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Longitudinal analysis of behavior patterns in a captive chimpanzee population

Amy Augusta Tirone
University of Texas-Pan American

LONGITUDINAL ANALYSIS OF BEHAVIOR PATTERNS IN A CAPTIVE CHIMPANZEE POPULATION

A Thesis

by

Amy A. Tirone

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CHIMPANZEE POPULATION

A Thesis
by
AMY A. TIRONE

Approved as to style and content by:

Valerie James-Aldridge
Chair of Committee

Gary Montgomery
Committee Member

Russell Eisenman
Committee Member

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ABSTRACT

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Data collected over an 11 year period were analyzed for behavioral constancy, reaction to environmental change, and the differential influence of environment and genetics in a group of captive chimpanzees using the framework of the Five Factor Model of Personality. Results suggested environment was a more influential factor in behavioral production, although expected reactions of specific individuals were not evidenced. Improvements upon this research include use of a more chimpanzee-specific personality model and more detailed data collection to support more precise conclusions regarding behavioral etiology.

DEDICATION

This thesis is dedicated to my mother, Nancy Tirone, who has worked tirelessly to raise me to be a driven, intelligent, contributing individual and to my father, Stephen Tirone, for always trusting my abilities and supporting my endeavors with exuberance.

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CHAPTER I

INTRODUCTION

Historical Concepts

The question of what makes humans beings similar to or different from other animals has been the subject of religious, philosophical, and sociological inquiry for generations. The bases of comparison between humans and other animals are of two general classes: the biological and the behavioral. The biological comparison among species is relatively straightforward – humans possess physical characteristics, the same attributes, to a greater or lesser degree than other species. For example, humans are larger than most animals but have less hair. There is generally wide acceptance of different degrees of cross-species similarities in biology, including similarity of humans with other species (Nelson & Jurmain, 1985).

Though comparisons have been made across a wide variety of species, a very specific biological comparison has been made between humans and their closest living relative, the chimpanzee. Considering the nonrepeated portions of DNA, chimpanzees and humans share in common ninety nine percent of their genomes (Nelson & Jurmain, 1985). This biological similarity has provided a basis for an extensive cross species comparison beginning with biological make-

up of chimpanzees and humans and extending into the more subjective realm of behavior.

The behavioral comparison between humans and other species is more complicated and controversial than the biological comparison. Humans, unlike other species, display behavioral manifestations of biology such as communication through abstract language and symbols. Humans also excel beyond any other species at modifying the environment in which they exist. Researchers have been reluctant to ascribe advanced or abstract behaviors to non-human primates. Despite this reluctance, these "human" behaviors have increasingly been evidenced in chimpanzees (Nelson & Jurmain, 1985).

Environmental modification, such as tool making, was once thought to be a skill unique to humans. Goodall (1986) gives examples of chimpanzees using tools, making tools, and transporting tools over large distances. The apparent forethought of bringing a twig to a termite mound for fishing or of bringing a rock to a tree with encased fruit for smashing are examples of the rudimentary similarity chimpanzee tool use, once thought to be an exclusively human behavior, has with human tool use.

Chimpanzees excel in tool use, but tool use is not the most abstract behavior of which chimpanzees are capable and it is likely found in species other than chimps and humans. Comparisons of more intellectually complex behavior, such as abstract representation, have been attempted with chimpanzees such as Washoe, a chimpanzee (*Pan troglodytes*) who learned to communicate using American Sign Language. Over the course of four years, Washoe learned over

130 signs and was able to engage in short dialogues with her trainer (Gardner & Gardner, 1979). The Gardners report that Washoe began to produce multiple word combinations soon after she began to learn single signs and that she even "invented" some sentences of her own. While the Gardners had only referred to the refrigerator as the combination of signs for "cold" and "box", Washoe began to sign "open food drink" in reference to the refrigerator. She also signed "open key" for a locked door and "please open hurry" (p. 192).

Washoe is not the sole example of symbolic representation in chimpanzees. There are multiple examples of chimpanzees using symbolic representation through sign language in the literature. This window into chimpanzee ability serves to present, in a humanly understandable format, the probability of cross-species behavioral similarity between chimpanzees and humans far beyond simple tool making and use (Gardner & Gardner, 1975; Rumbaugh et al., 1982).

Acknowledging the potential for behavioral similarity between chimpanzees and humans, primatologists, anthropologists, and other researchers have extended work further into more specific areas of behavioral similarity. Research on chimpanzee memory, learning, personality, and temperament has become increasingly common in the body of work on this species.

Anthropological History

Modern apes and humans last shared an ancestor in common somewhere between 4 and 14 million years ago. Both human and ape behaviors have changed since that time with human behavior changing to a much greater degree, as culture

became a significant factor. Thus, clues to hominid behavior prior to the influence of culture may be found in the behavior of the closest relatives of humans, the apes comprised of gorillas, orangutans, and chimpanzees (Nelson & Jurmain, 1985).

The study of chimpanzees is motivated by the fact that the more that is learned about the evolutionary history and adaptations of other primate species, the more knowledge will be gained regarding the processes that shaped the human species (Lancaster, 1975). The knowledge gained from the study of chimpanzee behavior, personality, and temperament is not only of value to the understanding of human behavioral development, but also to the general body of scientific knowledge regarding chimpanzees themselves, making chimpanzee research doubly important.

Pan troglodytes

Beyond sharing a common behavioral lineage, chimpanzee social structure mirrors human social structure in its intricate and fluid complex of relationships. *Pan troglodytes*, or common chimpanzees, are highly social animals adapted like all other species to their specific ecological niche. The male dominance hierarchy, with changing leadership due to maturation of young males, injury or illness of the leader, and the death of old males, characterizes relationships and the social structure among chimpanzees.

The basic social unit of chimpanzees is a fluid membership group, within which is a strongly bonded group of adult males and females in their prime as well as females past their prime. Chimpanzee females are usually nurturing

mothers whose infants travel clinging to the belly of their mothers and, later, riding on the backs of their mothers for many years after birth (Nelson & Jurmain, 1985).

The relationship between a chimpanzee mother and daughter is very close until the daughter is at least 7 years old. Female chimpanzees often spend their infancy, childhood, and early adolescence – through age 10 or 12 – in close proximity to their mothers, beginning to stray further away as they mature. Like their female counterparts, male chimpanzees begin to stray further from their mothers and spend time with other males, working into the dominance hierarchy, and pursuing cycling females, as they grow into early adolescence at about 10 years of age (Nelson & Jurmain, 1985).

Primates solve major adaptive problems in a social context. A few major aspects generally characterize chimpanzee social interactions: grooming, displays, dominance, the mother-infant relationship, the male-female sexual bond, and role separation between adults and young (Nelson & Jurmain, 1985).

Chimpanzees exhibit much social interaction. Excepting male-female consortships – itself a social event of sorts – in which a male lures an estrus female away from the rest of the group members for a few days or even upwards of one month, chimpanzees are almost always found in the company of multiple fellow chimpanzees. Family units consisting of mothers, daughters, and infants are also often seen in close company (van Lawick-Goodall, 1971).

Chimpanzees are rarely left completely alone. Even during times of great illness or death, such as that of *Mr. McGregor* of the Gombe Stream Research

Centre in Tanzania who was stricken with polio and paralyzed during Goodall's early research, chimpanzees will remain together: "In that whole period [of *Mr. McGregor's* illness] *Humphrey* seldom moved farther than a few hundred yards away. When the others moved away up the valley . . .*Humphrey* abandoned his attempts to follow the big group and built his nest close to *Gregor's*" (van Lawick-Goodall, 1971, p.223-224).

Though much of chimpanzee interaction is quiet and peaceful, communication through vocalization, silence, displays, and facial expression is extensive and complex. Further, there are frequent, yet usually brief, bouts of violence among chimpanzees, even within a seemingly coherent group. Chimpanzees become violent in response to multiple stimuli. Their reactions may range from mild irritation to rage and may be a reaction to a feared stimulus or a threat. Goodall (1986) gives an example of *Goblin*, a Gombe chimpanzee who exhibited a frustrated redirection of aggression by attacking all nearby females. Fear of strangers and action to support a friend or ally are also common reasons for aggressive behavior in chimpanzees.

Much of the social interaction among chimpanzees stems from a variety of factors including the influences of environment, genetics, personality, and temperament. How these forces interact to produce changes in behavior over time is relevant to the discussion of the similarities and differences in chimpanzee and human behavioral profiles and subsequent conclusions regarding divergent or convergent evolution of the two species.

CHAPTER II

REVIEW OF LITERATURE

A Framework for Understanding Personality

To discuss personality and temperament in chimpanzees and humans, a framework of personality and temperament assessment has been developed. A new discipline is emerging that provides a grand framework for personality psychology, a framework that has been missing almost entirely from the core conceptualization of personality psychology. This discipline, termed "evolutionary psychology", provides a powerful heuristic for identifying central human goals and the psychological and behavioral means used to obtain these goals. Anchored in evolutionary theory, evolutionary psychology theory may assist in the unification of seemingly arbitrary personality theories by anchoring human personality in evolution (Buss, 1991).

According to Buss (1991), although behavior is highly context-dependent, there is no such thing as a purely environmental or situational cause of behavior. Accordingly, differences among species in response to a given environmental input are shaped by psychological mechanisms. Difference or similarity in response, assuming identical environmental input, can be construed as evidence of difference or similarity in psychological mechanism.

Buss (1991) further asserts these psychological mechanisms are plastic and evolve because of their behavioral consequences. Evolved psychological mechanisms have accompanying behavioral strategies and specific adaptive problems they were designed to solve. In humans, mate retention as an adaptive problem may lead to a behavioral strategy and psychological solution such as females drawing attention of other males in order to preserve the attention of, or provoke jealousy in, the partner. Looking at the whole of evolutionary theory, psychological mechanisms may well play a similar role in other species' social interaction and behavior, especially in those most closely related to humans.

Beyond evolutionary psychology, personality theories in the literature are somewhat divergent. Popular theories include psychodynamic theory popularized by Freud, trait theory represented by Costa & McCrae's Five Factor Theory, and cognitive theory discussed by Kelly (see Whitbourne, 2001, for discussion). Evolutionary psychology theory may well provide a unifying base for various theories of personality and some personality theories may already be viewed in the light of evolutionary psychology.

For example, research on trait theory in the form of the Five-Factor Model of personality (Costa & McCrae, 1988 cited in John, 1990) is robust across time, context, culture, and data sources (Buss, 1991). Although human personality, or chimpanzee personality, is likely not limited to the five factors in the model – they serve only as a possible basis of personality – the factors, neuroticism, extraversion, agreeableness, conscientiousness, and openness to experience,

emerge repeatedly in different situations and therefore may have an evolutionary basis.

The five factors may summarize the most important dimensions of the social landscape to which humans have had to adapt. The core of this view is that perceiving, attending to, and acting upon differences in others are crucial for solving problems of survival and reproduction. Buss (1991) hypothesizes that humans have evolved psychological mechanisms sensitive to individual differences in others that are relevant to survival and reproduction. It is likely not the case that humans are the sole species capable of this type of social structure and interaction, especially when considering closely related and highly social species like the chimpanzee.

Human groups are often intensely hierarchical with important reproductive resources closely linked with position in the hierarchy. Hierarchies are evidenced in subtle social organization ranging from friendship to business ventures to family structure and are often affected by subtle changes and actions by members of the social group. Hierarchies are extremely important features of the human adaptive landscape (Buss, 1991). Hierarchical organization of group members, as discussed above, is also clearly seen in the dominance hierarchy of male chimpanzees. It is sometimes the case that females may also be characterized as more or less dominant based upon how strongly they are favored by males (see Goodall's description of *Flo* for example, 1971, p.79-88).

According to an evolutionary psychology perspective, basic psychological mechanisms that have evolved because they solved problems of survival and

reproduction will be relatively stable over time. Thus, in addition to observance of overt behavior as evidence of personality, consistency in personality may be sought at the level of basic psychological mechanisms and the events that activate them (Buss, 1991). This stability of personality may be evidenced using a tool such as Costa & McCrae's Five Factor Model of Personality.

One of the important contributions that evolutionary psychology can make in its formation of a base for personality theory lies in its formulations of a crude map of personality. Although the present discussion of personality both in humans and other species may be wrought with theoretical, empirical, and conceptual holes, Gosling and John (1999) believe it is better to begin with the available research and work ahead than to surrender to the challenge of organizing and describing personality in all animals.

With the "map" of personality that may be derived using models such as the five factor model, researchers can refine the conceptualization of personality, investigate which species display what personality factors, and extend the map to form new and more complete theories of personality (Gosling & John, 1999). Contributions to the body of literature on chimpanzee personality increase the comprehensiveness of the map of human personality theory.

The Five Factor Model of Personality

As mentioned, the five factor model of personality has a rich empirical history. As a model for adult human personality, it has been used in different languages across cultures in different situations for many years. In addition to the robustness of the five factor model across divergent human populations, the

evolutionary continuity between humans and chimpanzees suggests that some dimensions of personality may be common across a wide range of species. The five factor model has thus been extended to work with other species, including chimpanzees (Gosling & John, 1999; Gosling, 2001).

