Figure 3.3), SWB was influenced by additive genetic ($h^2 = .27$), heritable maternal ($m^2 = .31$), non-heritable maternal ($c^2 = .07$), nonshared environmental ($e^2 = .32$), shared zoo ($z^2 = .03$), and age effects ($a^2 < .01$).

Dominance in this model was influenced by additive genetic effects ($h^2 = .64$), heritable maternal effects ($m^2 = .03$), nonshared environmental effects ($e^2 = .29$), shared zoo effects ($z^2 = .02$), age effects ($a^2 = .01$), sex effects ($s^2 < .01$), and the age by sex interaction ($i^2 = .01$).

The additive genetic effects were correlated ($r_g = 1.00$) as were the heritable maternal effects ($r_m = 1.00$). The correlation among nonshared environmental effects was small ($r_e = .04$).

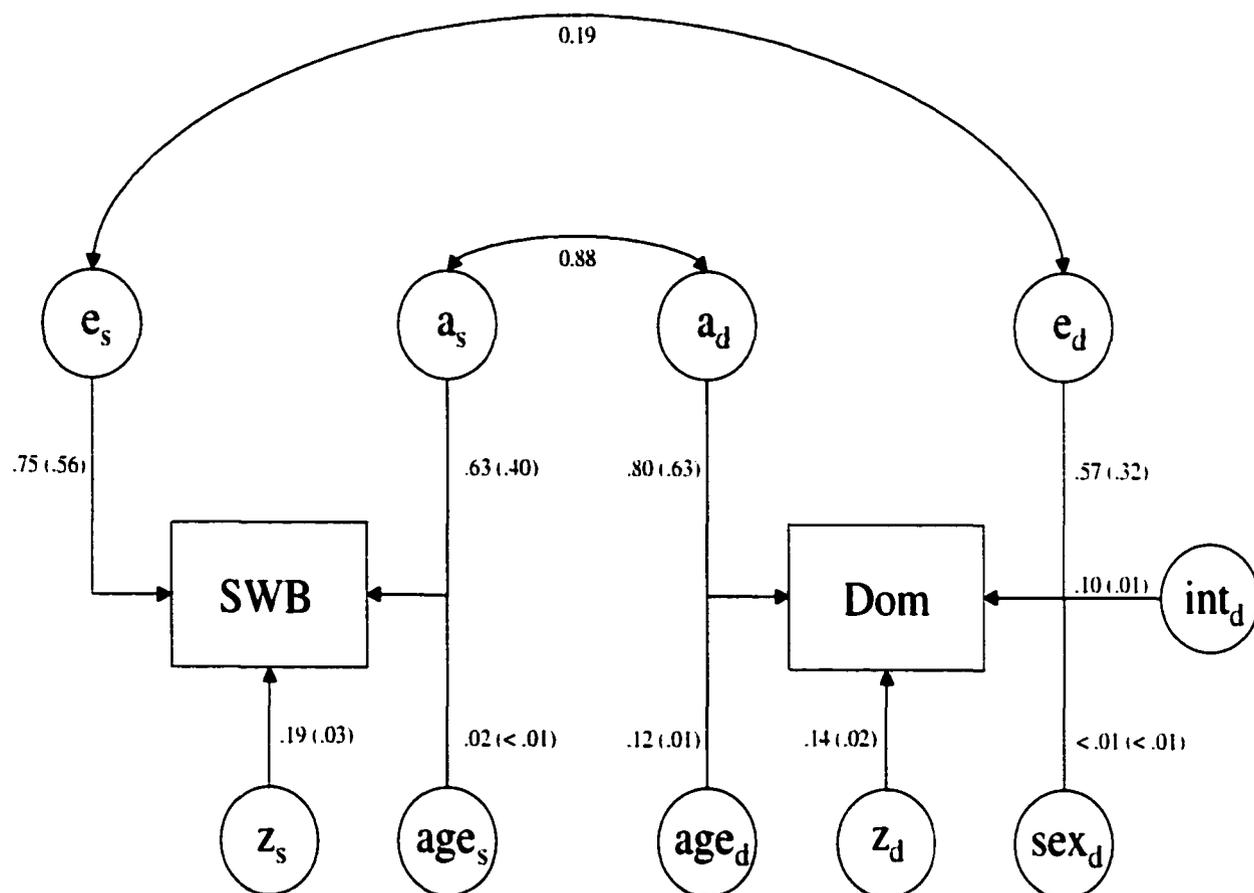


FIGURE 3.2. Model 8: The Model with the Lowest *AIC* and Best Fit as Determined by Difference Chi-square Tests

