Macaque Personality: Structure, Development, and Relationship to Social Behavior

Adrienne Sussman

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Reading Committee:

Renee Robinette Ha, Chair

James Ha

Thomas Burbacher

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Abstract

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Adrienne Sussman

Chair of the Supervisory Committee:
Renee Robinette Ha, Ph.D.
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In this work, we use behavioral observations to quantify individual differences in infant and adult macaques. We demonstrate that these differences, which we refer to as *temperament* in infants and *personality* in adults, explain differences in behavior between individuals. Using infant pigtailed macaques (*Macaca nemestrina*), we show that temperament changes in predictable ways throughout the first 10 months of life. We also show that temperament scores are predictive of social behaviors in 4-month-old infants. Next, we show that adult personality also changes predictably with age, though individuals' personality scores are stable over shorter periods of up to a year. We measure adult personality in three closely related species of macaques – *Macaca nemestrina, M. mulatta*, and *M. fascicularis* – and demonstrate that mean personality scores differ between the three species. These personality differences reflect species differences in social behaviors. To further investigate the relationship between personality and social behavior, we observe social behaviors in pairs of adult macaques, as well as large breeding groups of adult macaques. We show that personality is a strong predictor of social behavior in pairs, but is a weaker predictor in larger groups. However, the variance in personalities present within a large social group does predict the group's rates of aggressive and affiliative behaviors. Moreover, the personality scores of adult female pigtailed macaques predict their behaviors within a social group. Overall, our findings suggest that temperament and personality in animals share many of the developmental features documented in humans. In addition, these results support the idea that differences in personality are an individual-level trait that predicts group differences in social behavior. We propose that personality is the target of selection that leads to such social behavior differences.

Chapter 1: Introduction

Introduction/ Historical Background

One of the most important trends in animal behavior in the last decade has been the increasing shift in focus from the population or group level to the individual level. A growing number of studies acknowledge that individuals within a species differ in their behavioral patterns and tendencies, and great attention has been given to quantifying and explaining this variation. Of course, individual variation in itself is not a new concept, and is, in fact, the cornerstone of Darwin's theory of evolution by natural selection. However, while Darwin himself gave examples of both physical and behavioral inter-individual variations [Darwin, 1872] subsequent theories tended to emphasize behavioral differences between species, rather than variation within species. Despite the chasm of theoretical dispute between the comparative psychologists and ethologists during the mid-twentieth century (most notably, the roles of nature and nurture in producing behavior), both sides agreed that animals tended to follow predictable, generalizable behavioral rules. This philosophy characterizes much of the animal behavior research of the 20th century, with an emphasis on work that describes evolutionary patterns or species-typical behaviors. In such work, there is a tendency to treat species or populations as homogenous behavioral groups.

This generalization was not the rule among primatologists, who published on personality differences in chimpanzees as early as the 1930s [Crawford, 1938; Yerkes, 1939]. Some bird researchers of the same period also reported individual differences in their subjects [Talbot, 1922; Lincoln & Baldwin, 1929]. However, many researchers studying animals in the early 20th century treated animals as ruled by either instinct [e.g., Tinbergen, 1948; Lorenz, 1957] or learned behaviors [e.g., Skinner, 1938], and dismissed variation among individuals.

According to Kuhn [1970], scientific change most often takes the form of a paradigm shift: *anomalies* that do not fit the prevailing paradigm are noted, and eventually, enough anomalies lead to a *crisis* in which researchers are forced to confront issues with the existing paradigm. Finally, a *new paradigm* is proposed, and wins out over the old paradigm. In the last few decades, the study of individual differences has followed these phases, and might be considered a paradigm shift in the field of animal behavior.

Beginning in the 1970s and 1980s, primate researchers applied concepts of human personality research to their own subjects more frequently than before [e.g., Chamove, Eysenck, & Harlow, 1972; Stevenson-Hinde & Zunz, 1978; Nash & Chamove, 1981; Martau, Caine & Candland, 1985]. This research was primarily focused on identifying individual differences, comparing them with similar constructs in humans or other primate species, and occasionally identifying their proximate mechanisms (i.e., physiological correlates). The research was well received within the primatology community, but was not widely adopted by researchers working with other study systems.

Concurrent with this movement among primatologists, researchers working with other species in the wild, generally from a behavioral ecology approach, also began to observe some patterns of individual differences at this time [e.g., Fox, 1972; Barash, 1976]. The mounting evidence from these studies, in both primates and other species, eventually led to the recognition by animal researchers of an *anomaly*: individuals differ in their behaviors. Throughout the late 1980s and 1990s, studies of individual differences began to appear in increasing numbers, and by the early 2000s, several syntheses and theoretical frameworks for individual differences had appeared [e.g., Gosling & John, 1999; Sih, Bell, & Johnson, 2004, Dingemanse & Réale, 2005]. The proliferation of studies of this kind from 2000 on is most likely due to a combination of an evolving zeitgeist and increased use of more sophisticated statistical methods within the animal behavior community, which are necessary for parsing complex data. This period can be considered the *crisis* period within Kuhn's framework, with a number of theories suggested. For example, a framework in which individual traits are correlated in "suites" of behavioral patterns ("behavioral syndromes", [Sih et al., 2004]) has been suggested, as has a framework in which, instead of personality scores, individuals are assigned ranges of typical behaviors ("behavioral reaction norms"; [Dingemanse et al., 2010]). The debates as to how best to define, name, and measure individual behavioral differences are ongoing, as described below. Overall, though, the field appears to be in the final stages of a paradigm shift, where the concept of individual difference has so permeated the field that it is no longer questioned; indeed, studies of individual difference are quite ubiquitous today, and considered by many to be a basic theoretical concept.

The research presented here arises from that final stage of paradigm shift. While the idea that individuals of most (or all) species differ in their behavioral tendencies has become widely accepted, the theory linking those individual differences to larger group, population, and species behavioral patterns is still developing. In addition, our understanding of how to best measure these differences, and how they change within individuals over time and across contexts is as yet under-developed. Our understanding of how individual-level differences relate to the rest of animal behavior research grows slowly because it is complex, rather than simple, divisive, rather than unifying. However, this shift follows a number of similar shifts in animal behavior and evolutionary biology towards increasingly complex models.

With each major theoretical addition to the field of animal behavior, we have come more and more to embrace complexity. Following acceptance of Darwin's theory, we saw phenotypic variation where before species were considered more or less perfect iterations of a "type"; following the introduction of theories of kin selection by Haldane, Hamilton, Fisher, and others, we saw differences in behavioral patterns depending on kinship of the participants [Fisher, 1930; Haldane, 1957; Hamilton, 1970]. Now, with the paradigm shift in thinking about individual differences, we will have to embrace within-individual complexity, with behaviors differing depending on age and context.

The research presented here explores this complexity from a number of fronts. Several of the studies explore the stability of individual differences over time and contexts. One study examines how patterns of individual differences vary among species. Finally, we explore how individual differences might predict social interactions between pairs of animals, and how these pair-wise interactions compare to patterns observed in larger groups of animals.

Personality: terminology and concepts

Definitions

A number of terms have been used to describe individual differences in behavioral patterns. The terms *temperament* and *personality* are often used interchangeably in the literature [see Réale et al., 2007], as both describe consistent individual patterns of behavior that are stable over time and differentiate individuals along one or more axes. These differences are usually understood to have genetic or physiological correlates. In the human literature, temperament and personality are better defined. In humans, temperament usually refers to individual patterns of behavior in infants or young children, and is considered to be a genetically rooted set of behavioral tendencies, which eventually develop into personality as these biological predispositions interact with experiences and environment [Rothbart & Bates, 2006; Rothbart & Derryberry, 1981]. The term personality is generally used to refer to individual differences among human adults or older children, which are impacted by experience and involve more sophisticated socially and cognitively based constructs [Putnam, 2011]. Some researchers have suggested that the traits associated with personality are unique to humans, and the existence of a trait in an animal model suggests that it is temperament [Zentner & Bates, 2008]. However, increasing evidence suggests that individual behavioral patterns are influenced by experience and environment in animals, as well, suggesting that these behaviors might be better referred to as personality than temperament [see for example, Veenema, 2009; Frost et al., 2007]. In this work, we use temperament to refer to traits identifiable in young individuals, and personality to refer to traits in adults, regardless of species.

Other researchers employ the term *behavioral syndromes* to describe individual patterns of behavior. Behavioral syndromes describe patterns of behavior that are correlated across contexts [Sih et al., 2004], such as aggression and boldness in the contexts of environmental exploration and mate defense. While the existence of such syndromes in invertebrates, fish, and some birds has been documented, few primate studies have attempted to correlate behavioral tendencies across contexts in this way. For this reason, we utilize traditional definitions of personality and temperament in describing individual patterns of behavior in primates.

Measurement

In addition to disagreement over terminology, proper methodology for measuring personality has been debated in the literature. In a recent review, Freeman and Gosling [2010] provide an overview of the methodologies used to measure personality in primate studies. They distinguish between two methods of data collection: first, data are either collected using an observers' (subjective) *ratings* of an individual's behavior or using an objective *coding* of an individual's behaviors. Freeman and Gosling found that coding was more commonly used in the published literature [2010]. While observer rating may give more holistic assessments of an individual's personality, coding behavior may give a more context- or time-specific picture of an individual's behavior [Weiss & Adams, 2013]. In addition to these data collection methods, Freeman and Gosling distinguish between three contexts of testing: using naturalistic behavior in the animal's familiar context, using a test-specific context, or using cumulative experience. The latter method requires testers who are very familiar with the individuals in question to rate the animals' personality based on their overall impressions of the subjects, rather than based on a specific observation period. While the distinction between these methodologies may seem stark, a comparison of results shows that these methods result in very similar repeatability scores and identify similar personality constructs [Freeman & Gosling, 2010], suggesting that all of these methodologies are valid. However, there are some limitations associated with these methods. For instance, accurate observer rating requires a number of trained observers to pool their ratings, and cumulative experience as a basis of personality scoring requires a number of observers familiar with all individuals involved in the study. Given these limitations, behavioral coding in either a naturalistic or test context may be the most appropriate methods of personality testing for studies with a large number of subjects and a small number of observers.

Once behavioral data have been collected using behavioral coding, there are several methods of statistical analyses that can be used to determine personality scores. Some researchers choose to simply group behavioral variables based on theoretical similarity, or they may name a personality trait for a single behavior (e.g., an open-field test). However, most researchers use statistical analyses to identify combinations of variables that describe the variance observed in individuals. The two most commonly used methods of identifying personality are principal components analysis (PCA) and factor analysis (FA). Both are methods of summarizing large sets of variables into smaller numbers of components or factors, which together explain the largest possible portion of the variance in the original set. Each component or factor is made up of variables that explain related portions of the overall pool of variance. Variables can contribute to multiple components, though this can hamper interpretation. Many researchers use rotation to ensure that variables contribute largely to only one component or factor. The benefit of using PCA or FA is that these methods can reduce the number of variables involved in an analysis, which in turn decreases Type I error rates [Cohen, 1992] and makes results more interpretable. The use of PCA or FA in personality research is also preferable to simply combining variables through averaging or pooling, as many researchers prefer to base the formation of their traits on the data, rather than their preconceptions of which variables will be related.

While both PCA and FA can be used as exploratory analyses, FA requires more theoretical input from the researcher. PCA divides up the total pooled variance among the variables included in the analysis, while FA also makes some assumptions about the structure of the error variance. In addition, FA usually requires that the researcher determine beforehand how many factors to identify. In personality research, FA is sometimes considered the sounder analysis option, as the structure of variance partitioning is more similar to what would be expected in personality theory (i.e., each individual has some underlying trait, and error is introduced in measurement). However, if the researcher wishes to describe how variables explain variance in a sample, without making assumptions about where error is being introduced or how many components are expected, PCA is a good choice. In practice, the results of PCA and FA are often similar [Arrindell & van der Ende, 1985; Velicer & Jackson, 1990].

Personality research in humans

A number of theories have been proposed regarding the structure and provenance of personality differences in humans. One of the most widely used models is the *five-factor model*, which divides human personality into five major categories: Conscientiousness, Agreeableness, Neuroticism, Openness, and Extraversion. This model emerged from several independent studies in the 1960s, which each concluded that human personality can be described by five broad spectra of variation [Norman, 1963; Borgatta, 1964; reviewed in Digman, 1990]. Costa and McCrae created the Neuroticism, Extraversion, Openness Personality Inventory (NEO-PI) in 1985, which formalized the measurements of these five traits, and became the foundation of a large portion of human personality psychology research. Later research showing that these five components can be identified across age groups and in many cultures, and has led to the wide-spread adoption of this framework [McCrae et al., 2002; McCrae & Costa, 1997]. However, some researchers have criticized the five-factor model for having a limited scope in describing human personality [Paunonen et al., 2000; Paunonen et al., 2003]. Many researchers have developed and continue to use different models, with two, three, four, or more personality traits, to describe human personality [e.g., Eysenck, 1968; Guilford, 1975; see Digman, 1990]. Some have also criticized the fact that the five-factor model was created to fit existing data, rather than being shaped by an actual theory of all the possible dimensions of human personality [Eysenck, 1992].

In addition to controversy over how many personality traits exist, and how they should be measured, there is also considerable debate over how stable personality is within an individual. A large literature suggests that personality changes predictably throughout adulthood [McCrae et al., 2000; Roberts & DelVecchio, 2000; Helson et al, 2002; Terracciano et al., 2005; Roberts et al., 2006]. These studies suggest that more change occurs during adolescence and early adulthood, and traits become more stable later in life. The most commonly described changes are an increase in social dominance, conscientiousness, and emotional stability (sometimes described as a decrease in neuroticism), and a decrease in social vitality [McCrae et al., 2000; Helson et al., 2002; Roberts et al, 2006]. Some investigators consider these changes to follow “intrinsic paths of development” [McCrae et al., 2000], but other evidence suggests that these changes are more strongly related to environmental factors, such as experiences that commonly occur in adulthood [Roberts et al., 2006]. While many agree that personality changes, some argue that the amount of change is negligible, and individuals' personalities are relatively stable over time [McCrae et al., 2000]. Another school of thought suggests that personality is actually quite *unstable* within an individual, and can vary dramatically depending on context and timing of testing [Mischel, 1969; Shoda & LeeTiernan, 2002].

The literature on temperament development in infants and children has historically occurred separately from adult personality research, confined to the field of developmental psychology. In that area, researchers have found that individual differences in behavior, or temperament, can be identified from a very young age. Differences in activity, for example, can be measured prenatally, and differences in distress and avoidant movements can be observed in newborns [Rothbart, 2007; Rothbart et al., 2000]. Other temperament traits emerge several years after birth [Izard, 1977; Rothbart et al., 2000]. These traits change considerably within individuals as they age, though infant traits are generally predictive of later behaviors [Rothbart, 2007]. Many infants become less extreme on certain temperament trait spectra, such as reactivity, as they age [Kagan, 1997]. While it is common for children to become less extreme in their temperament scores with age, it is not common for temperament scores to become extreme in the opposite direction. Likewise, while there appear to be some normative developmental paths for temperament, not all children develop in the same way, and some individuals maintain extreme temperament scores into adolescence [Kagan, 1997]. Infant and childhood temperament is a weak to moderate predictor of adult personality in several dimensions [Caspi & Silva, 1995; McCrae et al., 2000]; much of the variation in developmental stability here may be due to differences in environmental experiences.