Early attempts to assess animal personality were conducted in the 1970s (Stevenson-Hinde & Zunz, 1978). Following a lull in research during the 1980s, the 1990s and beyond have seen a relative surge in research into animal personality, ranging from guppies to chimpanzees (Gosling, 2001). In their cross-species review of personality dimensions in nonhuman animals, Gosling and John (1999) present a comprehensive review not only of animal personality research, but also of animal personality research based in theory on the five factor model of personality.

Gosling & John (1999) assert the evolutionary continuity between humans and other animals suggests that some dimensions of personality may be common across a wide range of species. The researchers review 19 studies of personality factors in 12 non-human species which use the human five factor model, plus the factor of dominance and an activity dimension, as a preliminary framework for non-human species' personality. Results of the review reveal that only chimpanzees display behaviors in all five of the human dimensions. The comparative approach used by Gosling & John (1999) offers a fresh perspective on human personality and should, the authors believe, facilitate hypothesis-driven research on the social and biological bases of personality.

Costa and McCrae (1988; cited in John, 1990) describe the five factor model in detail. Just as Gosling & John bill the five factor model as the most widely accepted and complete map of personality, Kail & Cavanaugh (2000) describe it as one of the most important advances in research on adult development, reasserting the empirical validity and reliability of the five factors: they are strongly grounded in cross-sectional, longitudinal, and sequential research. Costa & McCrae's five factor model does not summarize personality but, rather, simplifies the study of personality by providing information regarding the building blocks of personality. The five dimensions used in the five factor model are presented in Table 1 below (adapted from Whitbourne, 2001).

According to Gosling and John, the five factor model is the most widely accepted and complete map of personality structure. It has five broad factors (See Table 1), which present personality at its broadest level of abstraction. Each factor is bipolar (e.g. Neuroticism vs. Emotional Stability), and summarizes more specific factors (e.g. anxiety, depression) that are composed of even more specific traits (e.g. fearful).

Although Gosling and John reviewed 19 factor analytic studies of 12 different non-human species, they found that only the chimpanzee displayed traits comparable to all five factors in the five factor model. In addition to the five factors, dominance also emerged as a clear factor in the chimpanzee studies. Reading the descriptions of the five factors, clearly the factors are geared to assessment of human behavior. They are described in terms that seem applicable only to humans. For example, how is open versus closed to experience in a

chimpanzee determined when that factor is based on such behaviors as appreciation of art and having a vivid imagination and dream life? Gosling & John (1999) simplify the characterization of the factors (See Table 2).

Table 1: Five Factors of Personality, Descriptors, and Examples

Trait Name	Description	Examples
Neuroticism	Tendency to experience psychological distress, overreactiveness, and instability	Anxiety Hostility Depression Self-consciousness Impulsiveness
Extraversion	Preference for social interaction and lively activity	Warmth Gregariousness Assertiveness Activity Excitement seeking
Openness to Experience	Receptiveness to new ideas, approaches, and experiences	Actions Aesthetics Feelings
Agreeableness	Selfless concern for others, trust, and generosity	Trust Tender-mindedness Altruism Compliance
Conscientiousness	Organization, ambitiousness, and self-discipline	Competence Order Dutifulness Achievement striving Self-discipline

Source: Adapted from Whitbourne, 2001

Presented as they are in Table 2 below, the clarity of application of this formula to chimpanzee behavior and personality more readily emerges. The descriptors in Table 2 are more directly applied to chimpanzee behavior and personality: sociability and positive emotions may be evidenced when one

chimpanzee grooms another; dutifulness and order may be evidenced when a chimpanzee submits to a dominant male who is performing a "display", a behavior characterized by hair erection, loud vocalization, chasing and hitting others, waving tree branches, running about, slapping the ground, throwing things, and other various behaviors. Curiosity may be evidenced by extensive investigation of the environment, as if looking for something, or by observance of unusual environmental circumstances.

Evidence indicates that chimpanzees show individual differences that can be organized along dimensions akin to the five factors. Extraversion, Neuroticism, and Agreeableness all have chimpanzee correlates (Gosling & John, 1999), suggesting that general biological mechanisms are likely at work between chimpanzees and humans. The Openness factor in chimpanzees resembles openness in human toddlers, a logical finding in the sense that neither human toddlers nor chimpanzees use advanced language skills in the abstract sense.

Finally, of the 19 studies reviewed by Gosling and John (1999), Conscientiousness was found as a separate factor only in chimpanzees. It was characterized by lack of attention and erratic, unpredictable, and disorganized behavior. These findings reveal an example of how personality research in animals is important to the understanding of human personality: Conscientiousness as a personality factor may have appeared relatively recently in the evolution of Homininae, the subfamily comprising humans, chimpanzees, and gorillas and using the five factor model to investigate chimpanzee personality may provide evidence of this evolution (Gosling & John, 1999).

Table 2: The Five Factors Redefined

Neuroticism	anxiety, depression, vulnerability to stress, moodiness
Extraversion	sociability, assertiveness, activity, positive emotions
Openness to Experience	ideas/intellect, imagination, creativity, curiosity
Agreeableness	trust, tender mindedness, cooperation, lack of aggression
Conscientiousness	deliberation, self-discipline, dutifulness, order

Other attempts have been made to assess chimpanzee personality using models similar to the five factor model. Dutton and colleagues (1997) developed novel rating procedures for the assessment of chimpanzee personality. Dutton and colleagues assessed the personalities of captive chimpanzees using individually generated bipolar constructs similar in construction to the bipolar constructs of the five factor model. Experienced observers used these constructs to rate the personalities of chimpanzees and three, perhaps four, components appeared to emerge as characteristics of chimpanzee personality: dominance, sociability, machiavellianism, and, for two of the observers, anxiety. Knowledge of these components serves to support the categorization of behaviors into the five factor model of personality and specifically externally validates the extraversion vs. introversion (sociability) and neuroticism vs. emotional stability (anxiety) dimensions of the five factor model and its use with chimpanzees.

Animal research has played and continues to play a central role in many areas of psychology, including learning, perception, memory, and psychopathology (Domjan & Purdy, 1995). Animal research may play a similar

role in temperament and personality. Gosling (2001) presents a comprehensive analysis of recent literature in animal temperament and personality research, noting the lack of a coherent, multidisciplinary research enterprise, nascence of the field, and lack of agreement on a definition of personality and temperament in the literature. Animal research in personality and temperament is likely to contribute importantly to the human understanding of personality and temperament. Bard & Gardner (1996) argue that much can be learned about social influences on human development by examining chimpanzee development.

Why Chimpanzees?

Personality and temperament research has been conducted with animals ranging from ants (Retana & Cerda, 1991) to dogs (Cattell & Korth, 1973) to chimpanzees (Buirski, 1991). As biological, phylogenetic, and social similarities of species are often correlated, the chimpanzee, having the greatest percentage of genome in common with humans, represents the most appropriate candidate for research that will build a base for cross-species comparison with humans.

Captive animal species in general provide an ideal situation to investigate personality and temperament as longitudinal studies provide the most useful data for personality and temperamental characteristics (Roberts & Friend-DelVecchio, 2000).

Comparison of Apples and Oranges

The ultimate goal of a primatologist is to trace the evolution of our own mental complexity to its first beginnings in creatures very different from ourselves (Jolly, 1991). This goal entails physiological, behavioral, social, and

psychological comparisons between humans and other species. Researchers vary in their attitudes toward cross-species comparisons, ranging from those who argue that all comparisons between humans and other animals are misguided anthropomorphism to those who strongly favor the use of animal models in research on humans (Gosling, 2001).

While Robins et al. (1999) assert advanced psychological processes may depend on uniquely human features of the brain, Dethier (1964) counters that the reluctance to ascribe "higher" characteristics to distantly related organisms is speciesist and scientifically remiss. The most reasonable approach is likely a combination of both views: Many similarities exist between humans and chimpanzees; the crucial issue is to determine which similarities are relevant for a given comparative analysis.

In past years, the concept of chimpanzee personality and temperament was taboo to those agreeing with Robins above in asserting the uniqueness of humans. Some humans struggle with the notion that another species possesses abilities in any way similar to their own or similar to what distinguishes humans from others. Despite ready acceptance of anatomical and physiological similarity, many researchers have been reluctant to ascribe personality traits, emotions, temperament, and cognitions to animals (Gosling, 2001). Though Darwin (1872/1998) argued over one hundred years ago that emotions exist in both humans and animals, some researchers choose to ignore the notion of any similarity among species beyond physiological similarity.

Despite this, for the past couple of decades, the concept of animal thought, personality, and temperament has become more widely researched with fascinating results (Gosling, 2001). Researchers appropriately assert personality and temperament may not be as uniquely human as was once thought (Barkow et al., 1992).

With the gradual acceptance of research in personality and temperament in animals, the question of relevance arises: How will this work contribute to the body of knowledge on human personality? Gosling explains that by examining what is similar about species sharing similar traits, researchers can reveal the origin of the trait, as discussed above. Cross-species comparisons of species-typical traits can help decipher the origins of personality and temperament (Gosling, 2001). Thus the comparison of chimpanzees with humans may be construed as a comparison of apples with oranges on one level, but the differences that emerge serve to more succinctly define human history.

Theory of Mind

Personality, like many other psychological constructs, is multiply determined. A coherent sense of self in humans is one defining factor in the development of the personality phenomenon. The sense of self has been investigated in chimpanzees as well and results show that chimpanzees have a sense of self and may, at times, participate in behaviors such as deception that support a moderately complex sense of self (see de Waal, 1989, p. 66 for example). The classic experiment of placing a spot of paint on the chimpanzee's

head while he sleeps, a spot that can only be observed in a mirror, presenting a mirror upon wakening, and observing any spot-oriented reactions (looking at the spot in the mirror, touching the spot and smelling the fingers), lends credence to the concept of self-awareness in chimpanzees (Gallup, 1979).

Premack & Woodruff (1978) delve more thoroughly into a theory of mind in chimpanzees with Sarah, a fourteen-year-old African-born chimpanzee. Sarah's success in tasks requiring that she impute mental states to others reveals that theory of mind in the chimpanzee may extend well beyond the sense of self and self-recognition revealed in the head-spot experiments.

In an even more complex test of theory of mind, Savage-Rumbaugh (1986) explored chimpanzees' use of video images to monitor their movements and actions as well as the movements and actions of human actors. Premack & Woodruff (1978) assert "assigning mental states to another individual is not a sophisticated or advanced act, but a primitive one." That is, it should not be surprising that the chimpanzee, one of the most social of species and the most closely related to humans, has a sense of self and demonstrates a theory of mind in varied situations.

Beyond self-recognition, planning a long sequence of behaviors to reach a future goal is commonly taken as a sign of consciousness (Jolly, 1991). Chimpanzees often travel long distances to widely dispersed food resources, evidencing a cognitive map, or transport tools from one location to another to facilitate eating: A slender twig may be selected and transported to a termite mound out of sight or a large rock may be selected and transported to a tree

bearing nuts in hard casings. Chimpanzees travel long distances to reach the appropriate resources and have been seen to bring appropriate tools to distant sites.

Beyond transporting tools to a location out of sight, symbolic behavior is likely the most complex example of a theory of mind. Symbolic behavior, although difficult to define and largely deriving from the use of language, is also construed as conscious behavior (Jolly, 1991). The most compelling example is that of Viki Hayes' pulltoy: Viki, a chimpanzee raised in an American home, had an imaginary pulltoy that she dragged about on the floor and which would sometimes get tangled on things. When her toy became entangled, Viki would recruit her (human) mother, Cathy Hayes, to help her untangle her (invisible) toy (Jolly, 1991). Interestingly, when Cathy Hayes tried her own experiment and began dragging an imaginary toy of her own around the house, Viki became terrified and never again displayed this unusual behavior.

With extended exposure to chimpanzee populations a theory of mind on some level is readily evidenced. When walking through a zoo it is easy to look at chimpanzees and only see the present and the external. They appear to be a group of hairy beings sitting around or sleeping and occasionally chasing each other, foraging, or playing. This superficial interpretation of visual input undercuts the complexity of chimpanzee behavior and social structure.

Extended observance of groups, such as that conducted over decades by Jane Goodall and her colleagues and students, reveals intricate and fluid relationships often characterized by behavior that can be attributed to a theory of

mind. When *Mike*, a chimpanzee at Gombe Stream in Tanzania, began using empty kerosene cans brought to camp by human observers in his displays, he moved quickly up the dominance hierarchy even though he was not a physically intimidating male – he simply figured out how to make a great deal of noise by running about, banging the cans, and scaring everybody else. Goodall asserts:

> "*Mike's* deliberate use of man-made objects was probably an indication of superior intelligence. Many of the adult males had at some time or another dragged a kerosene can to enhance their charging displays. . .but only *Mike* (had learned). . .to seek out the cans deliberately to his own advantage" (Goodall, 1971; p.114).

Temperament as a Basis for Behavioral Stability

Temperament is an ancient concept in philosophy but only very recent in empirical research on human development (Bates, 1989) and temperament and personality are closely related. Rothbart, interviewed in Goldsmith et al. (1987), defines temperament and personality as broadly overlapping domains of study, with temperament providing the primarily biological basis for the developing personality. This definition is not adopted uniformly and the definition of temperament is less defined in animal research (Gosling, 2001). Temperament may also be viewed as a subcategory of personality.