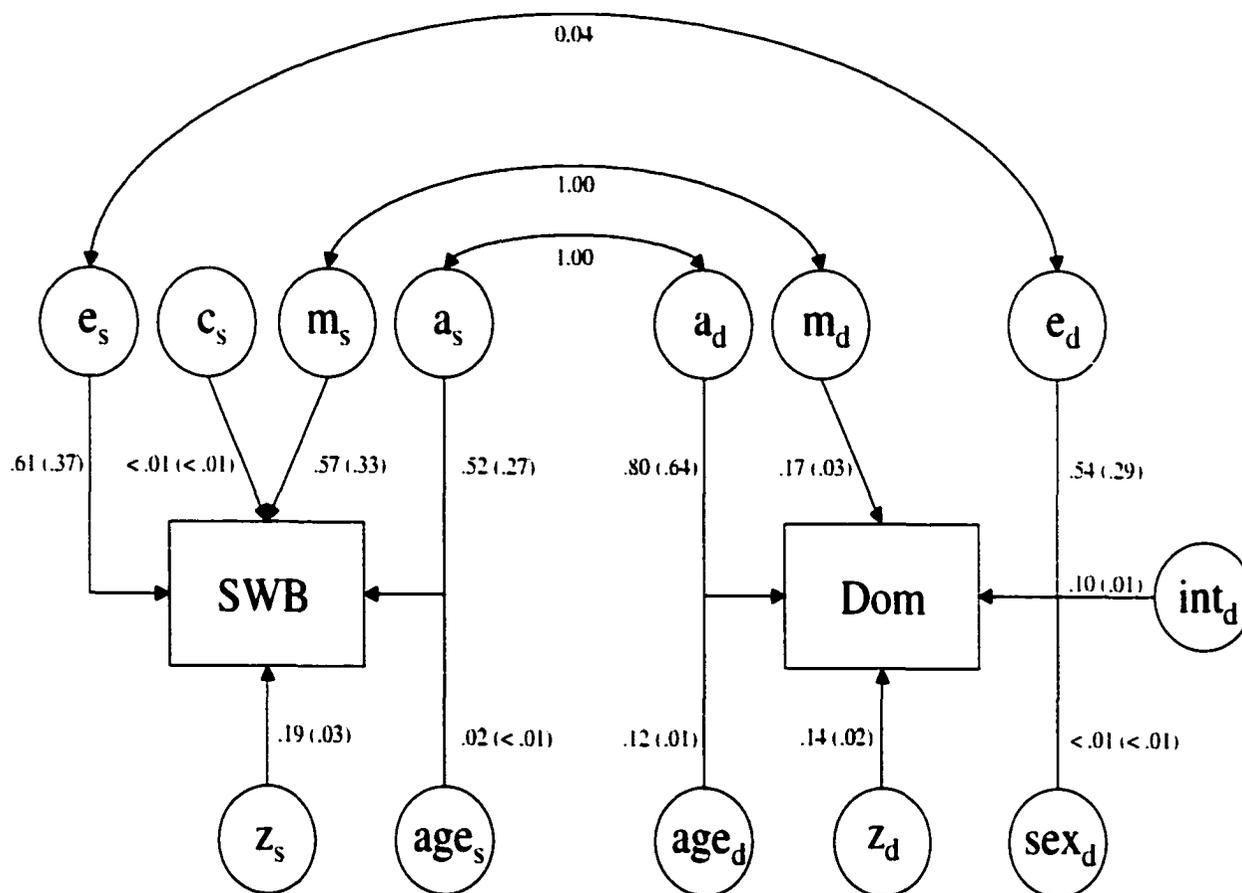


FIGURE 3.3. Model 2: The Model with the Highest p -value

Chapter 4

DISCUSSION

4.1 Environmental Analysis

4.1.1 Overview of the Environmental Analysis

To isolate unique predictors of Dominance and SWB, a sequential canonical analysis was used. In the first stage of the analysis, the demographic and environmental variables were tested as possible predictors of Dominance. In the second stage, Dominance, followed by demographic and environmental variables, was used to predict SWB.

All variables were hierarchically entered as predictors. Three classes of main effects were tested. The first were tests of demographic hypotheses, which included age, sex, the age by sex interaction, the density of males and females, mean male age, and mean female age. The second class involved tests to determine whether, as predicted by kin selection, the density of male or female kin influenced Dominance or SWB. Finally, the third set of variables included the chimpanzee's personality score on each of the remaining five factors and the mean personality scores in its zoo. The latter, when entered into the equation after the personality variables, was a measure of chimpanzee-environment fit.