The early appearance of temperament traits, as well as the cross-cultural explanatory power of the five-factor model, suggests that personality has a biological basis and is not a cultural construct. Indeed, there is substantial evidence to suggest this is the case. A review of twin studies and other analyses shows that human personality traits is heritable at about 50%, with almost no variance attributable to shared environment [Bouchard & Loehlin, 2001]. Several personality traits have been linked to specific genes. For example, novelty-seeking behaviors have linked to a specific exon repeat of a dopamine-receptor allele (DRD4) [Gelernter et al., 1997; Ebstein et al., 1996]. Similarly, a repeat sequence in a vasopressin receptor gene (avpr1a) is linked to more pair-bonding behavior in men [Walum et al., 2008], and an allele of the serotonin transporter promotor (5-HTTLPR) is a strong predictor of Neuroticism and depression and anxiety disorders [Sen, Burmeister, & Ghosh, 2004]. Several other genes and physiological measures are also correlates of personality, and research in this area is progressing rapidly.

At the same time, personality is not entirely dictated by genetics, and experience has measurable effects on personality. For example, stressful or traumatic events can alter personality even in adulthood [Mroczek & Almeida, 2004; Lockenhoff et al., 2009]. More mundane events, such as work experiences in midlife [Roberts, 1997] and changes in work and marital status [Costa et al., 2000] may also affect personality. As mentioned, some researchers believe that these effects of experience on personality may explain the observed changes in personality in adulthood. That is, these changes may not be related to physiological or gene-expression changes that occur with aging, but rather, to normal life experiences (e.g., getting married, having children, retiring) that occur at certain life points [Roberts et al., 2006].

With a well-developed metric for measuring personality, human social psychologists have been able to link personality trait scores to a number of correlates. For example, personality can be linked to job affinity, choice of geographic living location, , stress levels, mental illness and many others [Brandstatter, 2011; Matthews et al., 2006; Rentfrow et al., 2013; Krueger & Eaton, 2010]. Of particular interest to this project, human personality has been linked to the number and quality of social relationships an individual is likely to have. Trait scores can predict social status, for example [Anderson et al., 2001], with high Extraversion related to higher status, and high Neuroticism related to lower status in males. Several studies have suggested that Extraversion is also related to larger social network size [Bolger & Eckenrode, 1991; Swickert et al., 2002]. Another study, however, found no relationship between personality and network size after controlling for age [Roberts et al., 2008]. Personality may also affect the type of network an individual relies on (i.e., primarily peers, family, or mixed networks; [Doeven-Eggens et al., 2008]).

Personality research in animals: The state of the field

The study of personality in animals has a shorter history than in humans, and consequently, the field is less developed. Whereas human personality psychologists debate how many factors best describe personality, or whether personality changes over the lifetime, or over the hour (see previous section), animal personality psychologists are still at the point of identifying that personality exists and can be measured reliably. To that end, researchers have identified personality traits in dozens of species, including vertebrates and invertebrates [Gosling, 2001].

As described above, there are several methodologies for measuring these traits, but regardless of the method used, the traits identified in most published research are fairly reliable within individuals. Most studies that use multiple observers report high inter-rater reliability (R >0.9), though the range of reliabilities for specific traits is quite large (R =0-0.92; [Freeman & Gosling, 2010]). In addition to inter-rater reliability, most researchers also measure repeatability, or the amount of variance in scores within individuals over time. One meta-analysis studied measures of repeatability in many different species [Bell et al., 2009]. They found that measurements taken over short time periods were significantly more repeatable than measurements over longer time periods. They did not find a difference in repeatability with age, but their analysis included a large variety of taxa, including insects, which might not be expected to adhere to the same lifetime repeatability trends as humans or other primates. The average repeatability in the Bell et al. study was 0.37 [2009], while in an analysis of nonhuman primate studies the average repeatability was 0.58 [Freeman & Gosling, 2010].

The language used to name personality traits in animals is also more variable than in the human literature. Gosling and others have recommended that animal researchers also adopt the five-factor model, as most animal personality traits can be fit to this framework [Gosling & John, 1999; Gosling, 2001]. Instead of Conscientiousness, which has only been identified in chimpanzees, Gosling recommends that researchers adopt Dominance as the fifth personality factor [Gosling & John, 1999]. Despite this recommendation, few researchers have used this framework, and instead most published studies identify traits such as Aggressiveness, Reactivity, Activity, etc. (see [Freeman & Gosling, 2010] for a review of common trait names in primate studies). These descriptions are presumably chosen because they describe the animal's behavior and seem less anthropomorphic than the language of the five-factor model. In keeping with the conventions of the field, in the research presented here we use language that best describes the trait identified, and that is comparable to other names used in the animal literature, rather than using the language of the five-factor-model. However, we acknowledge that systematic naming conventions would be a boon to the field.

As in humans, there is evidence that personality in animals is shaped by both genetics and experience. Heritability values in primate studies tend to be comparable to the $h^2 = 0.5$ average in human studies (reviewed in [Weiss & Adams, 2013]). A study of rhesus macaques found heritabilities on reactions to anxiety tests to range from $h^2 = 0.47$ to 1.0 [Williamson et al., 2003]. A study of social impulsivity in vervet monkeys found slightly lower, but still significant heritability values, with Impulsive Approach heritable at $h^2 = 0.25$ and Aggression at $h^2 = 0.61$ [Fairbanks et al., 2004].

In addition to these similar heritability values, similar genes to those identified in humans have been identified as related to analogous personality traits in animals. An allele related to the serotonin reuptake transporter system (5-HTTLPR) has been linked to anxiety or Neuroticism in rhesus macaques [Bethea et al., 2004], while polymorphisms of the dopamine receptor gene (DRD4) are related to novelty seeking in vervet monkeys [Bailey et al., 2007]. Differences in cerebrospinal fluid concentrations of the serotonin metabolite 5-HIAA were related to differences in rhesus macaques in risk-taking and aggression [Higley et al., 1996a, 1996b; Westergaard, Suomi, & Higley, 1999].

While the physiological mechanisms that produce personality are fairly well understood in animals, less is known about the developmental trajectory of personality throughout an individual's life. One meta-analysis suggests that there is little developmental change in most animals [Bell et al., 2009], though this might reflect the diversity of species examined in that study. Several studies in primates suggest that personality does change with age in chimpanzees and great apes [King et al., 2008; Weiss et al., 2007; Weiss et al., 2012], and that, as in humans, it becomes more stable with age. Other studies reported that personality can be predicted by age in several species, including vervet monkeys [McGuire et al., 1994], capuchins [Manson & Perry, 2013], and callitrichids [Kendal et al., 2005].

A number of studies have also examined developmental change in temperament in young animals, similar to the human developmental psychology literature. Some of these findings suggest that infant temperament is fairly stable and highly predictive of adult personality. Suomi, for example, [1997] showed that traits such as impulsivity and reactivity persist from infancy into adolescence in rhesus macaques. Other work with rhesus macaques has shown that juvenile temperament measures translate into predictable adult behavioral patterns [Capitanio, 1999; Weinstein & Capitanio, 2008]. Similarly, responses to novel objects in infant squirrel monkeys were predictive of novelty seeking behaviors at 2.5 years [Parker et al., 2007]. However, other studies have emphasized developmental change. For example, a study of infant macaques and baboons found individual changes in behavior over the first 4 months of life [Heath-Lange, Ha, & Sackett, 1999], and Stevenson-Hinde et al.'s [1980] studies of infant rhesus macaques found significant change in behavioral traits during development. The developmental literature is strongest for primates; many studies of other systems do not distinguish between juvenile and adult individuals [Bell et al., 2009]. Of those non-primate studies that do look at development, most find that juvenile personality or temperament was no less reliable than adult personality [Bell et al., 2009].

The only theoretical area that has received more attention from animal behaviorists than from human personality psychologists is the adaptive value of personality. Given that similar types of personality dimensions can be observed in such a diverse array of species, researchers have suggested that variation along these axes must be maintained by evolution. Studies across systems suggest that the fitness value of personality traits varies depending on environmental factors like resource availability and predation pressure. For example, differences in exploratory behavior among great tits were found to be heritable [Dingemanse et al., 2004]. These differences in exploratory behavior have different fitness consequences, depending on food availability. In years with greater food availability, fast-exploring males and slow-exploring females survived best, and in years with low food availability, this pattern was reversed [reviewed in Dingemanse & Réale, 2005]. Another series of studies examined differences in Boldness and Docility in wild bighorn sheep, which were also found to be heritable [Lynch & Walsh, 1998]. These two traits were found to predict reproductive success, with ewes higher in Boldness or higher in Docility reproducing earlier than shy or non-docile ewes (Reale et al. 2000). They were also related to survival, with Bold ewes less likely to be predated on in years of high predation pressure [Dingemanse & Réale, 2005]. Finally, a few studies have examined fitness of personality traits in nonhuman primates, especially in the free-ranging rhesus macaque population on Cayo Santiago.

Cerebrospinal fluid levels of 5-HIAA (a serotonin metabolite related to aggression and risk taking behaviors, see above) predicted higher reproductive success but lower survival in this macaque population [reviewed in Dingemanse & Réale, 2005].

Personality and social behavior

Relationships between personality and individual fitness benefits are compelling, but clearly don't tell the whole story when it comes to highly social species. For group-living species, personality might predict not just individual behaviors, like tendency to explore novel environments, but also might be related to an individual's tendency towards certain social behaviors, like engaging in social aggression. An extension of this idea is that the behavior of a social group – for example, the average amount of aggression in that group – might best be explained by the personalities of the individuals within that group.

This idea has been proposed by a number of theorists. A group of researchers have modeled the differences in aggression between macaque troops based on individual differences in "thresholds" to perform certain behaviors; these computer simulations, which vary only in individual differences, mimic the differences between primate groups noted above [Hemelrijk & Wantia, 2005; Puga-Gonzalez, Hildenbrandt, Hemelrijk, 2009]. Some game-theorists have also explained differences in group behaviors in terms of group members' tendencies towards "hawkish" or "dovish" behaviors [Dall et al., 2004]. According to this theoretical model, the combination of Hawks and Doves in a group predicts the likelihood of conflict in that group.

In addition to these theoretical approaches, several researchers have found empirical evidence for a link between personality and group social behaviors. In a small-scale study, Capitanio [2004] found that the personality types present in newly formed groups of rhesus macaques affected the behaviors in the groups, including the amount of aggression and grooming. Differences in group behavior were dependent on both the group mean on traits such as sociability and the trait variance present within the group. Similar or supporting results have been found in other species, as well. Scheid and Noe [2010] found that personality predicted whether rooks would cooperate with conspecifics on a task. Several studies also demonstrate that personality affects social style in fish. For example, bold sticklebacks have fewer social interactions, but interact with more different individuals than shy sticklebacks [Pike et al, 2008]. Croft et al. [2009] found similar results for guppies, with shy individuals having a greater number of strong social network connections than bold fish. A recent study in great tits replicates this finding [Aplin et al., 2013]. Finally, extensive work has examined individual differences and social behaviors in water striders, including experimental manipulation of social groups to demonstrate the effects of personality [Sih & Watters, 2005]. This work found that groups made up of Aggressive individuals tended to be more active and more aggressive towards intruders (though the latter result was only marginally significant). This study examined differences in mean personality within a group, with variance held constant.

Macaques as a model system

The macaque monkeys are a wonderful model system to study the relationship between social behavior and personality because they are one of the best studied primate groups, and their individual differences and social behaviors are well studied. Moreover, they are widely kept in captivity as research subjects, so can be studied in controlled environments in large sample sizes. While our studies used captive macaques, it is important to understand an animals' natural history when studying its behavior.

Natural history of the macaques

Macaques are a diverse genus, with species displaying a broad spectrum of possible social dynamics. Researchers recognize 20 extant species of macaque, which are found throughout Asia and into northern Africa [Thierry, Singh, & Kaumanns, 2004]. This wide geographical range encompasses the most habitat diversity of any non-human primate [Thierry et al., 2000]. Regardless of habitat, macaques are very similar in many of their natural history attributes. All macaque species live in multi-male, multi-female groups with male dispersal [Hill, 1994; Melnick & Pearl, 1984]. The sex ratio in these groups is biased towards females, with differences in the typical ratios across species [Caldecott, 1986a; Thierry, 2000]. Unprovisioned groups across species tend to include about 18-32 individuals [Caldecott, 1986a], though provisioned groups can be many times this size. The macaques are semi-terrestrial and mainly frugivorous, though species vary in diet [e.g., Caldecott, 1986b]. The research presented here focuses on pigtailed macaques (*Macaca nemestrina*), but also includes rhesus macaques (*M. mulatta*) and long-tailed macaques (*M. fascicularis*) in some of the projects described. These three species differ on a number of dimensions, as outlined in Table 1.1.

The macaques show considerable variance in their social behaviors. These include species differences in dominance, nepotism, retaliation, and despotism, as well as species-typical displays of aggression, affiliative behavior, and reconciliation [Matsumara, 1999; Thierry, 2000]. Rhesus macaques, one of the species studied here, are considered to be among the most despotic, or rigidly hierarchical of macaque species

[Thierry, 2000]. Their societies have a strong power asymmetry, and most aggressive contests are unidirectional. When compared directly to other macaque species, rhesus macaques often show more intense aggressive behaviors. Both longtailed and pigtailed macaques, our other study species, show comparatively less social aggression, lower influence of kinship in determining female rank, and a higher frequency of clasping and appeasing behaviors than rhesus [Thierry, 2000; Thierry, et al., 2000; Maestripieri, 2005]. In captivity, for example, pigtailed macaques' hourly rates of aggression are about half that of rhesus macaques' [Bernstein et al., 1983], while their reconciliation rates are twice as frequent [Gouzoules & Gouzoules, 2000]. Not only the rates of aggression, but also the severity of aggressive behaviors appears to be more extreme for rhesus macaques. In reports of wounding among captive populations, rhesus macaques received more than twice as many wounds as pigtailed macaques [Ruehlmann et al., 1988]. Whereas longtailed and pigtailed macaque societies are not markedly different in terms of frequency of aggression, some evidence suggests that pigtailed macaques show higher rates of conciliatory behaviors than longtailed macaques [Thierry, 2000]. They also may make greater use of some affiliative gestures, such as conciliatory male-male mounting [Oi, 1990] and the "pucker" ([Maestripieri, 2005]; also known as the LEN, a species-specific facial expression of *M. nemestrina*; [Oettinger, Crockett, & Bellanca, 2007])

While the three species discussed here differ in social behaviors, research suggests that other macaque species are even more distinct in their social behaviors [Thierry, 2000]. For example, Tonkean macaques (*M. tonkeana*) are considered by some as one of the least despotic species in the genus, with notably low frequency and intensity of aggressive encounters, and high rates of reconciliatory behaviors [Bernstein et al., 1983; Thierry, 1986; Thierry, 2000]. For the purposes of this research, it is simply important to note that the species examined here inhabit only a range of the possible spectrum of macaque behaviors.

Ecological correlates of social behavior

Behavioral ecologists have linked the observed differences in social structure among macaques to the availability of resources within and between groups. Several theorists have suggested that optimal group size is tied to both resource availability and predation pressures [Terborgh & Janson, 1986]. Some have suggested that the amount of within- and between- group competition predicts the style of female philopatry within the group (i.e., how egalitarian or despotic the group is; [Sterck, Watts, & van Schaik, 1997]). Groups with low within-group competition and low or high between-group competition are expected to show more egalitarian behavior, while groups with high within-group competition for resources will be more nepotistic [Sterck et al., 1997]. The combination of high within-group competition and high between-group competition are expected to be the most despotic. Caldecott [1986a] also proposed that resource availability should influence within-group aggression, with groups in resource-poor areas showing a lower male: female sex ratio and more prolonged consortship relationships between females and males. Males in this scenario would be more likely to emigrate, and male-male aggression for control of females would be fierce [Caldecott, 1986a]. Conversely, in resource-rich areas, Caldecott predicted that sex ratios would be more even, and that male-male competition would occur through sperm-competition, rather than through male-male aggression [Caldecott, 1986a]. Wrangham argued that resource scarcity primarily affect female-female aggressive tendencies, which in turn determines the social structure and style of the group [1980]. Several similar theories have been proposed in the primate literature [e.g., Terborgh & Janson, 1986; Van Schaik, 1989].