The concept of temperament in humans originated from studies of infants and young children; children's behavioral tendencies are often described in terms of temperament (Bates, 1989). Thomas and Chess pioneered the modern

systematic application of temperament measurements of child individuality and other researchers have developed extensive theory of temperament and personality (Goldsmith et al., 1987; Costa & McCrae, 1992).

In human children, temperament may be defined as a characteristic response style to novel stimuli or challenging situations that is largely independent of immediate social or volitional influences and that is observable primarily in novel situations (Clarke & Boinski, 1995). Temperament is also defined as a concept serving to tie together a variety of primary behavioral dispositions commonly used to distinguish one individual from another (Bates, 1989). The term might be applied to infants, children, adults, pets, or livestock when talking about the characteristic mixture of activity, moods, and emotional responses of the individual (Bates, 1989).

In human infants, stability of temperament has been observed. Mebert's (1989) experiment addressed the stability of parents' perceptions of infant temperament between early pregnancy and 13.5 months postpartum and found stability across all measures during pregnancy and the postpartum period. Rothbart (1996) also reported longitudinal stability of infant temperament. This stability in infants is an important precursor to the argument for personality and temperament stability in adult humans and, further, in chimpanzees.

Ultimately, temperament is more than a complex concept describing behavior: it is, like most psychological terms, a set of hypothetical constructs, and many researchers theorize regarding the definition of temperament (Bates, 1989). Appropriate to this research is Rothbart's conceptualization of temperament as

relatively stable, primarily biologically based individual differences in reactivity and self-regulation (Derryberry & Rothbart, 1984).

Environment and Genetics in Temperament

There is evidence that both genetic and environmental variables are factors in the development of temperament (Higley & Suomi, 1989). Debate over nature versus nurture supports the biological base of temperament: It has been described in day-old infants, leaving only pre- and perinatal factors as possible environmental influences (Buss & Plomin, 1984). Buss & Plomin (1984) thus provide evidence for a biological basis of temperament.

Although social-developmental researchers have emphasized the influence of environmental variables in temperament, research during the 1960s (see Bell, 1968; Thomas et al., 1963) supports a biological basis of temperament. Also, researchers assert behavior traits referred to as temperament ought to have a clear genetic basis (Buss & Plomin, 1984; Bates, 1987). Bates' (1989) research discusses the effect children's own biologically-instilled tendencies may have on personality development. Though some research supports the biological nature of temperament, it is likely the case that temperament has a biological base, yet displays plasticity in reaction to new stimuli. Construing temperament in this way is consistent with evolutionary theory.

Conversely, in support of an environmental basis for temperament, conspecific primate infants reared in contrasting early rearing environments show differential temperamental characteristics. Differences in behavioral traits observed across species suggest temperamental attributes may be more related to

life history variables than genetic influence. Specific ecological, demographic, or other factors differing between localities that might cause differences in the selective regimes acting on temperamental reactivity are more likely to be identified in closely related populations. Thelen (1989) asserts that a dynamic systems approach may be appropriate wherein behavioral organization is less programmed than it is emergent, that is, less genetically defined than it is a reaction to environmental influences.

As temperament and personality are closely related, discussion of the origins of temperament may be extended to the origins of personality. Temperament and personality should be interpreted as less of a dichotomy of nature versus nurture and more of a two-part process: the individual possesses certain temperamental or personality traits that may be tapped by environmental input. The five factor model described above exemplifies a framework in which temperamental and personality behaviors may be classified and compared over time.

A Return to Personality

Some researchers differentiate between personality and temperament while others discuss significant conceptual overlap. This overlap is the basis for discussion of both personality and temperament in a study focusing on behavioral consistency. Personality is revealed by the specific social characteristics of an individual – descriptors such as gregarious, aggressive, confident, and playful are relevant to discussion of personality. Also relevant is the interpretation that there

may be no distinct practical difference between temperament and personality, it may only be a matter of which researcher is addressing which piece of behavior.

Human personality trait research waxed and waned between the 1960s and 1980s until the advent of the five factor model of personality described above (John, 1990). With the inception of the five factor model, behavior could be conveniently summarized and explicated. As an instrument for studying personality, the five factor model is important because of its successful longitudinal relevance to personality interpretation. It is also relevant to the study of chimpanzees as it has been previously used to study the personality characteristics of this species.

Individual Differences

As personality and temperament are ultimately personal constructs, the explication of individual differences is an important issue. Mischel (1990), in a brief review of three decades of personality disposition theory, cautions that the appearance of unpredictability in individual differences does not imply that individual differences are inherently unpredictable but, rather, that the nature and locus of predictability may be difficult to pinpoint and different from what has been assumed.

Mischel (1990) asserts the importance of specific expectancies of an individual in conceptualizing the construction of behavior in particular situations. The change of expected consequences, which leads to a change in behavior, makes predictable the lack of cross-situational consistency that may be perceived in behavior. This plasticity of behavior is highly functional whereas insufficient

sensitivity to changing consequences may be an indicator of maladaptive functioning (Mischel, 1990). That is to say, reacting differently in different situations is more adaptive than a lack of sensitivity to changing environmental conditions. Mischel practically exemplifies the juxtaposition of genetics and environment in behavioral output.

Temperament and Personality Research

Thus far, the account of temperament and personality has referred for the most part to human infants and adults with brief reference to nonhuman animals. Research in animal personality was once scarce. The past couple of decades, however, have seen expanding research on chimpanzee personality and temperament. Historically, researchers have been loath to humanize non-human primates through the use of human descriptors. However, a gradual accretion of evidence has resulted in the acceptance of at least some of the ideas of personality and temperament study in nonhuman primates.

Beginning with Goodall's decades-long research with the chimpanzees of Gombe Stream, Tanzania, chimpanzee personality research has bloomed in anthropological and psychological arenas. Goodall and colleagues spent thousands of hours observing the chimpanzees of Gombe and certainly acknowledged personality and temperament in Gombe chimpanzees. In the Shadow of Man (van Lawick-Goodall, 1971) and Through a Window (Goodall, 1990) are chimpanzee life chronologies with dozens of anecdotes revealing personality, temperament, and behavior profiles: matriarch *Flo* is consistently characterized by her sexual popularity, her child-rearing skill (which was also

seen in her daughter *Fifi*), and her general equanimity with other chimpanzees. Contrastingly, *Passion*, another adult female in the Gombe troop is characterized as an inattentive and incompetent mother and, later, a cannibal, killing infants of her cohorts.

Another researcher, Frans de Waal, describes chimpanzee personality and includes anecdotes with reference to a theory of mind (see example of *Nikkie* and *Luit* below). de Waal's book, Chimpanzee Politics (1989), discusses at length and in detail the social organization of chimpanzee groups. Although the chimpanzee mind has been made more accessible through experiments such as the dot-on-forehead and videotaped presentations described above, the highly subtle and complex picture of the chimpanzee social life is still disjointed (de Waal, 1989; p. 18). Thus, de Waal explains chimpanzees in terms of politics, drawing a parallel between human social organization and chimpanzee social organization.

Goodall's observations of individual behavior differences, like de Waal's description of chimpanzee politics, could be construed as overly anthropomorphic. Mitchell & Hamm (1997) argue that in some cases naive raters tend to classify mammalian behavior using the same descriptors, despite the species under observation. They note that the use of the same psychological terms across species, however, should not be seen as simply an anthropomorphic extrapolation. When an animal, a chimpanzee for example, behaves in a fashion similar to that of a human in the same context, Mitchell & Hamm (1997) assert a similar psychological interpretation of the two species is warranted.

In assessing chimpanzee behavior, critics note such descriptions as "[*Pooch's*] response to the rather mild threat seemed *unnecessarily* violent" (Goodall, 1986), a description which may incite criticism regarding the scientific validity of words such as "unnecessarily" when applied to nonhuman behavior. Jolly (1991) reacts asserting parsimony and scientific accuracy do not benefit from discarding our primate social sensitivity to species closely related to our own. Humans "have had millions of years of common evolution with chimpanzees during which time we were developing our sensitivity to just such cues" (Jolly, 1991).

Observer bias is another point of contention for critics of animal personality assessment. Emotional assessment in humans and chimpanzees alike often relies on interpretation from a secondary source. Thus, the question of the difference between the emotions of a chimpanzee and perceptions of these emotions by human observers arises (Higley & Suomi, 1989). Between one human and another the same judgment is made regarding emotions – verbal reports given by one individual are often inaccurate expressions of inner feelings and secondary sources must often interpret actions as evidence of internal processes (Higley & Suomi, 1989). The process by which these elements are combined and weighted to produce an inference is not well understood either with humans or nonhuman primates and is assumed to be equally valid.

Looking at interchimpanzee differences from a more quantitative point, Cervone & Shoda (1999) apply the five factor personality model to nonhuman primates. Findings indicate behavioral stability may be consistent within an

individual and, further, that its characteristics may be heritable (Goodall, 1971). Gray (1971) notes that strains of non-primate species bred for temperamental traits such as reactivity show aspects of emotionality can be bred for and the behaviors of individuals can be predicted across time and situation.

Experienced primatologists consistently describe chimpanzee behavior using the same terms applied to human personality and intention. van Hooff (1971) uses words to describe chimpanzee behavior such as affinitive, social-positive, aggressive, and submissive, the latter two heard often in human personality research. de Waal (1989) characterizes chimpanzee behavior from the perspective of politics describing chimpanzee behavior as political and planned, similar to human behavior. A specific anecdote serves to succinctly illustrate: During the change in alpha status among three males, de Waal notes characteristic behaviors for each of the males that seem human-like. Following an altercation, *Luit*, seated on the ground with his back to *Nikkie*, put his hand to his mouth and pressed his lips together with his fingers to conceal a "fear grin", a grin which occurs when a chimpanzee is frightened or distressed. This was repeated three times with *Nikkie* displaying a similar lip-pressing behavior to conceal his own fear grin (de Waal, 1989).

Luit and *Nikkie* exemplify the intricate social structure in which chimpanzees both in the wild and captivity operate. Each male attempted to hide the fear grin that emerged on his face by literally pressing his lips together with his fingers. This pair of males demonstrates the importance of appropriate action and reaction in the social environment. Showing fear in the presence of another

male during a change in alpha status likely does not work in favor of the male with the fear grin. The behaviors exemplified by *Nikkie* and *Luit* may also exemplify deception and attribution of awareness to others, an extension of theory of mind discussed above.

Chamove et al. (1972) argue that the omission of personality in experimental work with monkeys is a serious omission, similar to leaving out personality when working with humans. Chimpanzees, phylogenetically located "between" humans and monkeys, likely deserve the same conclusion: to study the species with disregard to personality factors is to ignore a major component of these animals. Also, considering the importance of individual differences, chimpanzee personality should be considered on an individual basis.

The idea that primates show emotions and have definite personalities is evident in the literature. A wide range of emotions expressed by chimpanzees includes anger, rage, surprise, motherly love, sympathy, affection, gratitude, and despair. Many field researchers discuss chimpanzee behavior in terms of emotion and personality descriptors in much the same manner that human personality is described (Van Lawick-Goodall, 1971). These findings provide further support for the use of the five factor model extended to work with chimpanzees.

Reliability

As noted, there is nothing in evolutionary theory to suggest that only physical traits are subject to selection pressures; Darwin, preeminent in physical trait selection theory, argued that emotions exist in both human and nonhuman animals (Gosling & John, 1999; Gosling, 2001). As behavioral consistency may

generalize across species (Rajecki & Flanery, 1991), non-human primates have been useful research models in studying and understanding human behavior (Higley & Suomi, 1989). The reliability of such research clearly becomes quite important in the study of chimpanzees if conclusions regarding chimpanzees may be generalized to any degree to human personality theory.

In his comprehensive literature review on animal personality research, Gosling (2001) asserts the accumulated evidence suggests that animal personality ratings can be made reliably. Interobserver agreement, in which two or more observers independently rated animal behaviors, was demonstrated in multiple cases. Test-retest reliability in which a chimpanzee behavior is rated on different occasions has also been demonstrated with various correlation coefficients between tests.

In many studies behavioral coding has been used in which behaviors are narrowly defined and chimpanzee behaviors are coded and recorded as they occur. Behavior coding was employed in the results to be presented below. Gosling (2001) presents a relatively exhaustive summary of research in animal personality describing reliability as the first psychometric requirement that must be met by any assessment instrument. Gosling (2001) goes on to discuss the reliability of trait ratings, as opposed to behavior coding reliability ratings, as researchers have largely ignored reliability issues in behavior coding (see Byrne & Suomi, 1995; Chamove, 1974; Jones, 1988 for examples of reliability in behavior coding; cited in Gosling, 2001). In his review of studies on animal

personality, Gosling (2001) concludes that reliability has been demonstrated in trait rating studies.

Buirski et al. (1978) also found experimental reliability in personality research in a study of chimpanzee personality. These researchers found personality ratings of chimpanzees can be reliably made between most pairs of relatively untrained observers. The observers in the study worked with the chimpanzees of Gombe Stream in Tanzania, the same group studied by Goodall. Buirski et al. (1978) attribute lower reliabilities to the fact that different ratings were made on different days, some times following only brief periods of observation. In some cases, life events such as the death of an infant occurred between observation periods, likely contributing to low reliability between ratings.