A number of two-, three-, and four-way interactions of these effects were also tested. These tested whether interactions of the persistent characteristics of the environment affected Dominance or SWB. A series of nested model comparisons was used to test whether the inclusion of these interactions improved model fit.

Tests of Main Hypotheses Of the demographic hypotheses that were tested, three were significant. Dominance increased as a function of age, and this increase was greater for

males than for females. SWB increased as a function of Dominance and as a function of age. None of the variables based on the kin selection or chimpanzee-environment fit hypotheses were significant.

Tests of Interaction Hypotheses With the sex by age interaction included in the main effects model, nested model comparisons showed that including two-, three-, and four-way interactions did not improve model fit over the main effects model. The nested model comparison ruled out these complex interaction effects. However, two of the four-way interactions were significant. The first suggested that male chimpanzees with female kin nearby are happier in enclosures with a high density of older males. The second suggested that male chimpanzees in zoos with a high male density are happier when they are surrounded by older female relatives.

4.1.2 Interpretation

The results of the environmental analysis did not support the contention that the paucity of environmental effects on human personality or SWB is due to the design of earlier studies which did not consider the possibility that individuals select environments that make them happy.

The chimpanzees in the study were unable to select the enclosures or enclosure-mates they were assigned to. Hence, the study should have been more sensitive to possible shared and nonshared environmental effects on chimpanzee Dominance and SWB.

Predictors Ruled Out Contrary to predictions, the density of chimpanzees did not increase behaviors that might lead individuals to give high Dominance ratings to chimpanzees. Density was also not an important predictor of SWB. This does not mean that enclosure size does not matter in absolute terms, but more likely indicates a threshold effect (see Rowe, 1994), *i.e.*, that after a necessary reduction in animal

density is achieved, further reductions make little or no difference. It is likely that all of the chimpanzee enclosures in the study achieved this optimal density.

The density of male or female kin also did not effect Dominance or SWB. This is surprising in light of a great deal of ethological research on chimpanzees and other primates highlighting the importance of kin in forming coalitions and alliances (de Waal, 2000). It is also contrary to human findings showing that the presence of kin can act as a protective factor (Figueredo et al., 2001). One possible explanation for this is that, as with small human societies (Sober & Wilson, 1999), small chimpanzee societies foster reciprocal altruism among related and unrelated members.

Another hypothesis that can be ruled out is that Dominance and SWB in chimpanzees are functions of how similar other chimpanzees are with respect to the other personality factors. This is contrary to what would be expected from hypotheses based on the "green beard effect" (Dawkins, 1976) which have been backed up by findings in humans showing that personality similarity is just one cue that indicates that two individuals share the same genes (Bouchard & Loehlin, 2001).

Finally, while it has been the mainstay of theorists who are opposed to genetic explanations for behavior (cf. Baumrind, 1993), the prediction that Dominance or SWB is sensitive to consistent, yet complex, characteristics of the environment was ruled out. However, results of the study do not speak to the effects of situations encountered over time as described by others (Mischel, 1968; Mischel & Shoda, 1995).

Predictors Ruled In The only predictors ruled in were the effects of age and the age by sex interaction. The human personality literature also contains findings of predictable, albeit small, age and sex differences in personality (Costa & McCrae, 2002).

On the other hand, whether age affects human happiness is, as yet, unresolved (Diener et al., 1999). One possibly crucial difference between this study and human studies is that age was a significant predictor of the proportion of SWB variance remaining after it had been residualized on Dominance. Hence, human researchers

may wish to see whether there is a difference between the sensitivity of the proportion of SWB variance shared in common with personality and the unique proportion of SWB related to age effects.

4.1.3 Conclusions from the Environmental Analysis

What can one conclude given these findings concerning the paucity of significant environmental effects on Dominance and SWB? Overall, it supports trait theories of personality (Allport, 1937; Digman, 1996; John, 1990; McCrae & Costa, 1997), and SWB (Diener et al., 1999; Lykken & Tellegen, 1996; Tellegen et al., 1988).

Demographic Predictors Human personality and happiness research has consistently found that demographic and shared environmental predictors do not account for as much variance as one would expect, especially if the effects of genes are taken into account (Diener, 1996; Lykken & Tellegen, 1996; Tellegen et al., 1988).

There are some exceptions in the human literature such as number of close friends and marital status (Myers, 1999, 2000). However, these effects may reflect the fact that agreeable extraverts are happier, seek out more friends, and are better suited to married life (see Diener & Lucas, 1999, for a review). These findings and work on niche picking (Scarr, 1993) suggest that these effects may not cause SWB, but are rather related to a cause of SWB.