It is clear that resource availability and to a lesser extent predation pressures are closely tied to primate social structure. However, such socioecological approaches can only approximate an explanation for the vast diversity of social behaviors observed among primates [Terborgh & Janson, 1986]. Furthermore, even within species, patterns of behavior vary greatly from one group to another [Sapolsky & Share, 2004; Ha et al., 2011]. Thus, while resource availability and predation may be the evolutionary pressures that push species towards one social structure or behavioral style, they are clearly not the proximate mechanisms that explain differences between groups in behaviors like aggression.

Correlates of aggressive behavior

In captivity, where resource availability is controlled, the relationship between group aggression and structure can be studied experimentally. Captive studies show that several group attributes can lead to higher aggression rates, including group sex-ratios, group size, and group stability. In captive rhesus macaques, larger groups showed greater levels of female-female aggression [Judge & De Waal, 1997]. A similar correlation between social housing density and aggression has been documented in pigtailed macaques [Erwin & Erwin, 1976]. In addition, the presence of a male appears to decrease the severity and frequency of aggression in a social group [Bernstein & Sharpe, 1966]. All-female groups of pigtailed macaques display more aggression than groups containing an adult male [Sackett, Oswald & Erwin, 1975; Ha et al., 2011], and males in pigtailed groups actively police female aggressive behavior [Dazey et al., 1977; Flack et al., 2005; Flack et al., 2006]. Finally, group stability also predicts aggression, with newly formed macaque groups undergoing periods of intense female-female conflict while the social organization is being established [Bernstein et al., 1974]. Presence of a sire, presence of other pregnant females, and greater group stability are predictive of positive pregnancy outcomes [Ha et al., 1999; Ha et al., 2011], most likely because these factors are indicative of lower aggression levels. In seasonally breeding species like rhesus macaques, time of year is a known predictor of female-female aggression [Beisner & Isbell, 2011], but it is currently unknown whether this is a factor in predicting aggression in non-seasonal species.

Evolution of differences in social behavior in the macaques

The ecological models of macaque behavior described above do not satisfactorily explain the persistence of species-typical behavioral differences in captivity [Thierry, 2000]. A phylogenetic analysis of social behaviors among the macaques suggests that some of the social differences between species vary with phylogenetic relatedness [Thierry et al., 2000]. This analysis found that species differences were better explained by phylogeny than by environment. Thierry et al. concluded from this analysis that differences in social behavior between macaque species are not the results of current ecological pressures, but rather the results of evolutionary processes. From this, they hypothesized that differences in social behavior most likely result from selection on behavior differences (i.e., personality) at the individual level. This conclusion, though reached through a study of phylogeny, is strikingly similar to the ideas discussed above that germinated from personality research.

Overview of this project

The studies presented herein explore this proposed connection between personality and social behavior in captive macaques. Chapter 2 presents work on the development of individual differences and the relationship between temperament and social behavior in infant macaques. In Chapter 3, we examine individual differences in adult macaques, looking at changes that occur throughout adulthood and differences in personality between three species of macaques.

In Chapter 4, we compare the personality components identified in Chapter 3 with social behaviors. This work begins by examining the behaviors of captive pairs of adult monkeys at the primate research center, and then scales up to larger groups housed at the primate center breeding colony. We attempt to explain variations in social behaviors between individuals using their personality scores, and also characterize group differences in overall social behaviors based on the mix of personalities in that group.

Finally, in Chapter 5, we discuss the major findings of this research and their implications for animal personality research, primate husbandry, and the evolution of species- and group-differences in social behavior.

Table 1.1 Phylogeny, ecology, and life history data for three focal species of macaques, genus *Macaca*.

Species	Species group	Natural range	Habitat type	Group size	Group sex ratio (M:F)	Breeding seasonality
M. fascicularis Longtailed	*fascicularis*[a]	Tropical forests of insular and peninsular South-east Asia [b]	Secondary and riverine forests [d]	7-100 (Mean =29.5, N=40)[f]	1:4[e], 1:3[g]	Non-seasonal[e]
M. mulatta Rhesus	*fascicularis*[a]	Eastern Afghanistan to eastern China and northern Vietnam [b]	Variety of subtropical forests [b]	8-98 (Mean=30.8, N=61)[f]	1:2[e], 1:3[g]	Seasonal[e]
M. nemestrina Pigtailed	*silenus*[a]	Tropical forests of insular and peninsular Southeast Asia [b]	*Diptero-carpacae* forests (masting, low productivity)[c]; primary forests, upland terrain [d]	15-40 (Mean =24.0, N=9)[f]	1:8[e]	Non-seasonal[e]

a – [Hoelzer & Melnick, 1996]; b – [Fooden, 2006]; c- [Caldecott, 1986b];
d- [Crockett & Wilson, 1980]; e- [Oi, 1996]; f – [Caldecott, 1986a];
g- [Ridley, 19

Chapter 2: Temperament and Social behavior in Infant Macaques

Overview

The studies presented in this chapter use archival data for infant pigtailed macaques (*Macaca nemestrina*) housed at the Washington National Primate Center (WaNPRC) Infant Primate Research Laboratory (IPRL). We used home-cage behavioral ratings to identify temperament components, and then tracked the development of temperament throughout the first 10 months of life (Study 1). We then compared temperament scores to social behavior in small play-groups (Study 2).

Part 1 – Temperament Measures

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Subjects and Housing

Infants at the Infant Primate Research Center (IPRL) in Seattle, WA were removed from their dams and placed in neonatal care immediately after birth, for either medical or experimental reasons. Subjects in this study were either control subjects in experimental studies or were placed in the IPRL for medical reasons pertaining to the dam, not the infant. Infants at the IPRL were housed individually but received 30 -45 minutes of socialization time in a play-group 5 days per week (described in greater detail below).

Infants were housed in plexiglass-front cages, generally adjacent to their social group partners. Cages contained a hanging, cloth-covered surrogate. Infants began the weaning process of transitioning from formula to biscuits and water at age 91 days; thus, subjects in this study received both diluted formula and soaked biscuits. All standard housing, feeding, and testing procedures for the IPRL are described in the IPRL research protocol [Ruppenthal & Sackett, 1992]. Throughout their time in the infant lab, subjects were monitored by a full-time staff that maintained records of their physical and cognitive development, as well as any medical procedures.

Behavioral scoring

All infants at the IPRL received daily temperament testing. We used data collected from birth through age 10 months to measure temperament. Temperament was measured 5 days per week between 9 a.m. and 12 p.m., during a daily weighing procedure. A trained tester recorded the animal's behavioral responses while being weighed. All responses were measured on 4- to 8- point Likert-type scales. The specific behaviors recorded are described in Table 2.1. For more detailed descriptions, see the standard operating procedures for the IPRL [Crouthamel et al., 2007].

Before collecting data, all new testers reviewed the standard operating procedures and observed a testing supervisor. The testing supervisor and new tester independently recorded scores for 8 consecutive days, with 80% agreement between the two scorers required to pass reliability. Reliability retesting sessions were performed in the same manner every 9 months.

Component Identification – Methods and Results

Only six of the measures recorded met assumptions of normality. These six variables were: approach, contact, exploration, vocalizations, irritability, and consolability (see Table 2.1 for definitions). We used a principal components analysis (PCA) to assess whether these measures contributed to any broader temperament components. First, multiple PCAs were run to check for structural stability of the components identified - that is, whether the same components existed at different stages of development. Variables with loading scores with absolute values greater than 0.4 were counted as contributing to a component. All components with eigenvalues greater than 1.0 were retained. This factor retention method was verified by assessing scree plots and by parallel analysis [Zwick & Velicer, 1986]. Components were rotated orthogonally with varimax rotation.

We used the PCAs from different measurement times as guides in creating composite behavior scores that corresponded to the principal components. We did not use the component scores calculated by PCA directly because we wanted to compare scores within individuals over time. Comparing scores from multiple PCAs and comparing component scores calculated from a single, sample-wide PCA were both statistically problematic. A single PCA would contain multiple measures from the same individuals, violating the assumptions of independence, whereas multiple PCAs would differ slightly in loadings and extraction values, because of sample-specific variation [Gorsuch, 1990]. Our PCAs showed that approach, contact, and exploration tended to cluster together, as did irritability, consolability, and vocalizations. Thus, we took the means of the behavior scores for these two variable groups to approximate the two components. We then mean-centered these scores on the basis of the sample-wide mean and conducted further analyses with these mean-centered scores.

Temperament scores were based on the six behavioral variables listed in Table 2.1. Each individual received a score on each variable for each month of testing (Months 1- 9). To determine the monthly score, we used the mean scores from the first week of the month. This method was chosen in order to provide a distinct “snapshot” of temperament for that month, rather than creating an arbitrary distinction between months. For exploratory analysis, we treated each month as an independent sample, and performed a principal components analysis (PCA) with the scores from each month. These multiple PCA analyses showed that the same variables tended to cluster together through time (Table 2.2). At Week 1 of Month 1, Month 3, Month 6, and Month 9, two similar components accounted for the majority of the variance (>60%). For Month 1 and Month 3, parallel analysis [Zwick and Velicer, 1986] confirmed that two components should be retained, whereas only one component and three components were significant above a randomly generated data set for Month 6 and Month 9, respectively. These differing findings indicate that there was some change in the structure and importance of these components over time. We chose to use two components, nevertheless, as these variable groupings did exist at all measurement times. However, our results should be interpreted with caution, as these traits may be better descriptors of early developmental temperament rather than temperament at older ages.

Overall, irritability, consolability, and vocalizations contributed to a single component, which we labeled *Reactivity*. Approach, contact, and exploration contributed to a separate component, interpreted as *Boldness*. These constructs were not identical throughout development, as shown in Table 2.2.

The names Reactivity and Boldness were chosen because of similarity to other trait names in the human developmental and animal literature. Both of these terms have been used to describe personality in rhesus macaques [Suomi, 1997; Weinstein & Capitanio, 2008]. Studies of human infants have shown that similar traits appear early in development [e.g., Kagan et al., 1984; Rothbart, 2007]. Moreover, these traits are present in evolutionarily distantly related animals as well. Reactivity has been identified in animals as diverse as horses and birds [Gosling, 2001], whereas differences in Boldness are seen even in invertebrates like water striders and squid [Sih & Watters, 2005; Sinn et al., 2008]. The pervasiveness of these traits across taxa supports the idea that Reactivity and Boldness are evolutionarily ancient dimensions of individual difference. This, in turn, is consistent with the idea that these traits are genetically influenced and, thus, would be observable in macaque infants as young as 1 week old, as demonstrated by our results.

Sex Differences – Methods and Results

We compared male and female behaviors using a general linear model (GLM). This method allowed us to test not only for broad sex differences for each trait but also for differences in trait combinations (i.e., high boldness and low reactivity) between the sexes. We analyzed sex differences at Month 1, Month 3, Month 6, and Month 9, using mean Reactivity, mean Boldness, and the interaction term of these two values as dependent variables and using sex as a predictor. We also examined sex differences in the extreme quartiles of each sample using t-tests. For this analysis, we looked at sex differences between infants in the top 75% and bottom 25% for each trait at 3 and 6 months, using an independent-samples t-test. These ages were chosen on the basis of our observation that the greatest amount of change occurred during this period (Figures 2.1 and 2.2).

The GLM with sex as a predictor and mean Boldness, mean Reactivity, and the interaction term as dependent variables found no significant sex differences at Month 1, Month 3, Month 6, or Month 9 (all *p*s < .1). We also examined male and female differences within the highest and lowest quartile scores for each trait. No sex differences were found at Month 3, top quartile Boldness: *t*(37) =1.65, *p* =.11; bottom quartile Boldness: *t*(37) =0.72, *p* =.47; top quartile Reactivity: *t*(36) =0.13, *p* =.90; bottom quartile Reactivity: *t*(38) =0.85, *p* =.40. There were also no significant sex differences at Month 6, top quartile Boldness: *t*(34) =1.81, *p* =.08; bottom quartile Boldness: *t*(36) =0.84, *p* =.41; top quartile Reactivity: *t*(36) =0.26, *p* =.80; bottom quartile Reactivity: *t*(37) =0.18, *p* =.86.

Change over time – Methods and Results

Hierarchical linear modeling software (HLM Version 6.0) was used to calculate individual linear growth curves for all subjects and to identify significant differences in baseline values (intercepts) or change (slopes) between individuals. We used HLM to create models with multiple observations nested within individuals and age in days as our predictor variable. We also tested a quadratic model, which included both age in days and squared age as predictors. All models had simple, random effects. Because of the large number of models tested, alpha was set at .01 for HLM analyses.

The HLM analysis of individual growth curves (based on individuals' monthly averages) indicated that although change for the group followed normative patterns, individual changes varied significantly (Table 2.4). Overall, reactivity growth curves showed a linear, negative trajectory for reactivity overdevelopment, with significant variance remaining in both intercepts and linear slopes (all chi-squares had $p < .001$, Figure 2.1). This indicates that there was significant individual difference on these items. A quadratic term did not significantly describe the group's pattern, although there was significant variance among individuals on their quadratic scores, indicating that a curve may have been a good fit for some individuals. Boldness did fit a quadratic growth curve, with scores increasing significantly over time but reaching an asymptote with greater age. This pattern can also be discerned in plot of Boldness means over time (Figure 2.2). Here again individuals differed significantly in their intercepts and in both linear and quadratic slopes, indicating that there is a great deal of individual variability in development (all χ^2 had $p < .001$).

Discussion of Temperament Findings

The results of our developmental analyses indicated that behaviors changed significantly over the course of development. On average, infants became less reactive and bolder as they grew older. These general trends toward calmer behavior and less avoidance mirror Heath-Lange et al.'s [1999] findings from a smaller study of IPRL animals and might be interpreted as habituation to the weighing procedure. In an HLM analysis, Reactivity showed a negative, linear trajectory, whereas Boldness had a positive, quadratic trajectory. These results indicate that over the first 10 months of life, infants, on average, increased in Boldness, with their rate of change slowing at later ages (Figure 2.1). The period of greatest change appears to be between about months 3 and 6 - consistent with past work showing changes in social behavior around this period [Sackett, 1966]. Infants also became significantly less reactive during this time, but the change in Reactivity did not asymptote during this period (Figure 2.2). In addition to these average patterns of change, we also found significant variability among individuals in both intercepts (initial behaviors) and both linear and quadratic slopes. Overall, then, our analyses show that behavior changes over the course of development, that these changes tend to follow a pattern, and that individuals vary significantly in their developmental trajectories.

These results fit well with the view of temperament seen in the human literature, which often describes normative changes in behavioral tendencies with development. However, such developmental change has not been fully explored in the animal behavior literature. Animal researchers often define temperament as a stable individual behavioral tendency, whereas human developmental researchers allow for significant change in temperament expression over development. For example, Kagan [1997] found that infants with extreme scores on reactivity as infants or preschoolers often became less extreme in their behaviors over time. Moreover, as Rothbart [2007; 2000] pointed out, some elements of temperament in human infants develop throughout infancy, with certain traits, such as avoidance, present at birth, and others, such as effortful control, appearing only after the first 2 years. Thus, not only are supposedly stable innate temperaments prone to change during development, other elements of temperament may appear only later, further altering the individual's behavioral tendencies. Earlier studies that traced primate behavior through development have also found change, with some behaviors in rhesus monkeys appearing to be more stable in adulthood than during early development [Stevenson-Hinde et al., 1980]. Our results contribute to a literature indicating that behavioral tendencies in young animals do not show temporal stability.

Part 2: Relationship between infant temperament and social behavior

For this study, we compared temperament scores (measured as described above) and social behavior in a sample of four-month old infant pigtailed macaques. We predicted that these temperament measures would be related to infants' frequencies of play, fear, and aggression in a social setting. In particular, based on other reports in the literature, we predicted that bold infants would display more play behaviors and fewer fear behaviors in their social groups, while reactive individuals would display more fear and more aggression than others.