The five factor model of personality used in assessing human personality traits has also been used as a basis for reliability assessment in animal personality studies. Drawing a comparison between humans and chimpanzees using a tool designed for human personality research is clearly difficult. Some personality domains in the five factor model are easier to compare than others simply due to their overt nature – the extraversion vs. introversion dimension, for example, is associated with high levels of interobserver agreement. This is easy to understand as extraverted behaviors are relatively overt.

Reliability across species has also been demonstrated. Discrepancies between human and chimpanzee behavior on different dimensions may in some cases be explained by socialization: differences in neuroticism may be due to

human socialization to inhibit overt signs of this trait (Gosling, 2001). Thus, discrepancy may result from the overt quality of a trait or lack thereof and the social factors influencing the expression of the trait.

When nonhuman primates have been classified using methods similar to the five factor model, similarities across taxa emerge. Manifestations differ between humans and chimpanzees, but the similarity between chimpanzees and humans across all five dimensions (Gosling & John, 1999) hint at biologically based characteristics.

Other measurement instruments designed to investigate human behavior have been modified for chimpanzees and have shown reliability of measurement. The Emotions Profile Index (EPI) as discussed by Buirski & Plutchik (1991) has been used for the evaluation of the distribution of emotions in human subjects as well as chimpanzees. This behavior rating approach has yielded reliable results with chimpanzees.

From the human EPI, reliable chimpanzee forms have been developed including adjectives such as belligerent, defiant, depressed, dominant, and fearful, among others (Buirski & Plutchik, 1991). *Passion*, a chimpanzee from Gombe Stream notorious for cannibalizing the infants of her peers, was found to deviate from normal on the chimpanzee EPI *before* her infant killing spree. The EPI rating scales are thus sensitive enough to detect deviancy in the organization of emotions in one chimpanzee (Lilienfeld *et al.*, 1999), lending support to the use of human personality models with chimpanzee population.

Validity

Evaluating the validity of personality or temperament measures is conceptually and methodologically challenging regardless of whether the targets are humans or animals. Identifying a validity criterion is difficult as is determining if the instrument with which validity is measured is itself valid (Gosling, 2001). One method of validation in chimpanzee study is association between personality or temperament as rated by observers and behavioral codings in which different behaviors are categorized.

To date there is limited evidence in the literature to provide support for the validity of personality and temperament ratings in animals (Gosling, 2001). Buirski et al. (1978) provide one example of validity in chimpanzee personality studies. Using the Emotions Profile Index, modified for chimpanzees, as a measure of personality, Buirski et al. discovered a clear correlation between personality descriptors and other information known about chimpanzees. For example, female chimpanzees were found to be more timid than males and males more aggressive than females. This seems appropriate as male and female chimpanzees differ in size, with males being stronger and more aggressive.

Buirski et al. (1978) also found that when chimpanzees were independently ranked for dominance by two investigators on the basis of brief behavioral descriptions, there was agreement in rank position for 9 of the 10 males rated. These results imply that personality descriptions of chimpanzees may reflect known sex differences and dominance status. For Buirski and colleagues, the findings support the validity of the trait measures based on the

Emotions Profile Index. They also bolster the validity of personality assessment in non-human animals.

In addition to the work of Buirski and colleagues, independent observers tend to agree about the relative ordering of individuals on a trait. Personality structure, differing among individuals, depends on the individual rated, rather than on the particular items in the rating instrument.

The body of evidence for validity in chimpanzee personality research is growing. Not only has validity of chimpanzee work been assessed but correlations have been drawn between human and chimpanzee personality using the EPI as an assessment instrument. The high correlations between human and chimpanzee personality profiles suggest that there may be a similar "normal" personality pattern in higher primate groups (Buirski et al., 1978).

Environmental Control

Clarke & Boinski (1995) note there are very few data clearly demonstrating within-species variations in temperament. A great deal of within-species variation in behavior has usually been explained as nongenetic response to local conditions such as habitat and food distribution and availability and other factors. To date, species-level comparisons have not offered many testable hypotheses. This is likely due to confounding effects of large phylogenetic distances of uncertain origin and inadequate knowledge of ecological and social conditions in the wild.

For the purpose of this study, many of the influential environmental factors listed above were limited in effect by the controlled captive environment

of the chimpanzees being studied. Within-species variation in temperament was addressed by studying individuals of the same species, the common chimpanzee (*Pan troglodytes*), in their shared captive home environment. In addition, excepting approximately the first six years of life of one individual, the environmental history of the animals was fully known. Differences in habitat and food distribution were also unlikely differential factors as the individuals lived in the same controlled zoological environment for the majority, if not the entirety, of their lives. Murray (1998) notes the benefit of studying animals in a captive environment: apes in captivity have more time to devote to social relationships. Observation at the individual level is appropriate as results may disappear when averaged across individuals but be evidenced by research with individuals (James-Aldridge, 1997).

Information about the ecological conditions and social structure of the group was readily available as research on the group of chimpanzees under study began in 1987. The individuals in this group were of two matrilines with one male believed to have sired all offspring. Essential to the purpose of this study on temperament and personality was the change in group structure that recently occurred in this chimpanzee group: On July 21, 2000, *Jeanie*, the eldest female of one family and matriarch of the entire chimpanzee group, died unexpectedly. It was the first and only death to occur among the group's mature adults.

Murray (1998) asserts the importance of the effects of group structure on personality in chimpanzees. The results of Murray's work suggest that chimpanzee behavior and personality reflect not only a composite of all previous

experiences but also must be considered in relation to the conditions in which the chimpanzees are maintained. Further, in captivity animals may be more likely to be affected by situational factors concerning their past and present experiences than in the wild. Murray also notes personality differences resulting from grouping conditions are not only evident in the discrete rating scale adjectives used in his work but also in the fundamental dimensions found to underline personality variation in this species (i.e. Confident/Apprehensive, Sociable/Solitary, and Excitable/Slow).

Theoretical Rationale for Data Analysis

To explore the etiology of behavior, the major influences of genetics and environment were explored by comparing various age cohorts and family pairs. *Rusty* and *Camille*, a mother and daughter pair, were compared with *Rusty* and *J.K.*, an unrelated pair of chimpanzees, and *Camille* and *J.K.*, who are half sisters, both sired by *Doyle*. The genetic commonality between *Rusty* and *Camille* and *Camille* and *J.K.* was fifty percent in either case. However, the half-sisterhood of *Camille* and *J.K.* is in essence different from the fifty percent relatedness between *Rusty* and *Camille*. This is a result of the fact that chimpanzees are raised by their mothers and the father has little contribution other than his genetic input. The social status of the mother effects the position of her offspring in the group hierarchy and, thus, *Camille* and *J.K.* are in some ways "less" related than *Rusty* and *Camille*. Although technically both pairs share fifty percent of their genetic composition, the extremely social context of chimpanzee existence emphasizes the mother's influence differentially from the father's.

Paired comparisons among *Rusty*, *Camille*, and *J.K.* were made both longitudinally and when all three chimpanzees were approximately 17 years old. That is, longitudinal comparisons compared the chimpanzees on the five factors of personality and on two validity scales, sociability and activity, over the course of the data collection period. Also, data from 1990 for *Rusty* were compared with data from 2001 for *Camille* and *J.K.* in order to compare all chimpanzees at age 17 and eliminate the confound of age difference. Group membership was a confound with this type of comparison: the members differed between 1990 and 2001.

From the paired comparisons, consistency over time and difference in proportions between genetically related pairs were determined. With genetics assumed to be the predominating influence in personality and temperament, either *Rusty* and *Camille* or *Camille* and *J.K.* were expected to display greater behavioral similarity than *Rusty* and *J.K.* when compared within the confines of the five factor model as well as when compared on the sociability and activity indexes. If the proposed similarity between mother and daughter or between half sisters did not differ from comparison between the two unrelated chimpanzees, this result would suggest that environmental influences strongly affect chimpanzee behavior or that the genetic composition of the chimpanzee is very plastic with respect to social interaction and overt behavior. This latter possibility is assumed to be so by some researchers, considering the highly social context of chimpanzee groups.

If neither of the two related pairs of chimpanzees evidenced greater longitudinal behavioral similarity than the unrelated pair of chimpanzees, the behavioral patterns among all three females may have resulted from random environmental influences, including the confound of group membership differences mentioned above. A greater similarity across the five factors between *Rusty* and *J.K.* than between *Rusty* and *Camille* would argue against genetics as the more influential factor in behavioral patterns and would implicate an environmental influence as the predominant factor influencing behavior.

The comparison of *Rusty*, *Camille*, and *J.K.* was made to assess underlying influences on behavior. Genetics and environment are separate influences that act in concert to varying degrees. By comparing these three chimpanzees at about 17 years of age instead of comparing them at different ages across years, the confound of age is controlled. The confound of differing group composition is impossible to control but, if group composition were the same during 1990 and 2001, the impact of environment and genetics would be somewhat clearer.

Objectives and Purpose

The specific objectives of this study were to interpret the stability of temperament and personality in broad based behavior categories in several adult female chimpanzees, to interpret any shift in temperament, personality, or behavior profile of the chimpanzees that may be correlated with a group member's death in July 2000, and to interpret results using the five factor model of personality for cross-species comparison of personality using two validity

scales created from the ethogram in Appendix A. The sociability and activity validity scales were developed using frequently occurring chimpanzee behaviors.

The purposes of this study were twofold: Firstly, to assess the stability of temperament and to assess whether an abrupt shift in temperament or personality could be correlated with the major event of the death of an individual. The consistency of behavior over time was determined to address stability of temperament. Differences in proportions demonstrated the degree of difference in paired comparisons of three chimpanzees.

Secondly, in order to draw a comparison between human and chimpanzee personality structure and stability, the five factor model of personality in humans was applied to the assessment of personality change in the chimpanzees in this study. The broad behavior categories delineated in the ethogram, or behavior categorization (see Appendix A), for the chimpanzees at the Gladys Porter Zoo in Brownsville, Texas, were subsumed under the five factor model of personality (see Table 3). Changes in behavior pattern under the five factor model were compared with changes in social behaviors and active behaviors to monitor validity of the five factor model for use with chimpanzees.

In order to integrate the human five factor model with chimpanzee data, the behaviors described in the chimpanzee behavioral ethogram designed by Dr. Valerie James-Aldridge for use with the chimpanzees at the Gladys Porter Zoo in Brownsville, Texas were subsumed under the five factor categories shown in Table 3.

Table 3: Chimpanzee Behaviors Categorized by Various Factors	
Neuroticism	coprophagy, regurgitation/reingension
Agreeableness	allogroom, contact touch
Extraversion	contact close, locomote, social play, vocalize
Openness	beg
Conscientiousness	submit, respond to display
Dominance	display
Sociability	groom, contact close, contact touch, social play
Activity	forage, manipulate, locomote

Hypothesis

The hypothesis of this research was a major change in group structure in a socially intricate species, the common chimpanzee, affected overt behavior of the group members in a quantifiable way such that the proportion of time spent in specific behavior categories showed a differential increase or decrease among the individuals in the group. It was predicted that *Rusty*, who prior to *Jeanie's* death was the second eldest female and who presently is the eldest, would display an increase in extroverted behaviors and an increase in agreeableness between the beginning and end of the data sampling period. It was also predicted that *J.K.*, *Jeanie's* eldest daughter, would display a decrease in extroverted behaviors and a decrease in agreeableness between the beginning and end of the data collection period. Extroverted behaviors are evidenced in the behavioral categories Contact Close, Locomote, Social Play, and Vocalize. Agreeableness behaviors are evidenced in Groom and Contact Touch behaviors.

Rationale for Selecting Specific Individuals

Rusty and *J.K.* were specifically chosen as focal chimpanzees because of their roles in the social structure of the group prior to *Jeanie's* death. As

discussed, the social status of a chimpanzee is greatly dependent on the mother's status in the social hierarchy. *Jeanie* was the dominant female in the Gladys Porter group and, subsequently, her daughter, *J.K.*, was able to behave in ways that other chimpanzees were unable to attain. For example, when *Jeanie* was alive and *J.K.* was an adolescent, she would tease *Rusty* until *Rusty* could no longer bear the teasing and would react in an unpleasant manner. *Rusty's* reaction to *J.K.* was usually met with an attack from either *Jeanie* or *Doyle* (James-Aldridge, personal communication).

To address the validity of results from the five factor analysis, comparison was made with social behaviors and active behaviors. The social behaviors category included the behaviors Contact Close, Contact Touch, and Groom (see Appendix A). The active behaviors category included the behaviors Forage, Manipulate, and Locomote.

The influence of genetics and environment was addressed through paired comparisons between *Rusty* and *Camille*, mother and daughter, *J.K.* and *Camille*, half-sisters, and *Rusty* and *J.K.*, unrelated chimpanzees, all at age 17. In addition to the direct comparison of behavior of *Rusty* and *J.K.*, it was hypothesized that, with genetics as the predominant influence on behavior, either the mother daughter pair or the half-sisters pair would show the most similar behavior profile both longitudinally and at age 17.