Environmental Context As with the demographic predictors, predictors such as kin density, the chimpanzee-environment fit, and their interactions with other variables were weak. These predictors fall under the rubric of potential nonshared environmental effects. That is, they are not shared among individuals in the same zoo or within the same family. The findings suggest that chimpanzee personality and SWB are, like human personality and SWB, traits that are largely independent of persistent characteristics of the environment.

The sole exception are the two possible four-way interactions which suggest that sexual resources, *i.e.*, female siblings, benefit males who are in a zoo with a high density of males. That is, these males may acquire favors from other chimpanzees by allowing access to their female relatives.

4.2 Genetic Analysis

4.2.1 Overview of the Genetic Analysis

The genetic analysis compared eight nested models which incorporated a common set of environmental and demographic fixed effects and covariates and different sets of random genetic and environmental effects.

The fixed effects included zoo effects which indicated whether chimpanzees that shared the same zoo were more similar than equally related chimpanzees at different zoos. The covariates for Dominance and SWB were determined in the environmental analysis. The covariates for Dominance included age and the age by sex interaction. The single covariate for SWB was age.

The proportion of variance in Dominance and SWB that was a function of random effects such as additive genetic, heritable maternal, non-heritable maternal, and nonshared environment effects was estimated. The analysis also estimated the covariances among additive genetic, heritable maternal, non-heritable maternal, and nonshared environmental effects.

Eight models with increasing degrees of freedom were tested. The *AIC*, *p*-value, and difference Chi-square statistics were used to determine which model had the best fit and most parsimony.

Model 8 Model 8 was the most restricted model and was selected on the basis of the *AIC* criterion and difference Chi-square tests. It included large additive genetic and nonshared environmental predictors for Dominance and SWB. It also showed that

almost all of the genes that contributed to Dominance variance contributed to SWB variance. Finally, it showed that the nonshared environmental effects were almost independent.

Model 2 Model 2 was chosen as the best fitting model using the p -value. It included the same effects as Model 8, but the proportion of SWB variance due to additive genetic effects was somewhat lower. Dominance and SWB variance were also accounted for by heritable maternal effects, although the proportion of Dominance variance accounted for by these effects was small. These maternal effects were perfectly correlated. Finally, the model included non-heritable maternal effects as a predictor of SWB, though these too were small.

While Model 8 had a lower p -value than Model 2, it estimated fewer parameters that were close to or equal to zero, therefore, it was chosen as the model with the best fit and most parsimony.

4.2.2 Interpretation

The genetic analysis ruled out shared zoo effects. That is, the shared zoo effect, which would capture any main effects of zoos that the environmental analysis failed to account for, accounted for a small proportion of variance in Dominance and SWB.

Predictors that are Ruled Out Like human personality and SWB studies (Bouchard & Loehlin, 2001; Lykken & Tellegen, 1996; Tellegen et al., 1988), none of the variance in Dominance or SWB was influenced by shared environmental effects. Thus, whether chimpanzees shared the same zoo or the same mother had no apparent bearing on either trait.

Because estimates of the nonshared environmental effects included error variance, the lack of a correlation among these effects suggested that some common method variance did not influence the Dominance or SWB ratings.

Predictors Ruled In The findings of this study are similar to those in studies of human SWB (Lykken & Tellegen, 1996; Tellegen et al., 1988) because they show that a personality factor and SWB are influenced by additive genetic effects and environmental effects that are not shared among relatives. These findings strongly support the temperament hypothesis.

Moreover, the finding that genetic effects are correlated whereas the nonshared environmental effects are independent is consistent with human studies of neuroticism, anxiety, and depression which show high genetic and low environmental correlations between neuroticism, anxiety, and depression (Kendler, 1996; Roberts & Kendler, 1999).

Ambiguous Findings An ambiguity arises with respect to the influence of heritable maternal effects on chimpanzee SWB. Studies of humans (Furnham & Cheng, 2000) and non-human primates (Higley & Linnoila, 1997; Higley & Bennett, 1999) have highlighted the importance of maternal effects. Also puzzling is the fact that a previous behavior genetic study of chimpanzee personality and happiness that used the same data also found that heritable maternal effects influenced chimpanzee happiness (Weiss, King, & Enns, under review).

These conflicting results might arise from the fact that, in the previous study of chimpanzee Dominance and SWB, age was not used as a covariate for SWB. If maternal effects are stronger for young chimpanzees, controlling for age would reduce the importance of maternal effects. This explanation would predict that the correlation between age and each mother's contribution to her offspring's SWB would be negative.