Infant social behavior monitoring

In addition to receiving daily temperament tests, as described above, infant macaques at the IPRL were also observed by trained animal technicians during their daily socialization. Infants received 30-45 minutes of socialization time in a stable playgroup of 3-5 individuals 5 days per week. Infants in each social group were shaved or dye-marked to make them individually identifiable. Subjects were observed through a two-way glass window with continuous 5-minute focal follows, in a randomized order. During each focal period, the observer recorded all social behaviors, and their recipients on a keyboard with a four-digit code (as described in [Ruppenthal & Sackett, 1992]). Inter-observer reliability was maintained at 85% kappa, and tested every 6 months for all observers.

While several social behaviors are recorded during the play time, for this analysis, we focused on three behaviors of interest: social play (including wrestling, chasing, rolling, gentle biting, or joint play with a toy); social fear (fear displays including submissive postures, fear grimacing, and shrieking); and social aggression (including threat displays, such as piloerection, open mouth, or “stiff” stance, as well as threat bark or biting). Other behaviors not included in this analysis are described in Worlein & Sackett [1997]. Because subjects differed in the number of focal sessions included, behaviors were measured as rates per observation minute, and normalized before analysis.

Scores on these scales were calculated as means of the contributing variables for ages 90-120 days (Month 4). Scores were standardized within the sample. Only subjects who had Month 4 temperament scores (Part 1) and had multiple observations from a social group during this month were included in this analysis (N=68). The age distribution and sizes of social group are illustrated in Figure 2.3.

Social Behaviors Observed – Results

Groups differed in their rates of behaviors (Figure 2.4). Among the 33 social groups observed, play behaviors were observed most frequently (M=16.65 times/day/animal, SD = 8.10), followed by fear behaviors (M=0.69 times/day/animal, SD = 0.49). Aggression was observed on average only 0.03 times per observation day per animal (SD = 0.06). The rate of fear behaviors observed in a group was significantly negatively correlated with the rate of play behaviors observed in that group, when both measures were adjusted for the number of observation sessions and the group size (ρ =-0.34, p=.05). Aggression rates were not significantly correlated with play or fear behaviors (p>.05).

Individuals also differed in their rates of behaviors. Infants displayed play behaviors most frequently, at a mean rate of 37.36 interactions per observation hour (SD

= 29.90/hour). Fear behaviors were observed on average 2.58 times per hour (*SD* = 3.29/hour), while aggressive behaviors were observed rarely (*M*=0.09/hour, *SD* = 0.20/hour).

Temperament and Social Behavior – Methods and Results

We measured the relationship between temperament and social behaviors using multiple regression at the individual level. We used aggression, play, and fear behaviors as outcomes (measured as behaviors/observation minute) and we included Boldness, Reactivity, and group size as predictors. We did not include sex as a predictor because there was no sex difference in this sample for either trait (Student's t-test $p>.05$). All tests were conducted in R (v. 2.15.1), with two-tailed α =.05.

Temperament and group size together predicted a significant portion of the variance (13%) in play behaviors and fear behaviors between groups (Table 2.4). The predictors did not significantly explain the variance in aggressive behaviors, and power was low for this analysis ($1-\beta = 0.43$).

Boldness was a significant independent predictor of both play ($\beta= 0.32$, $p=.04$) and aggression ($\beta= -0.34$, $p=.03$). Reactivity was a significant independent predictor of fear ($\beta =0.02$, $p=.01$). Group size was not a significant independent predictor of any social behavior.

Discussion of Temperament and Social Behavior Findings

We compared home-cage temperament measures with social behavior metrics for 68 infant pigtailed macaques. As predicted, we found that Boldness was a significant predictor of play and aggression behaviors, while Reactivity was a significant predictor of fear behaviors.

In contrast with past empirical and theoretical work linking Boldness with aggressiveness [Sih et al., 2004], we found a negative correlation between the temperament score and aggressive behaviors in a group setting. On the other hand, we did find that Boldness had a positive relationship with social play. This unexpected finding most likely reflects the developmental stage of our subjects, who very rarely engaged in social aggression at 4 months of age [see also Worlein & Sackett, 1997; Reite & Short, 1980]. Play is vital to proper social development in primates, and play relationships may lay the foundation for the later dominance hierarchy [Poirier & Smith, 1974; Paquette, 1994]. Several studies link Boldness, or similar traits such as “confidence”, to dominance rank in adult primates [Buirski et al., 1978; Konečná et al., 2008]. Thus, the relationships observed here might actually reflect a developing dominance hierarchy in our social groups, with bolder infants holding higher ranks. Further research is needed to explore these relationships and determine whether bolder infants also are more dominant or display more aggressive behaviors as adults.

Reactivity in our sample was predictive of fear behaviors, consistent with observed patterns in human children. In humans, infant reactivity is predictive of inhibited or fearful behaviors during childhood and adult social anxiety [Kagan, 1997; Kagan & Snidman, 1999]. Activity of the hypothalamic-pituitary-adrenal (HPA) system may be the underlying physiological cause for both fear and reactivity behaviors, suggesting that the relationship observed here may simply be two manifestations of individual variation in HPA activity [Byrne & Suomi, 2002; Capitanio et al, 2004]

The analysis here measured the relationship between social behavior and temperament at one point in development. However, as demonstrated in Part 1, temperament changes within individuals in predictable ways throughout development. Social behaviors are also known to change over the course of development [Worlein & Sackett, 1997]. An interesting area for future study would be to track the developmental trajectories of these two sets of behaviors. From our results here, it seems likely that developmental changes in temperament may be closely tied to the changes in social behavior, and could possibly be a causal factor in these social developments. However, it is also possible that social experiences affect individual behavioral patterns, or that both temperament and social behavior change as the brain matures. Future studies should try to identify the relationships and potential causality of these two areas of infant development.

Overall, our results demonstrate that early-emerging temperament traits measured in a home-cage context are predictive of behaviors in a social group. Not all infants at the primate center were temperament tested, so we did not have complete temperament profiles for all social group members. Consequently, we were unable to test whether the overall temperament make-up of the group impacted the amount of social interaction within that group. However, we did observe that groups differed dramatically in their behaviors, with some groups engaging in 9 times as much play behavior, or 15 times as much fear behavior as others, controlling for observation time and group size (Figure 4.2). As group membership was stable, these differences suggest fundamental variation between groups in behavioral frequencies. These fundamental differences in behaviors between groups might be due to the age make-up of the group, but also likely are related to the mix of temperaments within the group. The findings support the idea that social group dynamic is primarily dependent on the individual behavioral tendencies of the group's members.

Conclusions

Overall, our analyses demonstrated that individual behavioral differences in Boldness and Reactivity are measurable in young animals. These traits emerge early (within one month of birth) and are identifiable throughout development. They also show predictable changes throughout infant development, Boldness increasing overall and Reactivity decreasing. Boldness was more stable throughout development than was Reactivity. Though measured in a non-social context, these temperament traits are significant predictors of infant behavior in a social setting, as well. Boldness was a significant predictor of both play and aggression in a social setting, while Reactivity was a significant predictor of fear behaviors.

Table 2.1: Description of behavioral variables and levels of measurement for infant temperament test.

Variable	Description	Scale levels
Approach	Response to the tester's approach of the home cage; degree of withdrawal or approach. Low values indicate withdrawal, high values indicate approach.	6
Contact	Response to the tester's placing a diaper-covered arm into the home cage (first initiation of contact by tester); degree or withdrawal or approach, speed of contact. Low values indicate withdrawal, higher values indicate increasing quickness of voluntary contact.	8
Capture	Removal of animal from the home cage; degree of passivity or resistance; measure of capturability. Higher values indicate more resistance.	4
Cling	Degree to which animal clings to tester's arm when carried from home cage to weigh pan. High value indicates tighter cling.	4
Exploration	Reaction to the weigh pan environment within the first 5 s of being placed in the pan; amount of activity, visual, and tactile exploration. High values indicate more exploration.	5
Irritability	Irritability during the entire weighing process, measured by fussiness, agitation, struggling, convulsive jerking, grimacing, and distress vocalizations. High value indicates more irritability.	3
Consolability	How easily soothed or calmed the animal is; degree of relaxation. High value indicates difficult to console.	4
Vocalizations	Clear auditory sounds coming from the animal during weighing; degree of distress of vocalizations. High value indicates more distressed vocalizations.	4

Table 2.2
Results of principal components analysis of behavioral measurements at Month 1, Month 3, Month 6, and Month 9. For each analysis, each individual's behavior scores from the first week were averaged. Rotated component contributions are shown. Factor loadings (bold), eigenvalues, variances explained, and reliability (Cronbach's alpha) (italicized) are reported.

		Month 1 1-7 days (n=118)	Month 3 61-67 days (n=154)	Month 6, 151-157 days (n=146)	Month 9 241-247 days (n=126)
		Reactivity			
% variance explained		*35.59*	*33.45*	*46.09*	*40.79*
Eigenvalue		*2.14*	*2.01*	*2.77*	*2.46*
Variable:	Irritability	**0.95**	**0.89**	**0.89**	**0.93**
	Consolability	**0.88**	**0.88**	**0.90**	**0.93**
	Vocalizations	**0.64**	**--**	**0.75**	**0.79**
Cronbach's α		*0.68*	*0.90*	*0.69*	*0.69*
		Boldness			
% variance explained		*27.37*	*31.86*	*21.77*	*24.26*
Eigenvalue		*1.64*	*1.91*	*1.31*	*1.46*
Variable :	Approach	**0.72**	**0.70**	**--**	**0.78**
	Contact	**0.82**	**0.85**	**0.60**	**0.91**
	Explore	**0.54**	**0.52**	**-0.89**	**--**
Cronbach's α		*0.45*	*0.47*	*0.45*	*0.63*
Total % variance explained		*62.96*	*65.31*	*67.85*	*65.05*

Table 2.3

Results of HLM analysis showing linear and quadratic models of change in behavior over time. Reactivity and Boldness were outcome variables, while age in days was a predictor variable.

	Outcome variable	
Variable	*Boldness* (N=164)	*Reactivity* (N=164)
	Fixed Effects	
Intercept		
Coefficient	3.90**	1.69**
SE	0.05	0.04**
T ratio	83.19**	46.17**
Slope (linear)		
Coefficient	0.01**	-0.001**
SE	0.0002	0.0001
T ratio	27.79**	-6.59**
Slope (quadratic)		
Coefficient	-0.00003**	0.0
SE	0.000004	0.0
T ratio	-6.75**	1.65
	Variance	
Intercept: χ^2	4729.56**	3835.94**
Slope (linear): χ^2	2240.68**	2167.91**
Slope (quadratic): χ^2	5116.46**	2490.36**

* p< .01, ** p<.001

Figure 2.1: Mean Reactivity over first 10 months of development; points represent daily mean score, line shows mean linear equation derived in HLM .

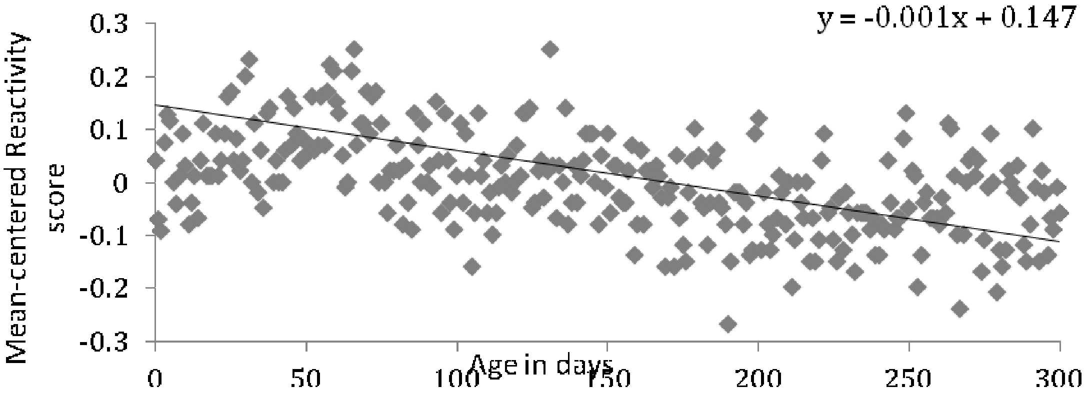

Figure 2.2 Mean Boldness over first 10 months of development; points represent daily mean score, line shows mean quadratic equation derived in HLM s.

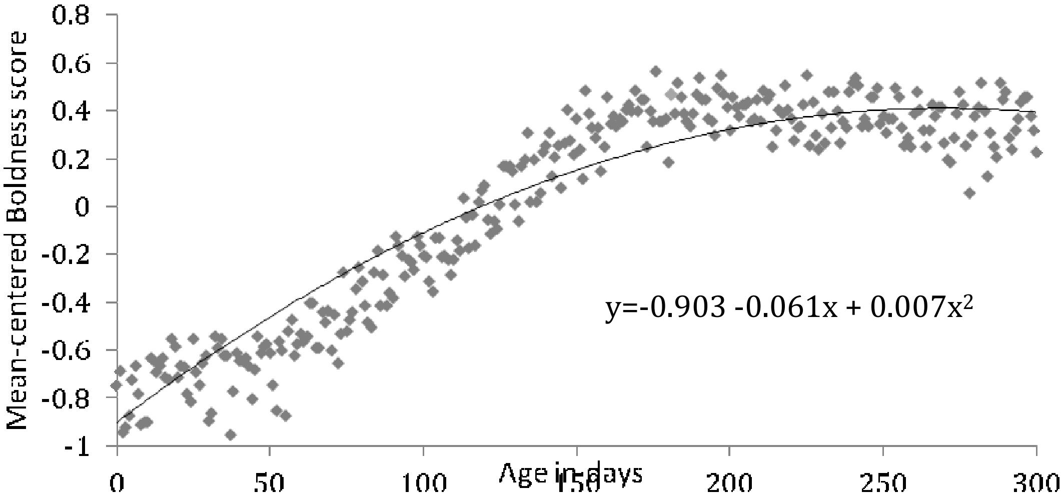

Figure 2.3: Age (a) and group size (b) distributions

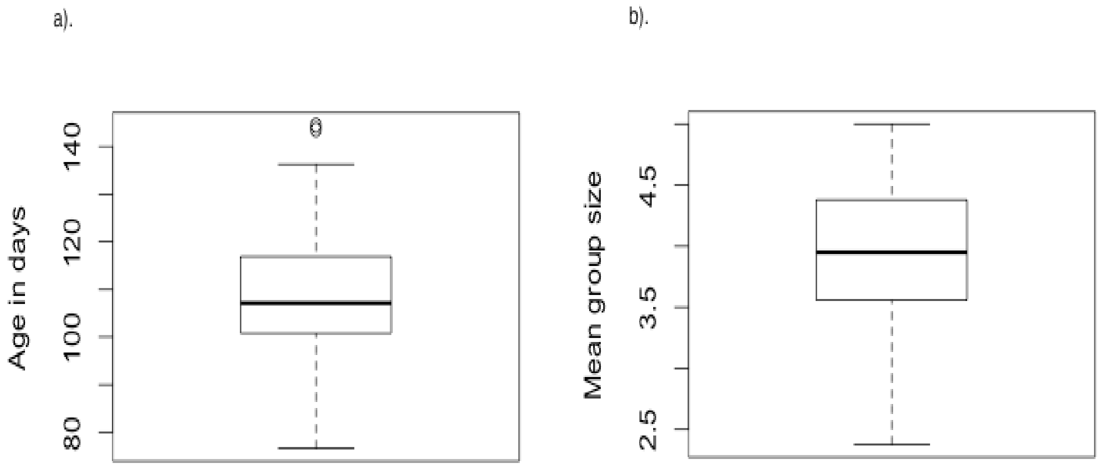

Figure 2.4: Histograms demonstrating the number of fear, play, and aggressive behaviors observed on average in one observation day for each group (adjusted for group size).