CHAPTER III

METHODS

Subjects

The larger of two chimpanzee groups (N = 7) housed at the Gladys Porter Zoo in Brownsville, Texas, was comprised of two matrilines plus an adult male believed to have sired all offspring in the group. The chimpanzees included in this study were *Rusty*, current age 29, and her daughter *Camille*, current age 19; and *Jeanie* (deceased), and her daughter *J.K.*, current age 17. See Appendix B for detailed descriptions of the chimpanzees.

Until *Jeanie*'s death, Family Jeanie was clearly the dominant matriline in the group (Guerra & James-Aldridge, 1999). *Jeanie* was clearly a central individual in the social structure of a group that has been very stable since 1984 (James-Aldridge, 2001). The event of her death served to reconfigure the social hierarchy of the chimpanzees at the Gladys Porter Zoo (James-Aldridge, personal communication).

Rusty, *Camille*, *J.K.*, and *Jeanie* were compared across years on the five factor behavior categories as well as the social and active behavior groupings. Though the ethogram contains many behaviors recorded for the chimpanzees at the Gladys Porter Zoo, many such as Hair Pull Autogroom and Present occur at such a low baseline rate that, without very large amounts of data, they contribute

little to the understanding of chimpanzee behavior. Thus, in addition to serving as validity scales for comparison with the five factor model and to glean a general concept of how the four focal animals spent their days, comparisons were made in the social and active categories.

Study Site

The chimpanzee outdoor daytime quarters at the Gladys Porter Zoo are comprised of a naturalistic island exhibit of approximately 404 square meters surrounded by a water moat. There are three palm trees with electrical deterrents wound about the trunks and a two-tiered large wooden platform structure with multiple areas for climbing and sitting. There is a one-tiered smaller wooden platform as well. The floor of the area is mostly grassy with some bare dirt areas and a small pool for drinking.

The length of one side of the grassy enclosure is bordered by a moat, which forms a semicircle around the west and south sides of the enclosure. A wooden path traverses the length of the moat and enables unobstructed viewing of the animals from the west and south sides. The north and east sides of the enclosure are bordered by a tan colored stone wall which the chimpanzees often lean against but cannot climb. The wall on the north side is the exterior wall of the chimpanzee night quarters. The east wall side of the enclosure has three large Plexiglas windows for observation from a covered vantage point. The enclosure cannot be viewed from the north side as there are no windows in the wall bordering that side.

The chimpanzees spend the daytime hours in the outdoor exhibit and all data to be analyzed were collected while the animals were in the outdoor exhibit. No measurements were taken in the chimpanzee indoor night quarters.

Procedures

Archived behavioral data were retrieved and analyzed for the years 1990, 1995, 1999, 2000, and 2001. Data were collected by means of focal animal sampling in which one animal was observed and behaviors recorded for three to 15 minutes. Behavior profiles were developed for *Rusty*, *Jeanie*, *Camille*, and *J.K.* with the years 1990, 1995, 1999, 2000, and 2001 selected for analysis to investigate behavior patterns across individuals, families, and years.

Each chimpanzee name was assigned a unique number. In focal animal sampling a random number sequence was used to select the order in which the animals would be observed in a given session. Behavioral data were recorded for each animal separately during a sampling period of 3 to fifteen minutes. The behavior codes listed in Appendix A were used for recording purposes.

Once raw data were collected, proportions of time spent in selected behaviors were calculated for 4 one-year periods (1990, 1995, 1999, and 2001) and 2 half-year periods (2000 "before" *Jeanie's* death and 2000 "after" *Jeanie's* death) in order to determine the proportion of time spent in a behavior. For example, if *Rusty* were observed as Stationary (S) at the beginning of a five minute sampling period, an "S" was recorded next to 5:00 on the data sheet. If 25 seconds later, *Rusty* began to locomote (L), an "L" would be recorded on the data sheet and the time, 4:35, was noted. The amount if time spent in a behavior

category over the course of a year was then divided by the total number of minutes of time the chimpanzee was observed during a given year. In this way, behaviors and the proportion of time they were emitted by the chimpanzees were determined.

If *Rusty* spent 165 of 820 minutes grooming during the data recorded in a given year, her groom proportion would be 165/820 or .20. Since it was possible for up to three behaviors to be recorded as occurring simultaneously (e.g. Groom and Contact Close), it was possible for proportions to sum to greater than 1.

Professor Valerie James-Aldridge, research assistants at the University of Texas – Pan American, and students in Primate Behavior classes at the University of Texas - Pan American collected data over the past 14 years, some of which was used in this research. Data output was broken down into proportions of time spent by each animal in each behavior category over the course of a year. Total proportions in each behavior category over the entire group were also calculated.

Students and research assistants collecting data were trained to recognize the chimpanzees individually and record behaviors using codes for behavior categories onto prepared paper data sheets (See Appendix A for behavioral codes). Each student completed interobserver reliability testing with Dr. James-Aldridge prior to actual data collection. During this process, Dr. James-Aldridge and the student simultaneously observed the same animals, recorded behavioral observations on separate data sheets, and then compared results until an agreement of approximately .9 was obtained between professor and students. The Primate Behavior course was taught every other spring semester, with only a

single observer available during other time periods. The density of the data thus varied on a cyclic basis depending on when student observers were available to augment data collection.

From the archived data, the proportion of time spent in behavior categories was compared for the focal chimpanzees *Rusty, Jeanie, Camille, and J.K.* during the selected years at the Gladys Porter Zoo. Proportion of time spent in the behaviors subsumed by the five-factor model categories was calculated by summing the number of minutes spent in each behavior category and dividing by the total number of minutes observed during the year. For example, to calculate the proportion of Extraversion, the sum of minutes spent in Contact Close, Locomotion, Social Play, and Vocalize was determined and this value was divided by the total number of minutes the chimpanzee was observed. Since the data were summarized using only proportions of time spent emitting a certain behavior, all analyses were based on descriptive measures.

Table 4: Total Minutes of Observation Time for Each Chimpanzee

	Years					
	1990	1995	1999	2000 before	2000 after	2001
Rusty	627	460	860	20	105	162
Camille	620	460	865	48	468	152
J.K.	613	450	860	48	463	152
Jeanie	609	440	855	48	0	0

Ethical Issues

Scrutiny of animal research is common and may be desirable (Domjan & Purdy, 1995). In the present study, ethical issues were kept at a minimum by the completely observational nature of the research. Of course, some may take moral issue with keeping chimpanzees in a zoo environment but, from a positive perspective, the animals are safe, well-cared-for, fed and watered regularly, and live in secure, sanitary conditions. No physical or biological manipulations with the animals were conducted in this research and no physical contact between humans and chimpanzees or exposure of chimpanzees to harmful or dangerous substances occurred.

Chimpanzees Present During Data Collection

Table 5: Chimpanzees Present During Data Collection and Birth Dates

Chimpanzee	Birth Date	1990	1995	1999	2000b	2000a	2001
Rusty	10/14/72	y	y	y	y	y	y
Doyle	06/13/70	y	y	y	y	y	y
Gladys	08/08/81	y	n	n	n	n	n
Camille	12/16/83	y	y	y	y	y	y
J.K.	06/06/84	y	y	y	y	y	y
Jeanie	06/23/61	y	y	y	y	n	n
Arbie	09/24/87	y	y	y	y	y	y
Jaby	12/21/89	y	y	y	y	y	y
Fiona	12/08/91	n	y	y	y	y	y
Freddy	03/09/96	n	n	y	y	y	n
Millie	01/22/00	n	n	n	y	n	n

Rusty, *Camille*, *Jeanie*, and *J.K.* were present during all sampled years. *Doyle*, resident male of the group and father of all chimpanzees born in this

group, was also present for all years. *Jaby* was *Jeanie's* younger daughter and *J.K.'s* little sister. *Gladys* and *Millie* were two of *Rusty's* children who have been sent to other locations. *Arbie* and *Fiona* were also *Rusty's* children, presently living with the group at the Gladys Porter Zoo. *Freddy* was *Rusty's* son who was ill and living in the health clinic at the zoo during 2001. For complete description of all chimpanzees, see Appendix B.

CHAPTER IV

RESULTS AND DISCUSSION

Data Analysis

Data analyzed were from the years 1990, 1995, 1999, 2000 – separated into before and after *Jeanie's* death, and 2001, for a total of five years sampled. Data analysis included three comparisons. First, *Rusty*, *Camille*, and *J.K.* were paired and compared on the indexes of sociability and activity. The sociability index included behaviors Contact Close, Contact Touch, Groom, and Social Play. The activity index included behaviors Forage, Manipulate, and Locomote.

Second, *Rusty* and *Camille*, a mother and daughter pair, *Rusty* and *J.K.*, two unrelated chimpanzees, and *Camille* and *J.K.*, half-sisters, were paired and compared on the five factor model. This second data analysis used years in which all chimpanzees were 17 years old: 1990 for *Rusty* and 2001 for *Camille* and *J.K.*

Third, comparisons were made of behavior profiles for *Rusty*, *Camille*, *Jeanie*, and *J.K.* as categorized above by the five factor model. *Rusty*, *Camille*, and *J.K.* were present for all years sampled while *Jeanie* was present during 1990, 1995, 1999, and 2000 "before" (See Table 5). Finally, comparisons were made between *Rusty* and *J.K.* to test the hypotheses of change in Agreeableness and Extraversion.

Since many proportions were quite small for behaviors, a decision criterion of .01 was chosen and scores of zero were not reported. Such a small decision criterion was chosen so that small deviations from zero would be present in the data.

The Sociability Index

Table 6: Difference Scores and Degrees of Similarity on Sociability and Activity

	Sociability	Degree of Similarity	Activity	Degree of Similarity
Camille-J.K.	.75 | .80	greatest	.21 | .32	greatest
Rusty-Camille	.46 | .75	middle	.17 | .21	middle
Rusty-J.K.	.46 | .80	least	.17 | .32	least

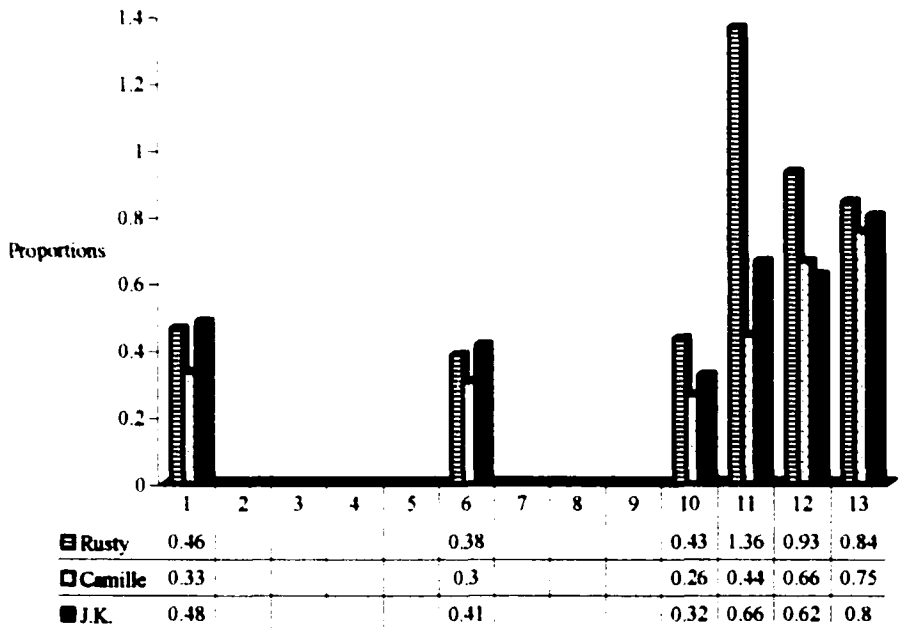
Table 6 above reveals that sociability and activity, very basic temperamental characteristics, seem to be greatly effected by genetic input. Unlike Table 8, which is comprised of data from a point comparison among the three chimpanzees when measured with the five factor model, Table 6 reveals that genetics may play the predominant role in temperament. Table 8 is a reflection of personality factors, thought to be influenced by environment to a greater degree, while Table 6 is a reflection of temperament, thought to be genetically determined.

In order to investigate the validity of measuring chimpanzee behavior using the five factor model of human personality, a sociability index was designed and *Rusty, Camille,* and *J.K.* were compared across years with respect to sociability. The yearly intervals on the X-axis in Figures 1 – 7 represent the years

sampled in the following way: Yearly interval 1 = 1990, 6 = 1995, 10 = 1999, 11 = 2000 before, 12 = 2000 after, and 13 = 2001. *Jeanie's* death occurred at the division of intervals 11 and 12. The only problematic feature of these comparison scales is that they may have accessed temperamental characteristics rather than personality characteristics.

In reference to Figure 1, upon first glance, the data seem to imply genetic input as the main influence in behavior. The same pattern is evidenced among all three chimpanzees in all years sampled except one – *Rusty* has the largest proportion, followed by *J.K.*, followed by *Camille*.

Figure 1: Sociability Index for Three Chimpanzees



Closer investigation reveals environmental influences are likely the predominant causal factor in behavioral output: Excepting yearly interval 12,

Rusty and *J.K.* were more similar across all years in proportions of social behavior. This pair is the only unrelated pair of chimpanzees included in the analysis of sociability showing genetic make-up is likely not the predominant factor influencing social behavior.