4.2.3 Conclusions from the Genetic Analysis

These findings are interesting because, like recent studies that factor analyze genetic and environmental correlations (see, for example, Livesley et al., 1998; McCrae et al.,

2001), they illuminate the source of common and unique variance among traits or factors. The most recent of these studies (McCrae et al., 2001) factor analyzed the covariances among genetic effects, nonshared environment effects, and method effects. They found that, while an analysis of the genetic correlations revealed five factors consistent with their previous studies, the analysis of correlations among nonshared environmental effects did not.

Similarly, this study decomposed the correlation between Dominance and SWB into common effects that accounted for the shared variance and unique effects that accounted for the unique variance.

Shared Variance The shared variance between Dominance and SWB was almost totally a result of the fact that the same genes contributed to both phenotypes. That is, it did not appear that Dominance causes SWB directly or via the environment.

Unique Variance On the other hand, the unique Dominance and SWB variance appeared due to almost totally unique nonshared environmental effects. That is, the environmental factors that contributed to Dominance were not those that contributed to SWB. Thus, while this study strongly argues against models in which personality directly or indirectly causes SWB, it does suggest that there are unique predictors of SWB that are not shared in common among biological relatives.

4.3 General Conclusions

4.3.1 Proximate Causes

The shared variance between Dominance and SWB in chimpanzees reflects the same innate genetic predisposition. The fact that Dominance and SWB are somewhat independent reflects the independent nonshared environmental effects. As with humans, neither personality nor SWB are affected by shared environmental effects (see Bouchard & Loehlin, 2001, for a review). This last fact is particularly striking when

one considers that the zoo chimpanzees do not have as much an ability to pick niches as humans. It is also striking because environmental variables included shared zoo characteristics such as the density of any given zoo and nonshared environmental variables such as the social and genetic characteristics of their enclosure mates.

The difference with respect to maternal effects between this study and our previous study (Weiss et al., 1999) suggests that these effects might be age dependent. If so, it is possible that other environmental influences on SWB are also age dependent and, therefore, fleeting.

The Temperament Model The traditional temperament model (Gray, 1981, 1991) attempts to explain the personality and SWB correlation as resulting from temperamental dispositions of extraversion and neuroticism that make one more or less sensitive to reinforcement or punishment, respectively. The interaction of this disposition with the world leads to varying degrees of happiness. For example, an individual with a high sensitivity to reinforcers and a low sensitivity to punishers will, over the long run, be happy.

The current model, on the other hand, suggests that personality traits and SWB spring from the same genetic temperament disposition, but are differentiated by the environment. This study and some human research (Furnham & Cheng, 2000) suggest that at younger ages maternal effects may contribute to SWB.

Perhaps the best causal candidate of this common temperament factor is the joint effect of the serotonin system on mood and temperament. Researchers have shown that serotonin is related to both depression and alcoholism in humans and primates (see Heinz, Mann, Weinberger, & Goldman, 2001, for a review). This appears to have a genetic basis as the short form of the serotonin receptor gene has been implicated in aggression, alcoholism, and depression in primates (Higley & Linnoila, 1997; Higley & Bennett, 1999).

A number of studies have also shown that serotonin is related to dominance in primates. Naturalistic studies by Higley et al. (1996), Higley and Linnoila (1997), Higley and Bennett (1999) and experimental research by others (see, for example, Raleigh, McGuire, Brammer, Pollack, & Yuwiler, 1991) demonstrate that serotonin levels are positively related to the acquisition of social dominance in rhesus macaques and vervet monkeys, respectively.

Other candidates for personality and happiness that have been explored in humans and rats, but not primates, are sex hormones. Research has shown that the effect of testosterone or estrogen on mood is mediated by their effect on the serotonergic system (see Fink, Sumner, McQueen, Wilson, & Rosie, 1998, for a review).

Future Directions Given these findings, the future direction of research on the relationship among personality factors and happiness should be broadened into a research program of *covitality* or how and why it is that positive traits, whether behavioral or physical, covary. The major possibility that this research suggests is that these traits are influenced by the same genes.

In the present case of the relationship between Dominance and SWB, human researchers should attempt to replicate these findings using twin samples. The ideal study would be to determine whether Extraversion, Neuroticism, Conscientiousness, Agreeableness, and SWB are caused by the same latent genetic factor or whether the effects of genes on SWB are indirect and mediated by personality.