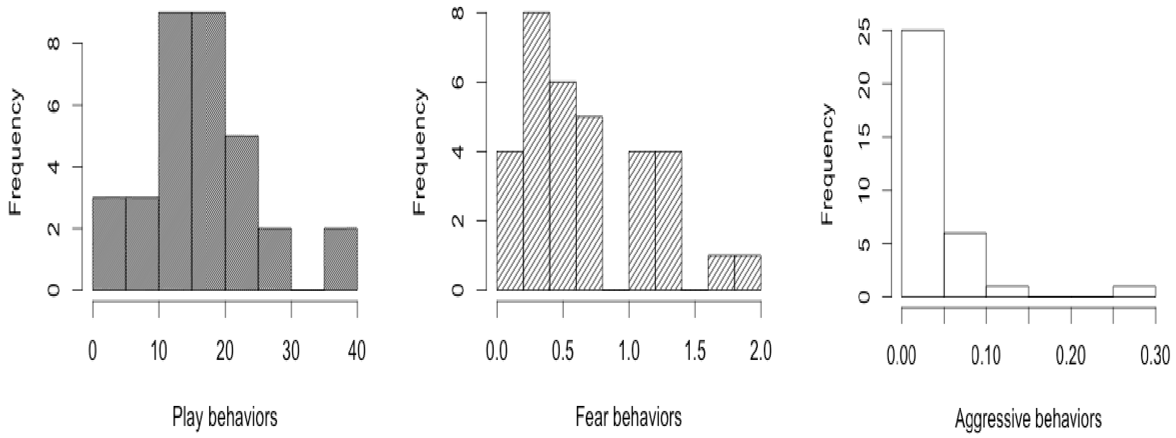

Table 2.4: Multiple regression analysis of group size and standardized temperament scores on social behaviors observed.

	Play			Fear			Aggression		
Variable	B	*SE B*	*p*	B	*SE B*	*p*	B	*SE B*	*p*
Boldness	0.15	0.07	.04 *	<0.001	0.01	.93	<0.001	<0.001	.03*
Reactivity	-0.04	0.07	.57	0.02	0.01	.01**	<0.001	<0.001	.20
Group size	-0.07	0.09	.46	0.002	0.01	.79	<0.001	<0.001	.50
R^2	0.13			0.13			0.07		
F(3, 63)	3.10 (p=.03*)			3.30 (p=.03*)			1.58 (p=.20)		
Cohen's f^2	0.15			0.15			0.07		
Observed power	0.74			0.74			0.43		

Chapter 3: Structure and Stability of Personality in Adult Macaques

Overview

In this chapter, we present several studies that used rapid cage-front behavioral observations to identify personality components in adult macaques. We compared scores on these components among three species of macaques, and found that species and sex differences were consistent with behavioral differences reported in social contexts (Part 1). We also examined the stability of personality components within individuals over time, and found that they were repeatable. Despite this within-individual stability, population-wide personality changed in predictable ways with age (Part 2).

Subjects and Housing

Subjects for this project were macaque monkeys housed at the Washington National Primate Research Center (WaNPRC) in Seattle. Subjects include pigtailed macaques (*Macaca nemestrina*), longtailed macaques (*M. fascicularis*), and rhesus macaques (*M. mulatta*). Most subjects were mother-reared, but some were reared in the WaNPRC infant primate research laboratory.

Animals were housed indoors in stainless steel cages appropriate for their weight, as specified by USDA Animal Welfare Regulations. In this study, subjects either were individually caged or had grooming contact [Crockett, 1997] with a partner. All subjects had visual access to other conspecifics in their rooms.

Room sizes varied and typically housed 12 to 30 monkeys, generally all of the same species. Animal rooms were maintained on a 12:12 h light:dark cycle. The ambient temperature was 22.2° to 25.6° C with a relative humidity of 30% to 50%. The subjects received enrichment as specified in the Environmental Enhancement Plan such as a portable toy and a foraging device hung externally on the cage, and fresh produce or foraging opportunities seven days a week. Commercial monkey biscuits were provided twice daily – once before 9:00 am and once after 2:00 pm, and water was provided *ad libitum* from water spigots.

The WaNPRC is a biomedical research facility, and as such, some of the animals used in our personality identification studies were research subjects. Though animals were in good health at the time of their assessment, the monkeys were subjects in a wide variety of studies, including AIDS-related research, developmental biology, functional genomics, immunology, reproductive biology, neurophysiology, and various primate disease models, among others (http://www.wanprc.org). Some monkeys were held in reserve for upcoming studies or assigned to timed breeding projects. Consequently, animals varied in the extent to which they experienced invasive procedures associated with biomedical research. The animal records available to us did not provide all specific project-related procedures performed on all subjects. We have no evidence to suggest that there is systematic variation between project-specific research experience and the variables examined in this study.

Rapid behavioral observations

The pilot study for a rapid, cage-front personality test was developed by Kathy Bentson, Carolyn Crockett, and Jim Ha. Data collection with these methods occurred from 2003 – 2006 [Bentson, 2003]. All monkeys were individually-housed at the time of the testing. During a 4-minute observation period, the observer (K.B.) recorded frequencies of 37 variables of interest using a PDA hand-held device. The observer stood directly in front of the subject's cage, but did not interact with it in any way. Prior to each 4-min cage-front observation, the tester stood in the middle of the room for 4 minutes. The observer was not known to the monkeys in any context besides personality testing.

Several behaviors, including posture/locomotion, facial/vocal expression, cage position, and responsiveness to the observer, were scored by instantaneous sampling every minute. Other behaviors were measured by whether or not they occurred during each minute of the observation period. At the end of each minute, the tester also made subjective assessments (i.e., ratings) of personality, as a means of validating and interpreting the behavioral measures during analysis. The tester assessed which of seven labels– "confident," "aggressive," "tense," "friendly," "fearful," "active," and "inactive" – best described the subject's behavior over the past minute. "Active" or "inactive" were used primarily when other personality ratings did not apply. All behavioral measures and subjective assessments occurred once each minute, so all variables ranged from 0-4. All behavioral variables measured in the pilot assessment, along with definitions, are described in Table 3.1.

Between 2003 and 2006, all monkeys, including pigtailed, longtailed, and rhesus macaques, received 1-4 personality assessments, depending on how long they stayed at the primate center and whether or not they were assigned to a project during that time. Monkeys that entered the WaNPRC during the three-year period were tested beginning 8 weeks after arrival, and typically retested about 10-12 weeks later, and then annually. Monkeys that were already at the primate center at the start of the three-year period were on an annual test schedule.

Part 1 - Personality component identification

As described in Chapter 1, both principal components analysis (PCA) and factor analysis (FA) are commonly used in the literature to identify personality traits. PCA was chosen over FA because these analyses were exploratory, and because the structure of the variance within the dataset was unknown. PCA is not appropriate for identifying latent "traits", but, rather, identifies suites of inter-related behaviors [Dunteman, 1989; Joliffe, 2002]; consequently, we refer to our results as "personality components" throughout.

When identifying personality scores from an initial list of behavioral variables, we performed a stepwise process to obtain the final list of components. Variables were removed if they did not load on any component at the 0.4 level, if they had extraction communalities < 0.5, or if they only contributed to one component which had no other variables contributing.

After establishing a list of variables that met the above requirements, we chose how many components to retain based on both eigenvalues (>1) and parallel analysis {Zwick and Velicer, 1986]. Components were rotated first with oblique (oblimin) rotation; in all cases, there was little or no correlation between components, so we used orthogonal (varimax) rotation to calculate the final component scores, in keeping with widespread practice. We used the regression method to calculate individual component scores. In several cases, we examined congruency between sets of scores (i.e., in split-sample analysis; to compare the scores calculated from obliquely or orthogonally rotated matrices; to compare scores calculated between different sub-samples such as species or age groups) using Tucker's congruence coefficients [Lorenzo-Sevo & ten Berge, 2006].

Adult macaque personality components - Results

PCA for the original personality test data revealed four components, which together explained about 64% of the variance in the data after rotation (Table 3.2), and incorporated 12 of the 37 behavioral variables. The same measures were identified in a split-sample validation, and the Tucker's congruence coefficients of the components on the two samples were all high (all > 0.95).

We included a comparison with the observer personality ratings to help us interpret our PCA components. The results were consistent with our interpretation of the components based on their variable make-up, and led us to name the four components Confidence, Cautiousness, Aggressiveness, and Fearfulness (Table 3.3). These names were chosen, when possible, from terms used in past studies.

Three of the four personality components we identified were similar to other named traits identified in the literature [reviewed in Freeman & Gosling, 2010]. Other studies that also used large sample sizes and similar statistical techniques have identified 3 to 6 personality traits in macaques [Capitanio, 1999; Rouff, Sussman, & Stroube, 2005; Weiss et al., 2011]. Our four components were consistent with this range. The limited social context of our study (subject responses to a human tester) suggests that our components should describe just a subset of all possible personality dimensions.

We interpreted and named our components based on similarity to other traits identified in the literature, and correlation with tester-rated personality descriptors. Where appropriate, we used component names from the list of personality dimensions identified by Freeman and Gosling in a recent review [2010]. In particular, two components were named Fearfulness and Aggressiveness, which were two of the most commonly identified traits in the literature [Freeman & Gosling, 2010]. Our first two components were less closely aligned to other dimensions described in the literature. Component 1 was interpreted as Confidence, because it describes tendencies to direct attention to the tester and reach toward the tester without threat or fear displays. The component that we named Cautiousness is similar, at the high end, to "reactivity" as used by Clarke and Mason [1988]. Monkeys scoring high on this component directed lipsmacks toward the tester while leaning or moving toward the tester. Monkeys scoring low on this component were in the front of the cage and did not change their behavior when the tester directed her gaze toward the monkey. These monkeys appear to be similar to ones described as equable or easy-going and passive [Capitanio, 1999].

Species differences - Results

Cross-species Validation

Species-specific PCAs demonstrated that the components identified from the RATR dataset existed in pigtailed, longtailed, and rhesus macaques, but with notable differences in structure. Congruence coefficients were highest for Fearfulness. Longtailed and pigtailed macaques were slightly more similar in their component structure, with structures for Cautiousness, Aggressiveness, and Fearfulness exceeding the suggested minimum congruence level of 0.85 [Lorenzo-Seva & ten Berge, 2006]. Rhesus and pigtailed macaques were least similar, with the lowest congruence on Aggressiveness (0.64). Differences in structure were mainly due to an apparent lack of importance of lipsmacks for rhesus macaques (this variable contributed to Cautiousness for longtailed and pigtailed macaques). Also, aggressive behaviors contributed to all components for rhesus macaques, while longtailed and pigtailed macaques had clearly defined "Aggressiveness" components. We proceeded with our cross-species comparison using the component scores obtained from the full sample PCA.

Species and Sex differences

The results of the GLM indicated that species and sex were both significant predictors of personality, after controlling for age and infant rearing experience (e.g., nursery vs. mother-reared). Species was a significant predictor of all four components, and sex was a significant predictor of Cautiousness and Confidence. There was also a significant species-by-sex interaction effect for Aggressiveness and Fearfulness. All main and interaction effects are summarized in Table 3.4.

Post-hoc Tukey-Kramer tests demonstrated that longtailed macaques were more cautious than other species (Tukey-Kramer 95% Confidence Interval rhesus: 0.27-0.74; pigtailed: 0.32-0.66), although rhesus and pigtailed macaques did not differ from each other (Table 3.4, Figure 3.1A). Pigtailed macaques were more confident than other species (95% CI longtailed: 0.50-0.84; rhesus: 0.15-0.56), and rhesus were more confident than longtailed macaques (95% CI: 0.08-0.55). Rhesus macaques were significantly more aggressive than either other species (95% CI longtailed: 0.01-0.51; pigtailed: 0.49-0.93) and longtailed macaques were significantly more aggressive than pigtailed macaques (95% CI: 0.27-0.63). Longtailed macaques were significantly more fearful than pigtailed macaques (95% CI: 0.01-0.39), but rhesus macaques did not differ from other species on this component. For sex main effects, males were significantly less cautious than females (95% CI: 0.002-0.24) and were significantly more confident (95% CI: 0.58-0.81, Figure 3.1B).

Examining interaction effects indicated that male pigtailed macaques tended to be less aggressive than other sex-species categories (Figure 3.2). Pigtailed males were significantly less aggressive than all other sex-species categories, including rhesus males (95% CI: 0.49-1.19), rhesus females (95% CI: 0.46-1.30), longtailed males (95% CI: 0.49-1.12), longtailed females (95% CI= 0.10-0.71), and pigtailed females (95% CI: 0.05-0.51). Pigtailed females were significantly less aggressive than rhesus males (95% CI= 0.21-0.91), rhesus females (95% CI=0.18-1.02), and longtailed males (95% CI: 0.21-0.84), but did not differ from longtailed females. Longtailed females were significantly less aggressive than longtailed males (95% CI: 0.03-0.78), rhesus males (95% CI: 0.03-0.83), and rhesus females (95% CI: 0.01-0.94). Longtailed males, rhesus males, and rhesus females did not differ from each other (all $p > 0.05$).

For fearfulness interaction effects, only the two most extreme sex-species categories differed significantly. Longtailed females were significantly more fearful than pigtailed males (95% CI: 0.01- 0.65), but no other pairwise comparisons were significantly different

Discussion of Adult species/sex differences

Overall, the species-specific PCA comparisons show that behaviors contribute to similar personality components in all three species. However, congruence coefficients indicate that component structure is most similar between longtailed and pigtailed macaques, and least similar between rhesus and pigtailed macaques. This is counter to our expectation that rhesus and longtailed macaques might be more similar given their closer phylogenetic relationship [Hoelzer & Melnick, 1996]. We found that lipsmacks are an important variable for defining behavior in longtailed and pigtailed, but not rhesus macaques. In addition, pigtailed and longtailed macaques have clearly defined "Aggressiveness" components, while in rhesus macaques aggressive behaviors are also somewhat related to Cautiousness and Confidence. The importance of aggressive behaviors for rhesus macaques is consistent with the results of our GLM, as discussed below.

As we expected, species and sex were predictors of the personality components examined, even after controlling for age and infant rearing experience. As elaborated below, our results are consistent with findings from the few past studies involving laboratory comparisons of these species. They are also consistent with reported differences in species' social behavior and socioecology in the wild, although some important field observations are lacking.

In our sample, longtailed macaques were notable for being more cautious and less confident than other species. They also tended to be more fearful than pigtailed macaques, and were intermediate in their aggressiveness. Rhesus macaques were more aggressive than other species (significantly more so than pigtailed macaques), and were intermediate in their confidence. Pigtailed macaques were much more confident and less aggressive than both other species. Confidence appears to be an especially important trait for pigtailed macaques, and an identical component may not exist in other species, based on the low between-species coefficients for these traits. The facial expression LEN

[Oettinger, et al., 2007] was not included in the PCA because it occurred only in pigtailed macaques. In an exploratory inclusion of LEN in the species-only PCA, LEN toward the observer loaded heavily with the confidence component and no others, suggesting that its exclusion understated the importance of the confidence component for this species.

The species categorizations and comparisons found in the present study are consistent with past work. In a similar laboratory environment, Clarke and Mason [1988] described longtailed macaques as more "reactive" than other species and rhesus as more "hostile." In captive social groups, rhesus macaques engage in more frequent and more severe intergroup aggression than other species [Bernstein et al., 1983; Thierry, 1985; Ruehlmann et al., 1988; Thierry, 2000;]. Both longtailed and pigtailed macaques show comparatively less social aggression, lower influence of kinship in determining female rank, and a higher frequency of clasping and appeasing behaviors than rhesus [Bernstein et al., 1983; Thierry, 2000; Maestripieri, 2005]. In captivity, for example, pigtailed macaques' hourly rates of aggression are about half those of rhesus macaques' [Bernstein et al., 1983], whereas their reconciliation rates are twice as frequent [Gouzoules & Gouzoules, 2000]. In captive groups, rhesus macaques received more than twice as many wounds as pigtailed macaques [Ruehlmann et al., 1988]. Some of these differences may be related to differences in captive conditions and in field study methodologies. However, the directions of these differences are consistent in most comparative studies [Thierry, 2000], and fit with our finding that rhesus macaques are more aggressive even when individually housed.