Interestingly, yearly interval 12 corresponds to the data sampling period 2000 "after" and this period is the only one in which *Camille* shows greater sociability than *J.K.*, further indicating the effect of environmental influence on behavioral output. The pattern of these results confirms results from the five factor analysis below in which *Rusty* and *J.K.* show more similar behavior patterns than *Rusty* and *Camille*.

The Activity Index

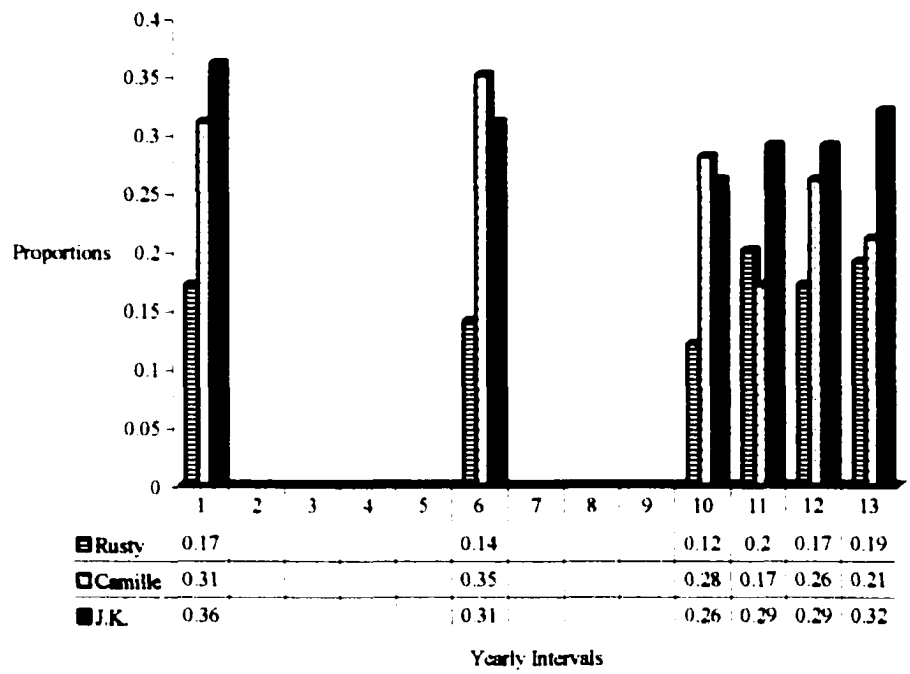
The activity index, comprised of the behaviors Forage, Manipulate, and Locomote, was also used as an index of comparison to establish validity of analysis using the five factor model.

In this instance, genetic influence again appears to be the predominant influence on first glance at the data. Closer inspection reveals this may not be the case. Firstly, *Camille* and *J.K.*, who are half-sisters, are closer in proportion of activity across all years except for yearly interval 11 in which *Rusty* moves ahead of *Camille*.

A second problem with interpreting genetics as the main causal factor in the behavioral similarities seen in Figure 2 is the confound of age. Throughout the entirety of the study, *Camille* and *J.K.* were approximately the same age and *Rusty* was approximately eleven years older than both of them. The concept that

Camille and *J.K.* are more active due to age than relatedness is confirmed by *Rusty* having smaller proportions of activity across all years, even while caring for an infant.

Figure 2: Activity Index for Three Chimpanzees



To control for the confound of age, proportions of activity were looked at for *Rusty* during 1990 (yearly interval 1) and for *Camille* and *J.K.* during 2001 (yearly interval 12) when all chimpanzees were 17 years old. Here, *Rusty's* proportion of activity is .17, *Camille's* is .21, and *J.K.'s* is .32. There again is no consistent implication that genetic influence is predominant. If it were, the difference in proportion between the mother and daughter pair should be similar to the difference in proportion between the half-sisters considering both pairs share fifty percent of their genetic composition. The difference between the half-

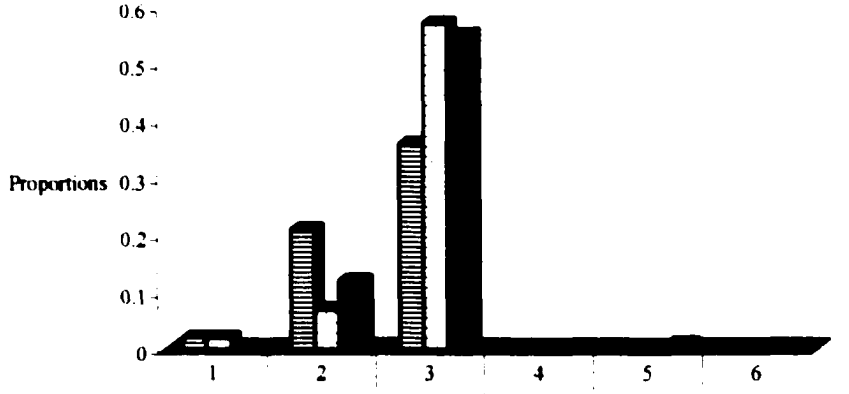
sisters is in fact much greater than the difference between the mother and daughter pair.

Of all comparisons in the sociability and activity indexes, this last comparison of chimpanzees at age 17 was the strongest evidence of a genetic influence. As it is not consistently observed across other data comparisons, however, behaviors in general continued to be interpreted as predominantly influenced by the environment.

Influences of Environment and Genetics: The Five Factor Model

To further investigate the influences of environment and genetics, comparisons were made among three chimpanzees, *Rusty, Camille,* and *J.K.* as above, across the five factors of personality. For this comparison, the age confound was controlled for by comparing the chimpanzees when all three were 17 years old. The following graph illustrates this comparison:

Figure 3: Five Factor Comparison of Chimpanzees at Age 17



	1	2	3	4	5	6
Rusty (1990)	0.02	0.21	0.36	0	0	0
Camille (2001)	0.02	0.07	0.57	0	0	0
J.K. (2001)	0	0.12	0.55	0	0.01	0

Five Factors Plus Dominance

The factors, numbered 1 through 6 in Figure 3 above, are the five personality factors plus dominance: 1 = Neuroticism, 2 = Agreeableness, 3 = Extraversion, 4 = Openness to Experience, 5 = Conscientiousness, and 6 = Dominance. Only one behavior from the ethogram in Appendix A was categorized into each of the latter three personality factors (See Appendix A). This may explain the extremely small proportions for all three chimpanzees on the three factors Openness, Conscientiousness, and Dominance. The former three, Neuroticism, Agreeableness, and Extraversion, show non-zero proportions that were analyzed for comparison of the three chimpanzees.

Table 7: Proportions of Three Chimpanzees on Five Factors Plus Dominance

	Neur.	Extr.	Agre.	Open.	Cons.	Domi.
Rusty	.02	.21	.36	0	0	0
Camille	.02	.07	.57	0	0	0
J.K.	0	.12	.55	0	.01	0

Agreeableness and Extraversion were comprised of commonly occurring behaviors in chimpanzees and they showed the greatest proportions of time spent. Agreeableness was comprised of Groom and Contact Touch, while Extraversion was comprised of Contact Close, Locomote, Social Play, and Vocalize.

Directionally *Camille* and *J.K.* are more similar to each other than *Rusty* is to *Camille* (See Table 8). Both pairs are related, though, so this result is non-contributory to the determination of the predominant factor influencing behavior. *Rusty* falls above the mean score in the Agreeableness factor, while *Camille* and *J.K.* fall below the mean. In fact, *Rusty* is more similar to *J.K.* than she is to her

daughter *Camille*. This result supports a strong environmental influence in chimpanzee behavior.

The data used to comprise Figure 3 were taken from the year 1990 for *Rusty* and 2001 for *Camille* and *J.K.* The comparison of *Rusty* and *J.K.* should have shown the least amount of similarity if genetic influences were predominant. In the case of Agreeableness above, *Rusty* and *J.K.* fall in the middle with the second largest amount of similarity between them, after *Camille* and *J.K.* who show the greatest similarity in behavior profile over the factor of Agreeableness. Again, all chimpanzees were 17 years old at the time of data sampling but *Camille* and *J.K.* had data sampled from the same year with environmental circumstances more similar to each other than to that of *Rusty*.

The pattern of similarity seen in Agreeableness and the conclusions drawn are bolstered by the pattern seen in Extraversion, which is exactly the same. Here, *Camille* and *J.K.* again are the closest to each other in deviation from the mean of the three chimpanzees than any other paired comparison of chimpanzees and *Rusty* and *Camille* the least similar.

These two comparisons strongly favor the influence of environment as predominant over genetics. It is difficult to determine the role of genetics directly with this set of data as in both factors *Rusty* and *J.K.*, completely unrelated, show greater similarity than *Rusty* and *Camille*, mother and daughter.

Five Factor Analysis of Data for Four Chimpanzees

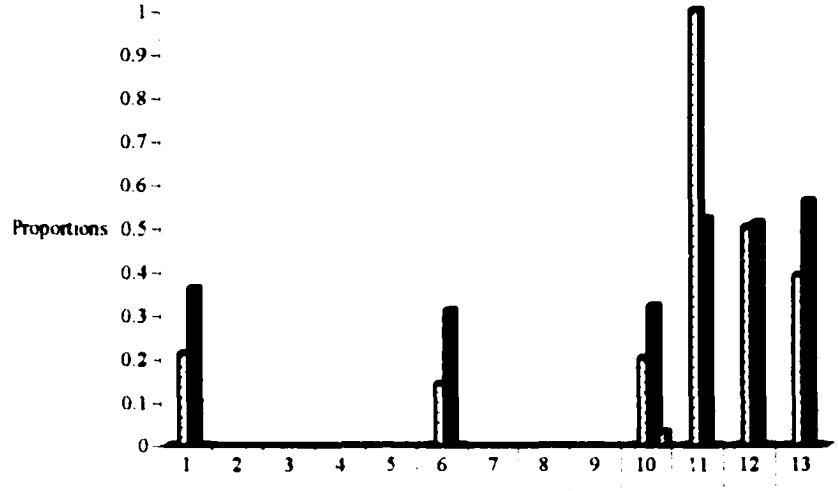
When subsumed under the five factor headings as listed above in Table 3 (page 41), much variation occurred among the longitudinal behavioral profiles of

four chimpanzees, *Rusty*, *Camille*, *Jeanie*, and *J.K.* The factors Conscientiousness and Dominance showed great consistency for *Rusty*, *Camille*, *Jeanie*, and *J.K.* in all years sampled, and thus were not included in the four figures below: All proportions for these factors were zero. The factor Openness to Experience also showed relative consistency with proportions ranging between zero and .04 (See Figures 4 – 7).

Neuroticism showed slightly more variation than Openness to Experience with proportions across chimpanzees ranging from zero to .07. Agreeableness and Extraversion showed by far the greatest variation, both intra- and interindividually. Figures 4 through 7 below illustrate behavior profiles for *Rusty*, *Camille*, *Jeanie*, and *J.K.*

Rusty and *Camille*, although showing similar patterns of Openness and Neuroticism, differed greatly in Agreeableness and Extraversion as discussed above. Agreeableness and Extraversion were comprised of frequently occurring behaviors such as Contact Close, Groom, and others. Since these were frequently occurring behaviors in a mother and daughter, a similarity in behavior profiles based on genetic commonality might have been expected but one was not evidenced.

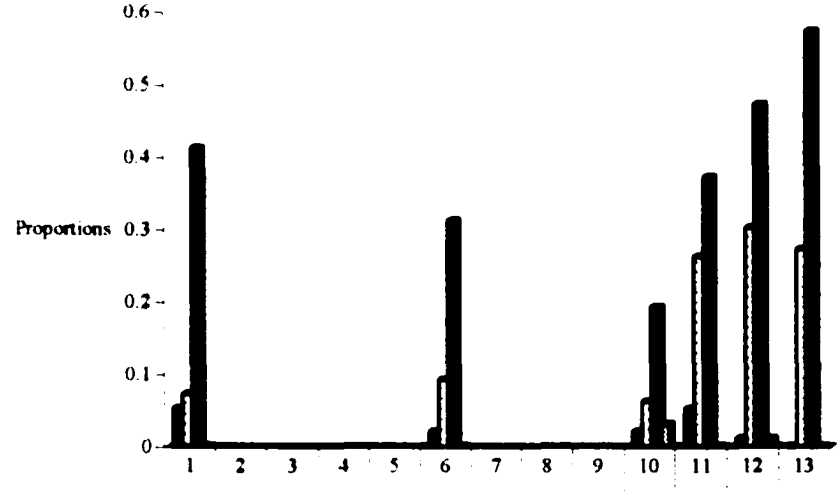
Figure 4: Rusty Behavior Profile



	1	2	3	4	5	6	7	8	9	10	11	12	13
Neuroticism	0					0				0	0	0	0
Extraversion	0.21					0.14				0.2	1	0.5	0.39
Agreeableness	0.36					0.31				0.32	0.52	0.51	0.56
Openness	0					0				0.03	0	0	0

Yearly Intervals

Figure 5: Camille Behavior Profile



	1	2	3	4	5	6	7	8	9	10	11	12	13
Neuroticism	0.05					0.02				0.02	0.05	0.01	0
Extraversion	0.07					0.09				0.06	0.26	0.3	0.27
Agreeableness	0.41					0.31				0.19	0.37	0.47	0.57
Openness	0					0				0.03	0	0.01	0

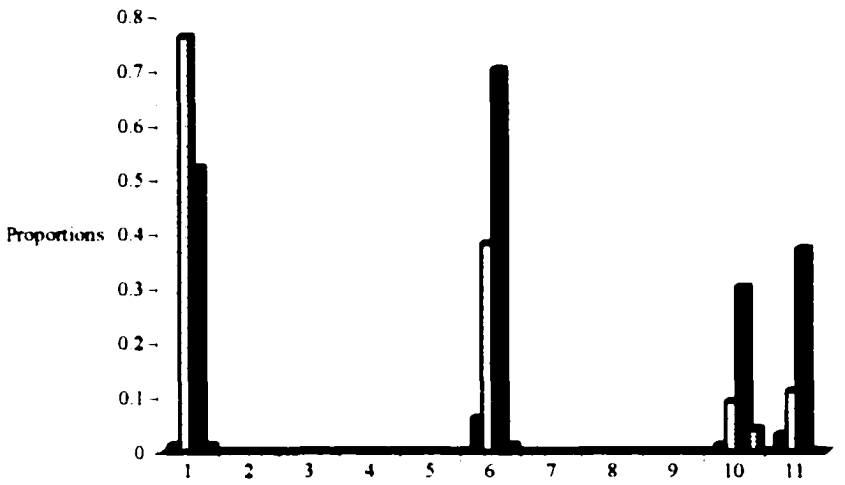
Yearly Intervals

Jeanie and *J.K.* also differed greatly in behavior profiles. Of all four chimpanzees, *J.K.* showed the greatest behavioral consistency over the course of sampled years. *Jeanie*, on the other hand, displayed great variation, especially in the factor Agreeableness in which she ranged from a proportion of 1.69 during 1995 to .01 during the year of her death. Again, the similarity, which may have been expected to result from genetic commonality, was not seen.