Other plausible tests of the current hypothesis include determining whether levels of certain neurotransmitters and hormones are phenotypically or genetically correlated with personality in humans or primates. Molecular genetic studies could also help resolve whether the shared genes model of temperament and SWB is correct.

There should also be more research on potential environmental effects that differentiate temperament into personality and affect. Previous research suggests that maternal effects are a good potential candidate for one of these effects (Bard & Gard-

ner, 1996; Furnham & Cheng, 2000). This study found no heritable maternal effects. However, it is unclear whether this was due to low statistical power or whether maternal effects, like shared environmental effects (Rowe, 1994), weaken over time.

One major methodological confound that plagues human research on environmental causes of SWB is that the researchers who study maternal effects (Bard & Gardner, 1996; Furnham & Cheng, 2000) work primarily with young individuals whereas the researchers who study other potential environmental effects (see Diener & Lucas, 1999, for a review) work with older individuals. Thus, the findings of various studies fail to generalize to older or younger subjects.

There are two developmental approaches that could resolve these conflicting findings. One would employ a longitudinal design that would determine whether the strength of different environmental influences change over time. Ideally, this would be a genetically informative design in which possible gene by environment correlations would be ruled out as confounds. The second approach would employ a cross-sectional design to study whether environmental predictors of happiness are constant across different age groups or whether they differ.

4.3.2 Ultimate Causes

One question that is still being debated is whether happiness has any adaptive value. Currently, most theories concerning the evolutionary origins of emotions focus on the adaptive value of negative emotions such as fear and how they help mobilize defense mechanisms (Bolles, 1970; Cosmides & Tooby, 2000).

Current Hypotheses Interestingly, the models that have been proposed for the evolutionary origins of happiness are similar to the models regarding its proximate origins. That is, these evolutionary theories view happiness as a product of environmental circumstances or a by-product of the beneficent interaction of individuals and their environments (see Diener & Lucas, 1999, for a review). Buss (2000) suggested the

possibility that happiness may be improved when there are more kin nearby. Buss also suggested that happiness is marked by the absence of evolutionary important emotions such as sexual jealousy. This study was unable to test the latter, but was a strong test of the former hypothesis and found it to be wanting. As a result, it is necessary to rethink potential evolutionary origins for happiness in light of the current findings.

Sexual Selection and Happiness As stated earlier, dominance in chimpanzees is related to their survival and reproductive success (Pusey et al., 1999). This leads to the intriguing and testable possibility that happiness in chimpanzees and humans is a sexually selected fitness indicator.

Miller (2000) outlines two prerequisites for something to be a sexually selected fitness indicator. The first is that the trait must be an honest signal, that is, hard to fake by individuals that are less fit. Clearly, if happiness is genetically correlated with a fitness-related trait such as Dominance, it will be difficult to fake as only those with genes for Dominance will have genes for happiness. If chimpanzees were, in some way, able to fake happiness to the point where it was indistinguishable from real happiness, the genetic correlation would be diminished and happiness would no longer be an honest indicator. The second prerequisite is related to the first in that the trait should be readily detected. Considering that humans are able to make reliable judgments of chimpanzee happiness (King & Landau, in press) and that the ability for humans to detect happiness and other emotions is universal (Ekman et al., 1987; Elfenbein & Ambady, 2002), it would be a fair assumption to suggest that our primate cousins are also capable of this feat.

4.3.3 Predictions

As with any hypothesis, one critical issue is whether it generates testable predictions. There are several predictions that can be tested. These predictions fall into

several domains of existing research including evolutionary biology, behavior genetics, perception, developmental, and cognitive psychology.

Genetic Correlations Between Happiness and Fitness The most critical prediction to be tested before further research is conducted stems directly from sexual selection theory. That is, if something is a sexually selected trait, it should be genetically correlated for preference for that trait in a partner. Bakker (1993) tested this prediction by estimating the genetic correlation between the ornamentation of male sticklebacks and female sticklebacks' preference for ornamentation. He found a high genetic correlation and concluded that male stickleback coloration was a sexually selected trait. Behavior genetic research in humans can easily test this prediction using twin or sibling studies.

Another prediction is that happiness is genetically correlated with physical traits related to fitness. Thus, human and chimpanzee researchers could test whether happiness is correlated with fluctuating asymmetry, an indirect measure of immune system function (Thornhill & Gangestad, 1993). Another possibility is to test whether the phenotypic correlation between health and happiness (Watson, 1988) is due to common genes.