Some evidence suggests that pigtailed macaques are less aggressive and show higher rates of affiliative behavior than longtailed macaques [Thierry, 2000]. Male-male affiliative behaviors in socially housed pigtailed macaques, lead to increased cooperation and intragroup tolerance relative to rhesus macaques [Maestripieri, 2005]. Pigtailed macaques also appear to have a larger affiliative vocabulary than some other species, including a species-specific affiliative greeting, the "LEN" [Oettinger et al, 2007], and extensive use of male-male affiliative eyebrow raises [Maestripieri, 1996]. Anecdotal reports also suggest that pigtailed macaques are "friendlier" than other macaque species, and more easily habituated to human presence in captivity. Oettinger et al. [2007] found that captive pigtailed macaques were likely to direct the LEN greeting towards human observers. In Sumatra, wild-caught pigtailed macaques were more easily trained to complete a task (picking coconuts) than longtailed macaques [Crockett & Wilson, 1980]. Again, these differences are all consistent with our categorization of pigtailed macaques as more confident and less aggressive than other species.

Whereas our study investigated captive macaques, some of the trends we identified show interesting parallels to ecological species differences in wild populations. One potential difference between the species in the wild, for example, is predation risk. Although no studies have directly compared predation rates among these species, it is likely that longtailed macaques are under greater predation pressures, as they are smaller than the other two species and occupy habitats with many possible predators [Crockett & Wilson, 1980; Caldecott, 1986b]. Cheney and Wrangham [1987] presented estimated predation rates for numerous primate species gathered directly from field investigators. The only macaque species included was the longtailed macaque, and it had one of the highest estimated suspected predation rates, second only to the vervet monkey (*Cercopithecus aethiops*). We propose, from the limited evidence available, that of the three species, longtailed macaques are most vulnerable to predation (most likely by felids, but crocodilian predation has also been reported [Galdikas and Yaeger, 1984]). Although primarily arboreal, longtailed macaques are edge species and come to the ground along rivers and forest margins [Crockett & Wilson, 1980], where they are more likely to be vulnerable to predators. The larger-bodied pigtailed macaques, given their quiet behavior and smaller group size [Crockett & Wilson, 1980], may be less likely to attract predators. Pigtailed macaque groups also have much larger home ranges, usually in upland primary rainforest, making their location much less predictable to a predator [Crockett & Wilson, 1980; Caldecott, 1986b]. It is difficult to generalize predation rates on rhesus macaques across their large geographical distribution. Compared to longtailed and pigtailed macaques, though, rhesus favor open habitats where they are likely to be terrestrial [Fooden, 2006], and thus may benefit from defending themselves by aggressive confrontation with some smaller predators.

Past work has suggested that reactivity, fearfulness, or novelty-aversion may be adaptive under conditions of greater predation pressure [Sih et al., 2004; Dingemanse & Réale, 2005; Réale et al., 2007; Smith & Blumstein, 2010]. This suggests that the personality type most typical of longtailed macaques in our sample – high Cautiousness and high Fearfulness scores – might be adaptive when predation risk is high. Similarly, the extreme aggressiveness we identified in rhesus macaques could be related to the adaptive benefit of aggressive troop defense strategies in the wild.

We also noted some sex differences. We found that females were significantly more cautious and less confident towards humans than were males, which is consistent with past work: Female rhesus macaques are less “confident” and more “excitable” than males [Stevenson-Hinde, et al., 1980], and longtailed and pigtailed macaque females are more novelty-averse than males [Montgomery et al., 2005]. Others have reported that the direction of sex differences in related traits varies by species [e.g., hyenas and humans, Gosling & John, 1999; rats and cichlids, Schuett et al., 2010]. This variability in findings is partially explained by the difference in the traits described, and partially related to species-specific differences. Males are the dispersing sex in macaques, [Melnick & Pearl, 1987], which might make relatively lower cautiousness and novelty aversion especially adaptive for males in leaving their home troops and integrating in new social groups.

Males in many species are more aggressive than females [Schuett et al, 2010]; however, in our sample the trend varied by species. Although longtailed males were more aggressive than longtailed females, rhesus macaques showed no significant sex difference, and pigtailed macaques showed a significant difference in the opposite direction. This lack of a main Aggressiveness effect in males may reflect a sex difference in response to the human observer overall. Males overall were also significantly more confident, less cautious, and had a non-significant tendency to be less fearful. Together, these findings suggest that male macaques in these housing conditions are more confident and comfortable with the human observer than females.

Species and sex only explained a small proportion of the variance in personality. All significant relationships had small effect sizes (Table 3.4), suggesting that much of the individual variation in personality remains to be explained. Within any species, individuals should vary on every trait, with some being more aggressive, some more confident, etc. Thus, much of the variance in personality is expected to exist on the individual level, not the species level. Considering that these species are closely related and have similar social systems (all are on the aggressive end of the despotic-egalitarian continuum [Thierry, 2000]), it is actually surprising to find as much personality differentiation as we see here.

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Part 2 - Personality change over the lifetime in macaques

In addition to identifying personality components and sex differences, we were also interested in measuring how personality changes over the lifetime, as described in Chapter 1.

Here, we used our personality-tested captive population to identify population-wide patterns of change over the study period, and the extent to which these changes were related to age, sex, and experiences besides age – especially tenure in the current primate facility. We predicted that, as in humans, pigtailed macaques' personality would show population-wide trends of change with age. We believed that tenure might affect personality as animals habituated to individual caging and proximity of humans at the primate facility, as habituation is well documented in macaques [Capitanio et al., 2006; Crockett et al., 1993, 1994]. Relative to longtailed or rhesus macaques, pigtailed macaques at WaNPRC for at least a year scored high on Confidence and low on Cautiousness (Part 1). We were interested to learn whether Confidence increased and Cautiousness decreased as the animals habituated to the facility, and whether there were any additional changes with increasing time there. Finally, we predicted that, as in previous studies, individuals would differ in their personality consistency, as demonstrated by a significant random effect of individual ID in our model.

Methods

Subjects and Housing

The sample used in this analysis included 293 mother-reared pigtailed macaques (*Macaca nemestrina*) that were at least 4 years old at time of first testing. The subjects were a subset of those used in the study above (Part 1). We restricted our analysis to the species with the largest sample size, and excluded nursery-reared subjects to reduce the number of variables in our analysis, and an independent analysis found nursery-reared subjects to differ somewhat from mother-reared macaques in levels of identified personality components.

Prior to arriving at WaNPRC, subjects were housed in various domestic and international breeding facilities where they were typically housed outdoors in social groups. The majority were captive born in Bogor, Indonesia or in Louisiana, and were of captive born Sumatran genetic stock. Details of individual animals' early life experiences were generally unknown, but they were assumed to be mother-reared. Although they may have occasionally experienced caged indoor laboratory housing in the prior facilities, we considered that the move to the WaNPRC facility represented a significant change in the social and physical environmental conditions for these animals. To capture the effect of experience at the WaNPRC biomedical research facility, we used the variables "tenure at first test" and "time elapsed since first test," described below.

Statistical Methods

Each monkey in our sample received two to four tests over the course of three years. Monkeys that entered the WaNPRC during the three-year period (N = 140) were tested beginning 8 weeks after arrival, and typically retested about 10-12 weeks later, and then annually. Monkeys that were already at the primate center at the start of the three-year period (n = 153) were on an annual test schedule. Our use of growth curve modeling allowed us to combine data for individuals with different numbers of tests into a single, population-wide model [Rogosa et al., 1982]. Such models can estimate population-wide patterns of change even when individuals differ in their number of samples.

In the analysis in Part 1, we used only a single observation for each individual (the first test conducted when the subject had been at the facility for at least a year), and did not attempt to assess the repeatability of the measures. Given the goals of the present study, we wanted to make sure that the structure of the personality components was the same at each of the testing periods within pigtailed macaques before proceeding. To do this, we performed PCAs, using the twelve variables previously identified, and specifying four components. We performed a separate PCA for each of the first three behavioral observation sessions. We compared the structure of the orthogonally rotated component matrices for the first, second, and third tests using Tucker's Congruence Coefficient [Lorenzo-seva & ten Borge, 2006]. The fourth test was not included in the component congruency analysis because of small sample size. We also compared all three tests to the structure of the full-sample PCA from our previously published study, which included a much larger number of subjects (n=899), and subjects from three species of macaque, including some monkeys that had been nursery-reared.

We found that all comparisons between observation periods were congruent, exceeding the minimum congruence level of 0.85 suggested by Lorenzo-seva and ten Borge [2006]. In other words, this analysis shows that the same personality components existed for the first, second, and third tests. To maintain maximum consistency with our past work, we chose to calculate individual component scores for each test using the same methods as in our 2013 publication. We used the regression method to calculate individual scores, specifying the same equation values as in our previous analysis. We used SPSS 18.0 (IBM, 2008) for these analyses.

Repeatability analyses – Methods and Results

In addition to our model fitting, we calculated repeatabilities, or short term stabilities, for each of our personality components to compare to those published elsewhere in the literature. In the interest of maximizing comparability, we calculated repeatability using both Intra-class correlation (ICC) [Bell et al., 2009] and Pearson's correlations between tests [Freeman & Gosling, 2010]. These analyses were conducted in R 2.15.2 using version 2.1 of the "ICC" package.

Measuring repeatability using ICC, we found that Confidence and Cautiousness had fairly high repeatability, while Fearfulness was slightly less repeatable, and Aggressiveness was not very repeatable (Table 3.5). We obtained very similar values when using mean Pearson's correlations. The repeatability scores from ICC of three of our components (Confidence, Cautiousness, and Fearfulness) exceeded the mean repeatability of 0.37 reported in Bell et al.'s meta-analysis [2009]. Aggressiveness, with a repeatability of only 0.28, was our least repeatable component. Our test-retest correlation values also compared favorably with those reported in the primate literature, as reviewed by Freeman and Gosling [2010]; Confidence, Cautiousness, and Fearfulness were within their reported range of 0.35-0.88, although all were smaller than their weighted average of 0.58. Aggressiveness was, again, the least repeatable component with a test-retest correlation of just 0.28. In contrast, Aggressiveness tended to be among the most repeatable traits in other studies [Bell et al., 2009]. The discrepancy with our results is likely due to limited variance in our measure of Aggressiveness, which reduces ICC. Pigtailed macaques showed lower average scores on both Aggressiveness and Fearfulness, and less variance than longtailed and rhesus macaques.

Population-wide model – Methods

To investigate population-wide patterns of change, we fit linear mixed-effect models to each component score with the random effect of subject ID, and a set of predictors. Predictors included sex, age upon arriving at the current primate facility ("entry age"), tenure at the current primate center at the time of the first personality test ("1st test tenure"), and time elapsed between the first personality test and subsequent tests ("time elapsed"). All variables were measured in years. These predictors were chosen because they were not strongly correlated, but together encoded information on trends that occurred with age and with tenure at the facility. Entry age and 1st test tenure were correlated at $\rho = -0.22$, while the other variables were uncorrelated ($|\rho| < 0.10$). Although animals sometimes entered the current primate facility long before they received a personality test, entry age was highly correlated with the age at which they received this test ($\rho = 0.81$). The summed effects of all three predictors are equivalent to an animal's age at its current test, while the sum of 1st test tenure and time elapsed gives the animal's tenure at its current test. Therefore, to examine the effect of age while controlling for tenure, we looked at the only predictor that contributes to age but not to tenure (entry age). We interpreted a significant effect of entry age as a personality change purely related to age and experience in previous facility, while the effects of 1st test tenure and time elapsed reflected the summed effect of increasing age and increasing time spent at the current facility. A significant effect of 1st test tenure without a significant effect of entry age suggests that experience, or time at the current facility, is the main predictor of a personality component. The effects of time elapsed were interpreted based on their parameter values, and whether they more closely matched the size and direction of the parameters for the other components.

We examined only linear effects here, and included the interactions of each predictor with sex. We also tested the interaction effect of entry age and 1st test tenure to ensure that there were no unexpected developmental effects for younger or older animals entering the primate center. As no significant interaction effects were found, this term did not appear in any of our final models. All distinct subsets of effects were examined, under the usual constraint that no subset may contain an interaction unless it also contains the main terms. This resulted in a total of 35 models. All models were fit with R (2.15.2), using version 3.1-108 of the "nlme" package [Pinheiro et al., 2010].

The explanatory power of models was judged by the Akaike Information Criterion with small-sample correction (AICc, [Hurvich & Tsai, 1989]). As p-values can be inaccurate for nested data, this approach is preferable [Pinheiro & Bates, 2000]. Because of the large number of models compared and the real possibility that there would be multiple models with near-minimal AICc values, we followed a model-averaging approach as described by Burnham and Anderson [2002]. Each model is assigned an

Akaike weight inversely proportional to the exponential of its AICc value, and predictions are averaged across all models using these weights. This approach avoids overly privileging the single "best" model if it has very close competitors in AICc values, and has repeatedly shown superior predictive performance to the best-model approach [Burnham & Anderson, 2004]. Model averaging was performed in R (2.15.2) with version 1.27 of the "AICcmodavg" package.

For heuristic purposes, we assessed the goodness of fit of our model-averaged predictions using classical R^2. To assess the significance of each individual parameter, we again followed Burnham and Anderson [2002]. We examined the subset of models containing that parameter but not containing any associated interactions. The value and confidence intervals for this parameter were then found by averaging across this subset, using renormalized Akaike weights. If a value differs significantly from zero, this indicates that the parameter has a significant effect on the response in the most informative models that include it.

Model of population-wide change

A mixed-effects model was better than a repeatability measure for explaining within-individual variation in component scores. We identify the best fitting models for each personality component (identified by lowest Akaike weight) in Table 3.6, along with the significant predictors within that model. We briefly discuss trends in significant predictors below.

Population-wide model – Results

The best-fitting models for population-wide trends explained much of the variance in Confidence and Cautiousness, but not in Aggressiveness or Fearfulness.

Specifically, the best-fit model for the population trends explained 31% of the variance in Confidence and 18% of the variance in Cautiousness, but only 5% of the variance in Aggressiveness and 3% of the variance in Fearfulness (Table 3.6). These R^2 values increased dramatically when individual ID was added as a predictor variable. When ID was included, all models predicted >50% of the variance in the personality components.

There were mean-level differences in personality components within our samples based on sex. Males were significantly more Confident, but less Cautious than females.

There were also several directional relationships between our temporal measures (entry age, 1st test tenure and time elapsed) and personality. Entry age was a significant predictor of Cautiousness and Aggressiveness (Table 3.6). Animals entering at a younger age tended to be more Cautious but also less Aggressive (Unstandardized Coefficients of predictors are given in Table 3.7). For Confidence, there was a significant, disordinal interaction between entry age and sex. Females' predicted Confidence did not vary with increasing entry age, while male Confidence decreased with increasing age at entry.

Tenure at first test was a significant predictor of Confidence and Cautiousness. Animals that had been at the current facility longer at the time of their first test were less Cautious and more Confident. There was a significant, disordinal interaction effect on Confidence between 1st test tenure and sex. Predicted Confidence increased with increasing 1st test tenure in females, whereas it decreased slightly in males.

Time elapsed between tests was a significant predictor of Confidence and Fearfulness, but not of Cautiousness or Aggressiveness. Confidence and Fearfulness both increased with greater time elapsed between personality tests, and there were significant, ordinal interaction effects on both traits between time elapsed and sex; as time elapsed increased, predicted scores increased more strongly for females than for males. As a result, females tended to diverge from males on Fearfulness, and converge toward them on Confidence, as time elapsed increased.