These differences between mothers and daughters emphasize the workings of an influence other than biology in the behavior of the chimpanzees. The result that both pairs of mothers and daughters showed the same pattern of differences supports the well-documented notion that the environment is a strong influence in chimpanzee behavior. In the following two figures, the four data years in *Jeanie's* behavior profile were 1990, 1995, 1999, and 2000 "before", while those in *J.K.'s* profile include the above listed years as well as 2000 "after" and 2001.

As *J.K.* showed the greatest behavioral consistency, *Rusty* showed a similar behavioral consistency across most years – excepting Agreeableness during 2000 "before" when *Rusty* was caring for a new infant, both chimpanzees show relative behavioral consistency when compared with *Jeanie* and *Camille*, but they are not genetically related to each other.

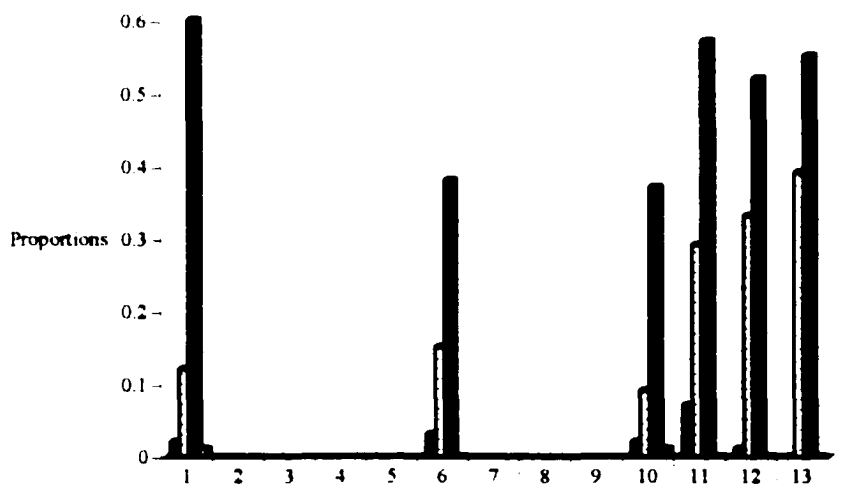
Figure 6. Jeanie Behavior Profile



Neuroticism	0.01					0.06				0.01	0.03
Extraversion	0.76					0.38				0.09	0.11
Agreeableness	0.52					0.7				0.3	0.37
Openness	0.01					0.01				0.04	0

Yearly Intervals

Figure 7. J.K. Behavior Profile



Neuroticism	0.02					0.03				0.02	0.07	0.01	0
Extraversion	0.12					0.15				0.09	0.29	0.33	0.39
Agreeableness	0.6					0.38				0.37	0.57	0.52	0.55
Openness	0.01					0				0.01	0	0	0

Yearly Intervals

Comparison of Rusty and J.K.

The following table depicts differences in proportion on Agreeableness and Extraversion, the two factors from the five factor model which showed the greatest proportions across chimpanzees. Figure 3 corresponds to the data in Table 6 and all chimpanzees were age 17 during the data reflected in Table 6.

Table 8: Difference Scores and Degrees of Similarity on Two Factors

	Agreeableness	Degree of Similarity	Extraversion	Degree of Similarity
Camille-J.K.	.07 | .12	greatest	.57 | .55	greatest
Rusty-Camille	.21 | .07	least	.36 | .57	least
Rusty-J.K.	.21 | .12	middle	.36 | .55	middle

This table reveals that the related pair of chimpanzees which were thought should possess the greatest degree of similarity, *Rusty* and *Camille*, actually showed the least degree of similarity from the three paired comparisons across both factors. This result fails to support the genetic influence as the predominant force in the production of behavior in this situation.

Following is a factor-by-factor comparison of results for *Rusty* and *J.K.*, two unrelated chimpanzees: Neuroticism, comprised of Coprophagy (ingesting one's own or someone else's excrement) and Regurgitate/Reingest (vomitus), showed extreme consistency for *Rusty* and *J.K.* Both had proportions of zero across all years. The behaviors included in Neuroticism are usually relatively

uncommon; it was thought that an excess of either could be construed as an indication of neurotic behavior or a reaction to change in the environment.

Agreeableness, the second of the five factors, comprised of Groom and Contact Touch, displayed some variation across years, especially for *Rusty*. During the measurement period of 2000 "before", *Rusty* displayed a noticeably increased proportion of the behaviors comprising the Agreeableness factor. This may be a result of the birth and care of an infant to *Rusty* during January 2000.

This spike in Agreeableness during 2000 "before" is the largest deviation from the pattern of Agreeableness displayed by *Rusty* across all years. *J.K.* showed some variation within the range of .33 to .56. This semi-consistency or movement within a small range of proportions may be evidence of an environmental circumstance superimposed upon a certain predisposition or genetic composition.

The third factor, Extraversion, was comprised of Contact Close, Locomotion, Social Play, and Vocalize. In addition to the oscillation of *Rusty* and *J.K.* from higher proportions of Extraversion, to lower, and back to higher throughout the study, there was a pattern of parallelism between *Rusty* and *J.K.* This pattern eventually converged in the years 2000 "after" and 2001 when the proportions of the two chimpanzees were virtually the same. Overall, *Rusty* showed an increase in Extraversion between the beginning and end of the years sampled, while *J.K.* ended at approximately the same level at which she began.

Openness to experience, Conscientiousness, and Dominance all revealed consistency of behavior across time. Each had quite small proportions, less than

one percent for both chimpanzees during all sampled years, which displayed consistency over time. Interestingly, the only indication of Conscientiousness (Submit and Respond to Display) exhibited by *J.K.* occurred in 2001 after her mother's death.

CHAPTER V

CONCLUSIONS

Data Comparisons

Three sets of data comparisons were made in this study. First, *Rusty*, *Camille*, and *J.K.* were compared on the indexes of sociability and activity. Second, *Rusty*, *Camille*, and *J.K.* were compared on the five factors of personality. Finally, *Rusty*, *Camille*, *Jeanie*, and *J.K.* were compared on the five factors of the five factor model of personality. Embedded within the comparison of the four chimpanzees on five factors, *Rusty* and *J.K.* were compared with each other on the five factors of personality.

The first set of comparisons showed genetics to be an unlikely candidate as the most influential factor in behavioral output. This comparison of the three chimpanzees on the sociability and activity indexes also illustrated that environmental factors are likely the more influential factors in chimpanzee behavior. The subsequent comparisons emphasized that environmental factors were likely influencing chimpanzee behavior.

Rusty and J.K.: Analysis of Five Factors of Personality

When data were analyzed under the five factor model categories, some factors showed strong consistency between *Rusty* and *J.K.* while others showed some deviation from consistency. For the first factor, Neuroticism, the behaviors

Coprophragy and Regurgitate/Reingest were selected to comprise the factor. These behaviors are not inherently neurotic, in fact, they are quite normal in chimpanzee groups. They were chosen to comprise this factor because in excess they may indicate some sort of distress. When *Rusty* and *J.K.*'s individual proportions for Coprophagy and Regurgitate/Reingest were compiled by summing the number of minutes for each behavior included in the factor and dividing the resultant sum by the total number of minutes sampled that year, creating two individual scores for each year sampled, proportions of zero were exhibited across all years for both individuals. Both spent very small amounts of time, amounting to less than one percent of any sampling period, in these behavior categories. Thus, consistency was found in the Neuroticism factor for *Rusty* and *J.K.*

Agreeableness, the second factor comprised of the behaviors Groom and Contact Touch, showed some deviation for *Rusty*, especially during 2000 "before". Note again that this is the time period during which she was caring for a new infant. *J.K.*'s proportions on this factor were moderately consistent over the entire sampling period, as illustrated by the relatively straight line shown in Figure 7.

The hypothesis that *Rusty* would increase in Agreeableness while *J.K.* would decrease in Agreeableness following *Jeanie*'s death proved to be inaccurate. That is, although *Rusty* showed an increase in grooming behavior following the major event of *Jeanie*'s death, she did not display an increase in Agreeableness, the factor into which grooming behavior is categorized. Following some fluctuation in the interim years, the Agreeableness factor in 2001

had approximately the same proportions for *Rusty* as in 1990. In other words, long-term stability of the Agreeableness factor was evidenced and *Rusty* did not show an increase in this factor following *Jeanie*'s death.

J.K. was predicted to show a decrease in agreeable behaviors following the death of her mother. In fact, she showed a slight increase in Agreeableness and, overall, remained very steady on proportions of Agreeableness throughout the course of the sampling period. Again, the event of *Jeanie*'s death did not appear to have a noticeable effect on the factor of Agreeableness for *J.K.*

Extraversion, including the behaviors Contact Close, Locomotion, Social Play, and Vocalize, showed similar consistency to Agreeableness for *Rusty* and *J.K.* An increase in Extroversion was predicted for *Rusty* following *Jeanie*'s death. Figure 4 shows that there was in fact a very slight increase in Extraversion for *Rusty*, but this increase is small compared with changes that occurred in other years. For example, there was a much larger increase in extraverted behaviors between 1999 and 2000 "before" than between any other years. Thus, although *Rusty* did display the predicted increase in Extraversion following *Jeanie's* death, it was small compared with increase seen in other years.

As Extraversion was comprised of Contact Close, Locomote, Social Play, and Vocalize, and *Rusty* was with her new infant during 2000 "before", the increased amount of close contact with the infant may have been sufficient to increase the entire factor by a noticeable amount. Infants are frequently powerful attractants for many group members. Therefore, *J.K.'s* parallel increase in

extraverted behaviors during this time may be a result of the birth of the new infant as well.

J.K. was predicted to show a decrease in the Extraversion factor following her mother's death. In fact, she had an increase between 2000 "after" and 2001. Also, she returned in 2001 to approximately the same proportion of Extraversion that she displayed in 1990. Except for some drop in extraverted behaviors in 1995 and 1999, *J.K.* remained in most part at about the same level of Extraversion throughout the course of the sampling period.

Openness to Experience, including Beg, was very consistent over time. Likewise in Conscientiousness, comprised of Respond to Display, behavior was very consistent. It is important to note that, although resulting from small proportions, the first time *J.K.* displayed a quantifiable amount of submissive behavior was during 2001, after her mother's death. The behavior Submit was only added to the ethogram in 2000; therefore, *J.K.'s* submissive behavior can only be compared among 2000 "before", 2000 "after", and 2001.

Finally, Dominance had proportions of zero for both *Rusty* and *J.K.* over all years sampled. A few minutes were spent in these behavior categories each year but the overall proportions did not equal even one percent in any given year.

Summary of Rusty and J.K.'s Changes in the Five Factors

The differential change proposed to occur between the behavior of *Rusty* and *J.K.* following *Jeanie*'s death was not evidenced. The factors of Agreeableness and Extraversion showed some fluctuation across the course of the data collection period but there was no distinct pattern of increase or decrease

matching that predicted in the hypothesis. In fact, where *Rusty* was predicted to increase in Agreeableness, she actually showed a decrease. *J.K.* overall had less fluctuation in her long term behavior patterns than *Rusty* as measured by the personality factors defined by the five factor model.

Comparison of Four Individuals on Five Factors

In general, results from analysis of the four individuals under the five personality factors reveal an environmental influence on behavior. Though Clark & Boinski (1995) assert differences in temperament at the individual level may be attributed to age, sex, and rank and differences at the species level may be attributed to the social system and ecology, the results of this study reveal that differences at the individual level may result from factors external to age, sex, and rank.