This hypothesis also predicts a positive relationship between fertility and happiness. Thus, one may look at phenotypic and genetic correlations between happiness and testes size in males and ovulation in females. Related to this is the question of whether the phenotypic correlations among testosterone levels and happiness (Carlson & Sherwin, 1998) comes about because of common genes. One could also test the degree to which inbreeding depression is negatively correlated with happiness because of its effects on fertility and health.

Correlations Between Happiness and Optimism Zehavi and Zehavi (1997) hypothesized that handicaps could also be honest indicators of happiness. Thus, the ability of an individual to survive with a handicap should be attractive to females.

Human research has shown that mentally healthy people have a less realistic perception of the world than those who are not mentally healthy (see Taylor & Brown, 1988, for a review). This is interesting and consistent with the handicapping principle as it shows another way in which happiness may be an honest indicator of fitness. This has two major predictions. First, happy individuals should be more likely to be found in dangerous situations. Second, happiness and how optimistically or realistically one sees the world should be genetically correlated. However, a recent review of the literature questions these findings and suggests that they may be specific to tasks that have little ecological validity (Albright & Henderson, 1993).

4.3.4 Change Over Time

Some developmental predictions also stem from the sexual selection theory of happiness. These come from the fact that, while the importance of some fitness-related characteristics such as health, are related to happiness throughout life, other characteristics may only be related to fitness during youth, adolescence, or old age.

Thus, one would predict that the importance of maternal effects would wane over time as the individual becomes older and less dependent on its mother for survival. This study and the previous study, which found maternal effects when SWB scores were not residualized on age (Weiss et al., under review), indirectly indicate this to be the case, but this needs to be tested more rigorously.

Conversely, it may be true that other factors, such as peer groups, physical attractiveness, or risk-taking become more important predictors of fitness as one enters adolescence. However, as the individual enters adulthood, these same factors may prove to be negatively related to fitness and, hence, negatively related to happiness.

The Theory of Affect If happiness is a sexually selected trait, it is possible that individuals may try to deceive others with respect to their happiness. The evolutionary consequences of this are similar to those of tactical deception (Ridley, 1993). That is,

they would lead to selective pressures for an increased ability to distinguish between real and feigned happiness. This, in turn, would lead to selection for an increased ability to feign happiness.

Several predictions come from this turn of events. First, the choosing sex should be better at discerning the emotional traits of others. In humans, females have been shown to be more sensitive to the emotional states of others, in particular men (see, for example, Erwin et al., 1992). It would not be too far a leap to imagine that this ability would include the detection of emotional traits.

Another prediction, consistent with the Brunswikian lens model (Brunswik, 1956), suggests that in the absence of facial or social cues individuals should be able to accurately discern a target's happiness using phenotypic traits that are related to fitness, and the use of cues should be directly correlated with how genetically correlated with happiness a cue is. Possible physical indicators include signs of health, fluctuating asymmetry, indicators of fertility in women such as their waist-to-hip ratio, and exterior signs of hormone levels such as square jaws in men and full lips in women. Another potential test would be to see whether, when asked to manipulate a computer-presented face to look happy, subjects create faces that have these characteristics. The amount of time spent working on changing each characteristic should be negatively related to how related it is to fitness because subjects would be more prepared to find the optimum value.

Considering that the theory of mind has been selected because a primate's social environment is rich in those who wish to deceive (Whiten, 1997), and behavior genetic research has shown these abilities to be genetically correlated with general intelligence (Hughes & Cutting, 1999), it would not be surprising if the same were true for a theory of affect. This leads to the possibility that the status of happiness as a fitness indicator and the need to detect happiness have acted, in part, to give rise to general intelligence. Thus, one could ask a final question about whether breeding a happier chimpanzee also leads to the breeding of a more dominant, sexy chimpanzee.

Chapter 5

APPENDICES

5.1 Chimpanzee Personality Questionnaire

5.1.1 Rating Definitions

Each item could be rated on the following 1 to 7 Likert scale:

1. Displays either total absence or negligible amounts of the trait.
 2. Displays small amounts of the trait on infrequent occasions.
 3. Displays somewhat less than average amounts of the trait.
 4. Displays about average amounts of the trait.
 5. Displays somewhat greater than average amounts of the trait.
 6. Displays considerable amounts of the trait on frequent occasions.
 7. Displays extremely large amounts of the trait.
-

5.1.2 Adjectival Descriptors

The following is an alphabetized list of adjectives and their definitions. The number in parentheses indicates the position of that item in the chimpanzee personality questionnaire.

1. (15) ACTIVE: Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.