Discussion of population-wide Patterns of Change

Our results suggest that, for the animals in this sample, both age and experience at the primate center predict personality. After controlling for the effects of tenure, the relationships observed between entry age and Cautiousness and Aggressiveness demonstrate that personality tends to follow some predictable changes over the lifespan of pigtailed macaques. Macaques entering at an older age were less Cautious and more Aggressive. These patterns occurred independently of experience at the primate facility, as entry age was largely uncorrelated with tenure at the facility, and there were no significant age-by-tenure interaction effects. These results are consistent with some age-related patterns of change observed in humans; the increase in Aggressiveness might be analogous to the commonly cited increase in social dominance with age [Roberts et al., 2006], and the decrease in Cautiousness parallels a decrease in Neuroticism in humans as they grow older [McCrae et al., 2000]. Some recent work indicates that behavior in rhesus macaques varies with entry age, in that study measured as entry into indoor housing from outdoor housing [Gottlieb, Capitanio, & McCowan, 2013].

Experience at the current primate facility was a significant predictor of both Cautiousness and Confidence, with animals being less Cautious and more Confident with increasing tenure at 1st test and more Confident with greater time elapsed between tests. This pattern suggests that most decreases in Cautiousness occur in a fairly brief period after arrival at the primate facility, while increases in Confidence occur on a longer time-scale. This pattern of change in Cautiousness is consistent with previously identified habituation responses in macaques. Past studies have demonstrated that, in rhesus macaques, behaviors and physiological measures become more stable after about 3 months in a given housing situation [Capitanio et al., 2006]. Urinary cortisol levels also continue to decline for more than a year after arrival at a new primate center in adult longtailed macaques, *M. fascicularis* [Crockett, et al., 1993]. The changes in Confidence identified here appear to occur on a longer timeframe than previously identified habituation changes. Recent work suggests that captivity alters behavior differentially across species [Mason et al., 2013], and the relationships between tenure and personality described here might be unique to pigtailed macaques. Some studies suggest that pigtailed macaques are receptive to human interactions. For example, pigtailed macaques are more neophilic than some other macaque species [Montgomery et al., 2005], are likely to direct social behaviors towards human observers [Oettinger et al., 2007], and are more easily trained to perform some tasks than longtailed macaques [Crockett & Wilson, 1980]. Comparative studies are needed to establish whether tenure at current facility is an important predictor of personality in other captive species. Based on the tenure finding, we encourage other investigators to include similar factors in their models of personality stability.

The patterns of change for Fearfulness in our study were more difficult to interpret than those of the other personality components. Fearfulness increased with time elapsed between tests, but not with other predictors. This unusual pattern might suggest that there are opposite directional effects of increasing age and increasing time spent in the facility (Table 3.7), which cancel out for monkeys within their first months or years at the primate facility, when physiological effects of habituation are occurring [Capitanio et al., 2006; Crockett et al., 1993]. However, after this initial period, the effects of further habituation appear to decline, and Fearfulness begins to increase again, perhaps due to sensitization for other reasons.

There were mean-level sex differences in Confidence and Cautiousness in our sample. In both cases, the differences were consistent with the sex differences we identified previously (Part 1). Males were more Confident towards humans and less Cautious than females. In addition, we identified several sex interaction effects, which suggested that females exhibit more change in their Confidence and Fearfulness scores with respect to tenure, but less change in Confidence with respect to entry age than do males. This latter interaction result must be interpreted with caution, as the male and female distributions for entry age differed considerably, leading to a correlation of 0.47 between entry age and sex. More females entered the primate center at older ages, while most males entered as young adults. Despite these issues of sampling validity, these effects are consistent with the theory that males have more stable personalities than females. Some researchers have suggested that males should be more stable in traits such as aggressiveness, which are strongly linked to male-specific hormones [Wingfield, 1994; Andrew, 1972], while others have suggested that sexually selected traits would be more stable in males than in females [Kokko, 1998; Garamszegi et al., 2006]. Such sex differences in personality change deserve further study.

Including individual ID in the model greatly increased the amount of variance explained to 51%-70% (Table 3.6), but a large amount of variance remained unexplained by either ID or the time-related predictors, indicating that individuals differed in the direction and rate of change of their personality scores over testing. The variance explained by individual ID is related to individual differences in intercept, while the unexplained variance can be interpreted as variation due to differences in individual slopes. Several other studies have noted that the repeatability or changeability of personality scores differ from one individual to another. In some cases this variability is considered a distinct personality trait, “consistency” [Dingemanse et al, 2010; Bell et al., 2009] or “intraindividual variability” [Stamps et al., 2012]. Similar individual differences in personality stability or consistency have been described in humans (reviewed in [Roberts & Mroczek, 2008]).

The relatively poorer model fit for Aggressiveness and Fearfulness and the lower unexplained variance for Confidence and Cautiousness may reflect slight differences in genetic contributions to personality between breeding facilities as well as differences in experiences before and after arrival at the current facility. For example, climate, size and composition of groups, animal density, substrate, and diet likely varied among breeding sites. Similarly, assignment of monkeys to a wide variety of projects after arrival influenced such factors as the number and type of veterinary and research procedures, room size, and number of moves within the facility that were experienced by each monkey. Since personality develops over time with interplay between genes and environment, it is remarkable that in spite of these variations in before- and after-arrival conditions, there were identifiable population-wide changes in some personality variables.

The sample used in this study consisted of captive animals that were typically mother-reared in outdoor groups. These animals are representative of pigtailed macaques held in captivity in the United States and we feel confident that our large sample allows us to generalize to this population. While our research is consistent with the literature in demonstrating that personality changes with age and experience, the patterns of change described here may be specific to laboratory animals with backgrounds similar to our subjects'. Further study of behaviors in the wild would be needed to assess whether or not personality changes in similar ways in wild animals.

Conclusions

In this chapter, we showed that personality can be measured in adult macaques using a rapid cage front behavioral observation. These observations gave a similar result to using subjective tester ratings. The scores derived from these tests were stable within individuals to a similar extent as other personality scores reported in the literature. However, we also showed that these scores change predictably with age and experience. This result, combined with our results on changes in infant temperament in Chapter 2, demonstrate that personality in macaques follows similar developmental trajectories as in humans, and suggests that researchers should consider the effects of age on personality in future studies.

In addition, we also demonstrated that personality differs between closely related species of macaques. The differences in personality identified in our study were consistent with observations of species differences in social behavior in other contexts, consistent with our hypothesis that personality and social behavior are closely linked. In the following chapter, we further explore this potential linkage.

One unexpected finding of here was that sex differences observed in adult personality were not in the directions hypothesized. Together with the lack of sex differences in infants in Chapter 2, this suggests that the home cage test does not capture some sex-typical differences observed in a social context.

Table 3.1: Description of variables measured in pilot personality testing. Coding is described as either "Point" (behavior recorded once a minute at a specified time; instantaneous sampling) or "One-Zero" (tester recorded whether or not behavior occurred any time in past minute). Point-score variables involved, (1) cage position, (2) degree and type of responsiveness to the observer or other monkeys, (3) posture/locomotion, and (4) facial/vocal expression. These categories were scored on the 15-, 30-, 45-, or 60-second interval, respectively. Related point score variables are grouped together by number in the Coding column. All scores range from 0-4. The behaviors listed in bold significantly contributed to personality components (see below for details on inclusion criteria).

Behavior	Description	Coding
Back of cage	Monkey was positioned in back 1/3 of cage.	Point (1)
Front of cage	Monkey was positioned in front 1/3 of cage.	Point (1)
Middle of cage	Monkey was positioned in middle 1/3 of cage.	Point (1)
Attention to others	Attention of monkey, as evaluated by eyes, was focused on conspecifics.	Point (2)
Attention to tester	Attention of monkey, as evaluated by eyes, was focused on observer.	Point (2)
Back to tester	Monkey was turned with back to tester	Point (2)
Ignore	Attention of monkey, as evaluated by eyes was ignoring the observer and conspecifics.	Point (2)
Lean or approach tester	Monkey leans or moves toward the observer, but does not lunge.	Point (2)
Lunge	Monkey lunged at observer.	Point (2)
Move away	Monkey leans or moves away from observer.	Point (2)
Crouch	Monkey was crouched.	Point (3)
Lie	Monkey was lying on floor of cage.	Point (3)
Locomote	Monkey was moving around cage.	Point (3)
Sit	Monkey was sitting on floor of the cage.	Point (3)
Stand on two legs	Monkey was standing on hind legs (without locomoting).	Point (3)
Stand on three or four legs	Monkey was standing on three or four legs (without locomoting)	Point (3)
Grunt	Monkey grunted.	Point (4)
LEN to other monkey	Monkey produced "LEN" facial expression (Lips forward, Ears back, Neck extended), directed toward a conspecific.	Point (4)
LEN to tester	Monkey produced LEN toward observer.	Point (4)
Lipsmack to other monkey	Monkey showed lipsmack toward conspecific.	Point (4)
Lipsmack to tester	Monkey showed lipsmack toward observer.	Point (4)

Open mouth	Monkey showed open mouth.	Point (4)
Quiet face	Monkey showed quiet face (mouth closed, no lip or jaw movement).	Point (4)
Grimace	Whether or not monkey showed fear grimace to observer.	One-Zero
Shriek	Whether or not monkey shrieked.	One-Zero
Grind teeth	Whether or not monkey ground teeth, without eating.	One-Zero
Threat	Whether or not monkey made a threat display (open mouth threat, lunge, and/or stamping foot with eye contact) to observer or conspecifics	One-Zero
Reach	Whether or not monkey reached out of the cage.	One-Zero
Avert gaze	Whether or not monkey averted gaze from observer (direction of gaze moved away from observer as observer directed eyes toward monkey).	One-Zero
Food	Whether or not monkey consumed food.	One-Zero
Groom	Whether or not monkey self-groomed.	One-Zero
Object	Whether or not monkey manipulated an object on or in the cage	One-Zero
Scratch	Whether or not monkey scratched self.	One-Zero
Shake body	Whether or not monkey shook its body.	One-Zero
Shake cage	Whether or not monkey shook cage.	One-Zero
Urinate	Whether or not monkey urinated.	One-Zero
Yawn	Whether or not monkey yawned.	One-Zero

Table 3.2: Results of PCA including all species, specifying 4 components and rotated with Varimax rotation. Variables that contribute with a loading of > |0.40| are shown in bold [Joliffe, 2002]. PC is principal component. Tucker's congruence coefficients (□) for species similarities are shown at the bottom of the table.

Behaviors	PC 1 Confidence	PC 2 Cautiousness	PC 3 Aggressiveness	PC 4 Fearfulness
Front of cage	**.82**	-.22	.04	-.04
Back of cage	**-.78**	.12	-.14	.03
Reach	**.64**	.28	-.19	-.05
Lipsmack to tester	**-.45**	**.60**	-.20	.11
Quiet face	**.41**	**-.67**	-.33	-.18
Ignore tester	.08	**-.76**	-.19	-.07
Lean or approach tester	.36	**.69**	-.06	-.14
Open mouth	-.05	.13	**.79**	-.05
Lunge	.03	-.02	**.72**	-.01
Threat (tester /conspecific)	.06	.04	**.78**	-.03
Shriek	-.06	.03	-.03	**.81**
Grimace	-.04	.04	-.04	**.82**
Eigenvalue	2.21	2.04	2.01	1.42
Variance Explained	18.44%	16.98%	16.72%	11.84%
Total variance explained	18.44%	35.43%	52.15%	63.99%
Longtailed vs. Rhesus	0.79	0.73	0.76	0.94
Longtailed vs. Pigtailed	0.79	0.86	0.95	0.91
Rhesus vs. Pigtailed	0.80	0.71	0.64	0.98

Table 3.3: Correlations between tester-rated personalities and PCA-derived personality traits (N=899). Correlations significant at $p < .05$ and with a "medium" or greater effect size [Cohen, 1992] shown in bold.

Tester Rating	Confidence	Cautiousness	Aggressiveness	Fearfulness
Confident	**.21**	**-.25**	-.14	-.16
Aggressive	.06	.10	**.78**	-.07
Tense	**-.31**	.11	-.08	-.02
Friendly	**.44**	**.42**	**-.22**	-.09
Fearful	-.16	.07	-.06	**.77**
Active	-.02	**-.21**	-.08	-.04
Inactive	**-.27**	-.13	-.13	-.08

Table 3.4: Main and Interaction effects of Species and Sex from GLM, after controlling for nursery rearing experience and age-in-months. Covariate effects for rearing experience and age are shown below. Significant differences (at the 0.05 level) are indicated in bold, and effect sizes (η^2) are noted.

		Personality Components							
		Confidence		Cautiousness		Aggressiveness		Fearfulness	
Predictors:	df, DF	F	η^2	F	η^2	F	η^2	F	η^2
Species	2, 891	**35.43**	.07	**56.22**	.11	**32.07**	.07	**3.21**	.01
Sex	1, 891	**47.86**	.05	**20.57**	.02	0.73	<.01	0.11	<.01
Species-by-sex	2, 891	0.94	<.01	1.00	<.01	**6.28**	.01	**3.86**	.01
Covariates:		F	η^2	F	η^2	F	η^2	F	η^2
Age-in-months	1, 891	0.06	<.01	**161.31**	.15	**4.27**	<.01	.48	<.01
Nursery experience	1, 891	**47.77**	.05	3.29	<.01	**15.26**	.02	.48	<.01

Table 3.5: Repeatability for four personality traits over 3 years (2-4 testing periods). Measures include ICC [Bell et al., 2009] and mean Pearson's correlation [Freeman & Gosling, 2010]. N=293; estimated k for individuals is 2.66

	Confidence	Cautiousness	Aggressiveness	Fearfulness
Single Measures ICC	0.54	0.53	0.28	0.42
95% CI for ICC	0.47-0.60	0.46-0.60	0.19-0.36	0.34-0.50
Within-Test Variance	0.40	0.40	0.30	0.25
Between-Test Variance	0.47	0.45	0.12	0.18
Mean Correlation	0.48	0.45	0.28	0.42
95% CI for Correlation	0.46-0.69	0.46-0.69	0.27-0.50	0.35-0.58

Table 3.6: Fixed estimates of the best fitting models of population-wide personality change. Equations show the best-fitting model, as determined by highest Akaike weight. Significant predictors are those variables with coefficients that differ significantly from zero in the more informative models. R^2 without subject ID describes the variance in personality explained by the model as shown, and R^2 with ID describes the variance explained by the model with "ID" included as a predictor. Root-mean-square error (RMSE) describes model residuals, and Cohen's f^2 is a measure of effect size.

Outcome:	**Akaike Wt.**	**Significant predictors**	**R^2**	**R^2 with ID**	**RMSE**	**RMSE with ID**	**f^2**
Confidence	= Sex + Entry Age + 1st Test Tenure + Time Elapsed + (Sex * Entry Age) + (Sex * 1st Test Tenure) + (Sex * Time Elapsed)						
	0.83	Sex *** 1st Test Tenure *** Time Elapsed *** Sex-by-Entry Age Interaction*** Sex-by-1st Test Tenure Interaction *** Sex-by-Time Elapsed Interaction *	0.31	0.70	0.83	0.57	0.45
Cautiousness	= Sex + Entry Age + 1st Test Tenure + (Sex * Entry Age)						
	0.25	Sex*** Entry Age*** 1st Test Tenure ***	0.18	0.68	0.91	0.60	0.22
Aggressiveness	= Sex + Entry Age + Time Elapsed + (Sex * Time Elapsed)						
	0.17	Entry Age ***	0.05	0.51	0.97	0.77	0.05
Fearfulness		= Sex + Time Elapsed + (Sex * Time Elapsed)					
	0.36	Time Elapsed *** Sex-by-Time Elapsed Interaction ***	0.03	0.65	0.98	0.64	0.04
*$p < .05$, **$p < .01$, ***$p < .001$							

Table 3.7: Unstandardized coefficients for predictors in the best fitting models of population-wide personality change.