Clarke explains that relative fitness results from both what an animal does *and* what others are doing; the important factor in success may be the differences between one individual and another rather than one's absolute level of response to a given amount of change. This characterization of animal behavior may partially explain differences observed among chimpanzees at the Gladys Porter Zoo. Behavior is likely not genetically programmed to be inflexible – though each individual carries family genes, the environment influences expression of these genes. Animals do not exist in a vacuum, their behaviors are often reactions to environmental circumstances. The analysis of *Rusty*, *Camille*, and *J.K.* support the conclusion that the environmental influences surrounding chimpanzees generally have a differential effect on their behavioral output. Thus, although the

experimental hypotheses were not supported by the data, it is very likely the case that *Jeanie's* death influenced the behavior of the chimpanzees at the Gladys Porter Zoo.

Murray (1998) further supports the notion that chimpanzee behavior is at least partially a result of environmental influence. Chimpanzee behavior and personality reflect a composite of all previous experiences. They must, however, be considered in relation to the conditions in which the chimpanzees are maintained.

Murray's perspective that animals in captivity differ in psychological state, personality, and overt behavior from their wild conspecifics due to limited stimulation may explain the concentration of chimpanzee behaviors in only a few of the five factors of personality. In a natural environment, chimpanzees are exposed to an infinite range of stimuli. Openness to Experience, for example, in the wild may be characterized by extremely various behaviors. Herein, Openness to Experience was limited to the behavior Beg.

It may also be the case that the five factor model, though it has been used extensively with animal species (Gosling, 2001), is not the most appropriate tool for chimpanzee personality assessment. Perhaps in a wild environment the factors of Neuroticism, Openness to Experience, and Conscientiousness would still be lacking in behavioral correlates. Dutton and colleagues (1997) designed and used a novel rating procedure with chimpanzees and found four factors: dominance, sociability, machiavellianism, and anxiety. Sociability and anxiety are subsumed by Agreeableness or Extraversion and Neuroticism, respectively. Dominance and

machiavellianism are difficult to construe under any of the five factors. Some combined assessment of chimpanzee personality using both the five factor model and Dutton and colleagues' model may be more appropriate for chimpanzees.

Behavioral stability was evidenced through the sociability and activity indexes used in this research. The five factor model, being a tool used for analysis of longitudinal behavior patterns is an appropriate approach to analysis of chimpanzee behavior. Further investigation into whether the specific factors in the five factor model are the most appropriate for chimpanzees is warranted.

Closing

Although extensive research is currently being conducted on chimpanzees, much of it is not for the benefit of both humans and chimpanzees but solely for the benefit of humans (in the context of medical research, for example). Sadly, chimpanzees in the wild that formerly roamed millions of acres of land mainly in central Africa, are an endangered species. The land surrounding their habitat is being slashed and burned or cut for timber and they are being relegated to increasingly smaller areas of forest. Careless elimination of any species, but especially of one so similar to the human species, is an irreparable loss.

This research illustrates the complexity of chimpanzee behavior and the reality of the complex social milieu in which they thrive. Preserving a species for longitudinal interpretation of its behavior and comparison of that behavior with human behavior is not as immediately gratifying as the exchange of currency resulting from a timber transaction. Patience and insight, however, bring unexpected results that increase human understanding of existence.

Suggestions for Future Research

Subsequent research in this area may further explicate the relationship between environmental variables, genetic variables, social structure, and chimpanzee behavioral output and personality. Compared with wild chimpanzee data, using captive chimpanzees as subjects for such work controls for many variables. Both populations have benefits and costs; however, working in a controlled environment where relationships between chimpanzees are known helps defer the potential confounds of differing environmental upbringing and living conditions.

Future research may improve upon results gleaned through the five factor model by beginning with a more extensive ethogram of behavior or by altering the five factor model such that it becomes more appropriate for use with chimpanzees. For example, concentration on dominance hierarchies among males or among families, directional interpretation of grooming behavior with respect to who is giving and who is receiving the grooming behavior, and recording of more dynamic processes such as movement of a chimpanzee toward or away from others, and which others, may supplement understanding of the complex factors effecting chimpanzee behavior.

As noted in the introductory section, the importance of this type of research rests on understanding of human development as well as on understanding of dynamics in the species most closely related to humans. The mysteries hidden either in DNA, archeological exploration, or in longitudinal behavior profiles will never be revealed if chimpanzee research ceases or the

species is eliminated. The ultimate goal of a primatologist, as described by Jolly (1991), of tracing human mental complexity to its first beginnings through comparison with the species most closely related to humans is of interest to all, not only to primatologists, and hopefully the opportunity to conduct this research will persist for many decades.

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APPENDIX A

BEHAVIOR CODES AND DEFINITIONS

G Allogroom – one individual picks through hair of another individual using fingers, teeth, and/or lips.

AuG Autogroom – individual self-grooms. Exclude occasional brief body scratching or nose swipes, but include scratching or facial cleaning that is intensive or repeated frequently within a single bout.

B Beg – individual solicits "contraband" from zoo visitor(s). Do not include begging from another animal in this category (see Contact Close).

CC Contact close – focal animal is near another animal (within "easy arm's reach," i.e., within approximately 1 meter from one another), but they are not actually touching one another. Include the close approach usually made when one animal begs something from another.

CT Contact touch – focal animal is touching or being touched by another animal. Include all types of holding, carrying, or huddling. Do not include grooming, contacts made in social play, or genital inspections in this category (see Allogroom, Social Play, and Genital Inspection).

Cop Coprophagy – eating one's own feces or drinking one's own urine, or consuming wastes that have been immediately captured from another. Record the consumption of old feces or urine as instances of Forage.

Dsp Displace – one individual approaches another causing the second to move away from his/her present position which is then occupied by the first. Record type of displacement, i.e., simple displace (Dsp), displacement accompanied by physical contact (Dsp T), displacement accompanied by vocalization (Dsp V).

D Display – a complex series of behaviors, typically performed by an adult male, which may include an upright stance, piloerection, swaggering, running, ground slaps, door pounding, etc. Occasionally accompanied by loud vocalizations which, under these circumstances, are not recorded separately.

Dr Drink – individual has lips in contact with water in pool or is bent over water.

F Forage/eat – individual repeatedly picks through grass, gravel, or dirt with fingers or lips selecting items, placing them in the mouth, and, apparently, eating them.

Gen Genital inspect – individual investigates the genital region of another animal, visually, olfactorily, and/or manually, or is so inspected by

another. This is a much more stylized behavior than is simple grooming of the genital region; genital inspections are usually much briefer than grooming sessions and the receiver is usually standing quadrupedally rather than lying or sitting down. Record other participant if possible.

HP Hair pull – an extreme form of grooming in which one animal plucks individual hairs from the animal being groomed, frequently with the teeth. The movements associated with hair pulling consist generally of short, sharp jerks of the head or hand in contrast with the more gentle movements associated with grooming. Record other participant if possible.

HPA Hair pull auto groom – a self directed version of hair pull (see above).

I Interact – attention is directed to zoo visitor(s) that is different from begging (see above). May include prolonged eye contact, mild displays, playing games at the windows, etc.

L Locomote – individual changes location by any active means by at least one body length; for example, walking, running, climbing, pirouetting, dangling by one arm, etc.

M Manipulate – individual closely investigates some physical object(s) (may include body parts, e.g., feet), handling it/them in some way. Object does not necessarily move (e.g., ladder or climbing structure). May include placing objects in the mouth, but animal is clearly "playing with" rather than eating the object (see forage above). Record object of manipulation if possible.

P Social play – one individual wrestles or gnaw-wrestles, plays chase games with, or leaps upon another animal in a context which is obviously nonagonistic. Typically accompanied by a play face; may be accompanied by quiet vocalization which is not recorded separately (see vocalize below). Do not use for instances of solitary play (see locomote and manipulate above). Record identity of play partner if possible.

Pr Present - one individual stands or crouches (usually quadrupedally) orienting the genital region toward another animal. Frequently followed by a genital inspection. Record receiver if possible.

RD Respond to display – individual interrupts ongoing activity and orients toward display being performed by another individual (including noisy displays from inside building). May include, for example, running or climbing to get out of displayer's way, a simple head turn, and/or vocalization, which is not recorded separately (see vocalize below).

RR Regurgitation/reingestion – animal regurgitates small amount of vomitus and reingests it. May be repeated several times per bout.

Sb Submit – individual obviously moves to avoid another animal and/or performs any of the following: bared teeth face, bared teeth scream, bob, crouch, back-up, flee, pant grunt, or present (in a nonsexual context, see above). The category Submit should be used in lower intensity social encounters not involving a full Display (see above) by another individual. Contrast with Respond to Display (above).

S Stationary – individual is being passive and is not performing ANY of the other scoreable behaviors, i.e., contact close, etc. Usually consists of lying down, sitting, or standing while alone. Pauses for urinating or defecating will also be recorded here unless, or until, they result in Coprophagy (see above).

V Vocalize – individual produces a clearly audible sound that is not included within a behavior category described above. Indicate gradations with V+ for a loud vocalization, V- for a soft vocalization.

NV Not visible – individual moves out of visual range during test period. If not visible for more than ¼ of the test, repeat test.

Oth Other – individual performs a behavior not described above, e.g., copulation, severe attack, leaping into a pool, etc. Always describe the nature of the "other" behavior on your data sheet.

APPENDIX B

CHIMPANZEES AT THE GLADYS PORTER ZOO

1 Rusty — Adult female: born on or about October 14, 1972, birth type unknown; acquired by GPZ on October 15, 1978. Generally thick coat of hair, especially around fact; has a very obvious pale, grayish-tan "saddle" across her lower back and bushy "sideburns" along her face. Both arms very bare at present. Clearly more mature than other females. Subject code: 1

3 Doyle — Adult male; born on or about June 13, 1970, birth type unknown; acquired by GPZ on June 13, 1980. Clearly larger than any of the other animals; prominent whitish scars and very heavy gray and pink mottling on upper lip. Subject code: 3

5 Camille — Adult female; born on December 16, 1983 at GPZ; mother-reared. Rusty's second offspring, believed to have been sired by Doyle. Has a very "square" dark face with highly contrasting white beard; very large, square teeth; is slightly smaller than JK and lack's JK's identifying "head spot". Hair short around face; coat is dark and generally in relatively good condition. Subject code: 5

6 JK — Adult female; born on June 6, 1984 at GPZ. Jeanie's first offspring at GPZ (second known birth); believed to have been sired by Doyle. Rather heavy set and stocky in build; vaguely "scruffy looking"; noticeably freckled; vague but detectable brownish saddle across lower back; has barely detectable small, white spot on top, center of her head where her hair parts. Heavy splotches of dark coloring on anogenital region. Walks upright more than others. Subject code: 6

8 Jeanie — [Adult female; born on or about June 23, 1961, birth type unknown, on loan to GPZ from Los Angeles Zoo since January 18, 1983. Her first offspring was a male born on 9/23/77 at Primate Foundation of Arizona; Jeanie was brought to GPZ because she had been reported to be an excellent mother. Clearly the oldest animal in the group; frankly homely, bald-headed, frequently droopy lipped; frequently has bare arms, but hair is thinning all over her body. Subject code: 8 Died July 21, 2000 of coccidiomycosis.]

9 Arbie — Young adult female; born to Rusty (her third) on September 24, 1987; mother-reared; believed to have been sired by Doyle. Long-limbed; generally slender. Longish hair around her face; look for a very small scar on upper lip. If trying to distinguish her from Jaby, check for the Rusty Family characteristic pink anogenital "figure 8". Subject code: 9

11 Jaby — Young adult female; born to Jeanie (her third at GPZ, fourth total) on December 21, 1989; mother-reared; believed to have been sired by Doyle. Still quite active. While younger than Arbie, Jaby is now as tall and is somewhat heavier than she is. Often has deep bare patches on both upper arms. Has the Jeanie Family's splotchy anogenital region. Subject code: 11

13 Fiona — Adolescent female; born to Rusty (her fourth) on December 8, 1991; mother-reared; believed to have been sired by Doyle. One of shorter animals in the group, but getting a little stout. Being younger, skin tones are overall lighter than those of older animals. Has an occasionally detectable white spot on the crown of her head and dark cheek patches under her cheekbones. Subject code: 13

14 Freddy — Juvenile male; born to Rusty (her fifth) on March 9, 1996; mother-reared, but with some initial difficulty; believed to have been sired by Doyle. Toddler sized. Subject code: 14

15 Millie — Infant female; born to Rusty (her sixth) on January 22, 2000; mother-reared; believed to have been sired by Doyle. Still tiny. Known on paper data sheets as Lily. Subject code: 15. Sent to Nebraska in August 2000 as a result of a combination of maternal neglect and sibling abuse during Summer of 2000.

VITA

Amy Augusta Tirone was born in South Carolina and raised in West Virginia. She attended Franklin & Marshall College in Lancaster, Pennsylvania, and graduated in 1998 with a Bachelors degree in Biopsychology, Concentration in Animal Behavior. Upon completion of her Masters degree in Clinical Psychology from the University of Texas – Pan American in August 2002, she will begin her legal education at the University of Miami – School of Law in Miami, Florida in August 2002.

The email address at which Ms. Tirone may be contacted is ballenita28@hotmail.com.