2. (21) **AFFECTIONATE**: Subject seems to have a warm attachment or closeness with other chimpanzees. This may entail frequently grooming, touching, embracing, or lying next to others.
3. (18) **AGGRESSIVE**: Subject often initiates fights or other menacing and agonistic encounters with other chimpanzees.
4. (6) **AUTISTIC**: Subject often displays repeated, continuous, and stereotyped behaviors such as rocking or self clasping.
5. (17) **BULLYING**: Subject is overbearing and intimidating towards younger or lower ranking chimpanzees.
6. (4) **CAUTIOUS**: Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviors.
7. (36) **CLUMSY**: Subject is relatively awkward or uncoordinated during movements including but not limited to walking, acrobatics, and play.
8. (29) **DECISIVE**: Subject is deliberate, determined, and purposeful in its activities.
9. (32) **DEFIANT**: Subject is assertive or contentious in a way inconsistent with the usual dominance order. Subject maintains these actions despite unfavorable consequences or threats from others.
10. (26) **DEPENDENT/FOLLOWER**: Subject often relies on other chimpanzees for leadership, reassurance, touching, embracing and other forms of social support.
11. (30) **DEPRESSED**: Subject does not seek out social interactions with others and often fails to respond to social interactions of other chimpanzees. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.

12. (40) **DISORGANIZED**: Subject is scatterbrained, sloppy, or haphazard in its behavior as if not following a consistent goal.
13. (2) **DOMINANT**: Subject is able to displace, threaten, or take food from other chimpanzees. Or subject may express high status by decisively intervening in social interactions.
14. (37) **ERRATIC**: Subject is inconsistent, indefinite, and widely varying in its behavior and moods.
15. (22) **EXCITABLE**: Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most chimpanzees.
16. (1) **FEARFUL**: Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.
17. (38) **FRIENDLY**: Subject often seeks out contact with other chimpanzees for amiable, genial activities. Subject infrequently initiates hostile behaviors towards other chimpanzees.
18. (20) **GENTLE**: Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.
19. (16) **HELPFUL**: Subject is willing to assist, accommodate, or cooperate with other chimpanzees.
20. (42) **IMITATIVE**: Subject often mimics, or copies behaviors that it has observed in other chimpanzees.

21. (23) **IMPULSIVE**: Subject often displays some spontaneous or sudden behavior that could not have been anticipated. There often seems to be some emotional reason behind the sudden behavior.
22. (43) **INDEPENDENT**: Subject is individualistic and determines its own course of action without control or interference from other chimpanzees.
23. (24) **INQUISITIVE**: Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about other chimpanzees, objects, or persons within its view.
24. (33) **INTELLIGENT**: Subject is quick and accurate in judging and comprehending both social and non-social situations. Subject is perceptive and discerning about social relationships.
25. (35) **INVENTIVE**: Subject is more likely than others to do new things including novel social or non-social behaviors. Novel behavior may also include new ways of using devices or materials.
26. (27) **IRRITABLE**: Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behavior.
27. (8) **JEALOUS**: Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged chimpanzees.
28. (39) **LAZY**: Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.
29. (19) **MANIPULATIVE**: Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Chimpanzee seems able and willing to use others.

30. (3) PERSISTENT: Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other chimpanzees.
31. (13) PLAYFUL: Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors with or without other chimpanzees.
32. (28) PREDICTABLE: Subject's behavior is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioral routine.
33. (34) PROTECTIVE: Subject shows concern for other chimpanzees and often intervenes to prevent harm or annoyance from coming to them.
34. (9) RECKLESS: Subject is rash or unconcerned about the consequences of its behaviors.
35. (31) SENSITIVE: Subject is able to understand or read the mood, disposition, feelings, or intentions of other chimpanzees often on the basis of subtle, minimal cues.
36. (10) SOCIABLE: Subject seeks and enjoys the company of other chimpanzees and engages in amicable, affable, interactions with them.
37. (14) SOLITARY: Subject prefers to spend considerable time alone not seeking or avoiding contact with other chimpanzees.
38. (5) STABLE: Subject reacts to its environment including the behavior of other chimpanzees in a calm, equable, way. Subject is not easily upset by the behaviors of other chimpanzees.
39. (7) STINGY/GREEDY: Subject is excessively desirous or covetous of food, favored locations, or other resources in the enclosure. Subject is unwilling to share these resources with others.

40. (25) **SUBMISSIVE**: Subject often gives in or yields to another chimpanzee. Subject acts as if it is subordinate or of lower rank than other chimpanzees.
41. (12) **SYMPATHETIC**: Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.
42. (11) **TIMID**: Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.
43. (41) **UNEMOTIONAL**: Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.

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