Component	Predictor	Estimate	Uncond. SE
Confidence	Sex	-0.29	0.05
	Entry age	-0.07	0.02
	1st test tenure	0.06	0.02
	Time elapsed	0.19	0.03
	Sex * Entry age	0.08	0.02
	Sex * 1st test tenure	0.09	0.02
	Sex * Time elapsed	0.08	0.03
Cautiousness	Sex	0.27	0.06
	Entry age	-0.10	0.02
	1st test tenure	-0.15	0.02
	Sex * Entry age	0.04	0.02
Aggressiveness	Sex	0.08	0.05
	Entry age	0.05	0.01
Fearfulness	Sex	0.08	0.05
	Time elapsed	0.12	0.04
	Sex * Time elapsed	0.13	0.04

Entry age, 1st test tenure and time elapsed are measured in years, and mean-centered. Sex is measured with females as 1 and males as -1.

Figure 3.1: Species and sex differences in z-standardized component scores, +/- SE. Letters represent significant differences. A. Species main effects; B. Sex main effects.

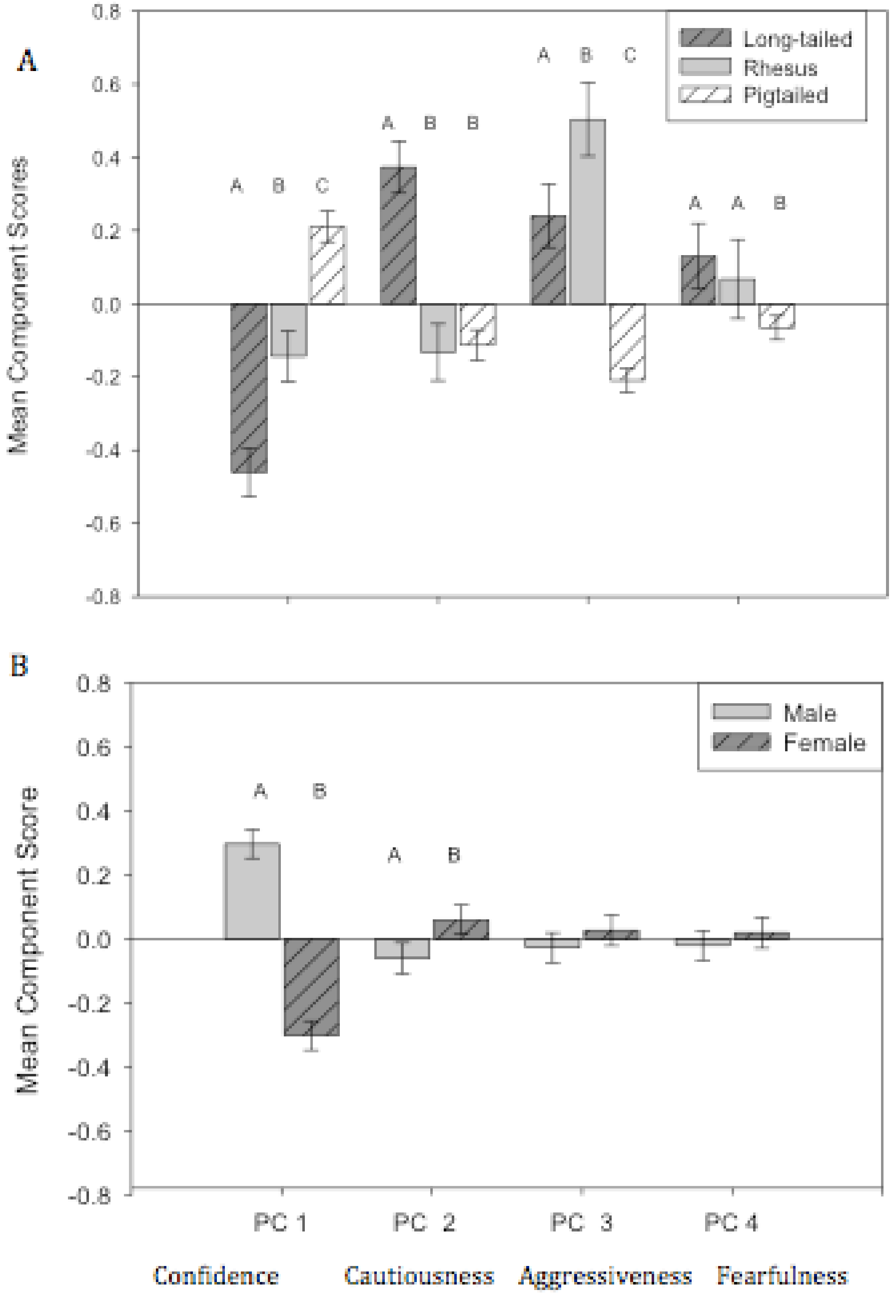
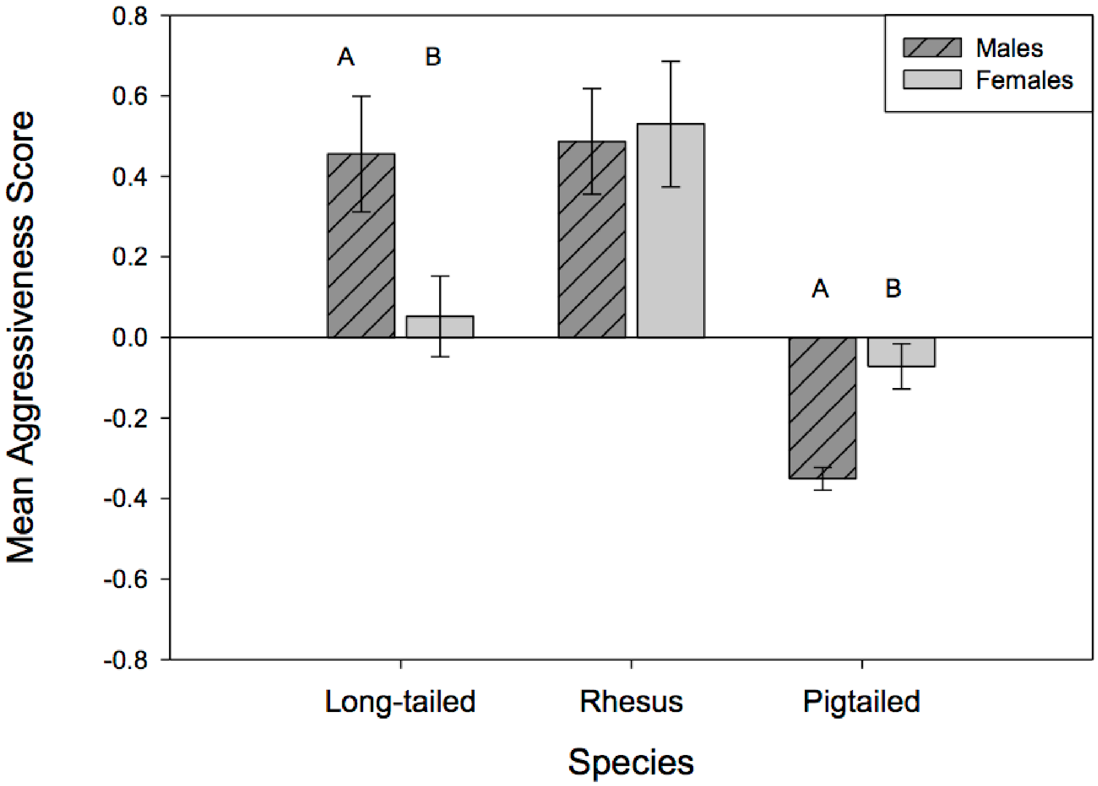


Figure 3.2: Species-by-sex interaction effects for z-standardized Aggressiveness, +/- SE. Letters represent significant differences.



Chapter 4: Personality and Social Behavior in Macaques

Overview

In this chapter, we present several studies that explore how personality relates to social behavior. In Part 1, we present the results of a personality test adapted from the test described Chapter 3. We demonstrate that the two tests give comparable results. Next, we use personality scores to predict the success of pair housing at the primate center, and the behaviors exhibited by adult macaques after they have been paired (Part 2). Finally, we examine the relationship between personality scores and behaviors exhibited in larger groups (Part 3). We test whether personality is predictive of individual behaviors in a group context. In Part 4, we test whether the mixture of personalities present within a group can predict the overall group dynamics.

Part 1 - Personality testing – adapted test

Our findings in Chapter 3 showed that a rapid cage-front behavioral observation could effectively describe differences between individuals, and between species. However, as described in that chapter, that test (hereafter referred to as "the pilot test") recorded 37 variables, only 12 of which contributed to personality components. We decided to adapt the test to streamline the methods and capture the most important portions of the behavioral variance between individuals. Like the pilot test, our adapted test was administered while animals were individually-housed, and took the form of a 4-minute cage-front assessment. Data were collected on tablet computers, using software created in NS Basic by Adrienne Sussman and Arthur Davis. As in the pilot test, behaviors were coded using either instantaneous sampling or based on whether or not they had occurred during the past time interval. However, in the adapted version of the test, time intervals were 30 seconds, rather than 1 minute. Thus, all behavior scores ranged from 0 – 8, rather than from 0 – 4, as in the previous version of the test. Variables that were not informative in the pilot test were removed from the adapted test. Other variables were modified, and several variables were added. All variables included in the adapted assessment, along with definitions, are listed in Table 4.1. Tests were administered by two observers, who had achieved an inter-observer reliability of $R = 0.9$. Each animal received the adapted test only once.

Animals in this study were housed either at the WaNPRC in Seattle or at the WaNPRC remote breeding colonies. Animals at the Seattle facility (N=79) were adults, who were tested prior to being paired with a social partner (see Part 2 for details). 72 of these subjects were female and 7 were male. Subjects in the remote breeding facilities (N=185, 13 male) were tested prior to being moved from a facility in Alice, Texas to a facility in Mesa, Arizona (described below). While these animals usually lived in large social groups, at the time of testing they had been moved to individual indoor cages for transportation. Animals had been housed in these cages for at least one week prior to personality testing.

The behavioral counts measured with the adapted test were again analyzed using principal components analysis (PCA), as described in Chapter 3. PCA obtained four components, which together explained 55% of the variance in the data after rotation (Table 4.2). The iterative PCA process retained 17 of the 37 behavioral variables measured. Nine of the twelve behavioral variables included in the pilot personality test PCA (Chapter 3) were also retained in this PCA, and seven additional variables were included in the adapted test PCA. The variables “Reach to observer”, “Lipsmack”, and “Ignore observer” were not included in the adapted PCA, while the variables “inactive”, “LEN to observer”, “LEN to conspecific”, “Yawn to observer”, “Grunt”, “Manipulate Object”, and “Eat/tooth grind” were included. There was high congruence between the obliquely and orthogonally rotated components for the adapted PCA (all Tucker’s congruence coefficients > 0.95), and no obliquely rotated components were correlated at R > 0.1. For these reasons, we chose to use orthogonal rotation for our final component scores.

Our interpretation of the four components was consistent with the interpretation of the four components in the pilot personality test, although the variables contributing differed slightly. The first component for the adapted personality test PCA was interpreted as Aggressiveness, the second as Confidence, the third as Cautiousness, and the fourth as Fearfulness (see Table 4.2).

Discussion of adapted test

Using an adapted version of the personality test, we again identified four personality components in adult pigtailed macaques. These components were very similar to those identified using our pilot personality test (Chapter 3). Although the sampling frequency was higher in the adapted test, and a larger number of behaviors were recorded, we found that the variables that explained the variance between individuals were almost identical between the two tests (see Tables 3.2 and 4.2).

There was a little difference in the variable composition of the components Confidence and Cautiousness between the two personality tests. In the pilot test, Confidence included the behaviors “Reach”, suggesting that individuals scoring high on this component were actively engaging with the observer. In the adapted test, this variable did not contribute to the final component, however. This might point to a difference in interpretation of these components in the two tests. In the pilot study, Confidence was related to the tester-rating “friendly”, but in the adapted version of the test, Confidence may be less closely aligned with friendliness to humans. For Cautiousness, in the pilot test analysis, the variable “Approach” contributed positively, while the in the adapted test this variable contributed negatively. Moreover, the adapted version of Cautiousness was also associated with the variables “Yawn” and “Eat/Grind teeth.” The pattern of variable contribution to the component in the adapted test version is more descriptive and, we believe, even better described as Cautiousness.

As described in Chapter 3, the components that we identified were similar to those described elsewhere in the literature [Freeman & Gosling, 2010], and the identification of four components is in keeping with other studies of macaques [Capitanio, 1999; Rouff, Sussman, & Stroube, 2005; Weiss et al., 2011]. The fact that not all behavioral variables described differences in variance between individuals, and that similar variables contributed in both of our tests, indicates that our initial results are replicable. Our next research step (Part 2 and Part 3) was to demonstrate whether the components identified here were informative in another context.

Part 2 - Pair social behavior

Subjects & Housing

We used examined the relationship between personality and social interactions of pair-housed macaques at the WaNPRC facility in Seattle. Monkeys in this sample had recently been paired with a new social partner. The socialization process at the WaNPRC operated as follows: after several days of being housed in adjacent cages, animals were introduced via grooming contact, and finally the doors between their cages were opened. During each step, animal technicians observed the animals for any moderate or severe aggression. If animals were wounded or aggression was otherwise severe at any point in the process, the socialization was deemed "unsuccessful" and animals returned to their individual cages. The entire socialization process took about 1 week. We recorded whether each pair-socialization attempted between 1/16/13 and 10/21/13 was successful or unsuccessful.

Once a pair was successfully socialized, an animal technician began video recording the pairs' interactions. We chose to use video monitoring for pair behaviors due to our anecdotal observation that animals at the primate center are conditioned to expect treats or food from human visitors, and so tend to respond to human presence in the room. We wanted to observe the animals' interactions without this influence. We used a Sony HDR camcorder with a wide-angle lens on a tripod mount to record video footage. Each social pair was filmed for 1 hour per session, with 2 sessions per week. Session timings varied depending on the animal technician's schedule, but the first session always occurred on Monday or Tuesday (beginning the week following successful socialization), and the second session occurred on Thursday or Friday of that week. Each pair was monitored for one month post-socialization, or up to 8 hours of recording per pair. Some pairs were separated early for assignment to research projects.

Videos of pair interactions were viewed and coded at a later date by A.S. All social behaviors described in Table 4.3 were recorded in a spreadsheet during observations. For the purposes of this project, only social behaviors directed towards an animal’s social partner were recorded – we did not record behaviors directed towards animals in other cages. 10% of all videos were re-coded for reliability, and overall coding reliability was R=0.85. We did not include results for the two least reliable behaviors, LEN and lipsmack, in our analyses below. Without these behaviors, reliability was R=0.91. Durations for social contact and grooming were accurate to +/- 15 seconds per hour.

Personality and Socialization Success – Methods and Results

We examined the outcomes of 44 socialization attempts that occurred during the study period to test whether personality predicted socialization success. After removing the records of 5 socialization attempts in which the socialization was cut short because of project assignments or health issues, we performed two logistic regressions. Socializations were deemed successful if the monkeys progressed from grooming contact to a full run-through cage without any aggressive incidents. Pairs where socialization was terminated at any point due to aggression were considered unsuccessful (N=9). We calculated both the difference and the means for each of the four personality components within each pair. We then performed two logistic regressions, using personality differences as predictors in the first, and personality means in the second. We separated our analyses into two logistic regressions to preserve statistical power, given the large number of predictors.

Our results showed that neither differences in personality nor similarities in personality component scores (measured by mean) significantly predicted the success of the socialization. Results of the two logistic regressions are given in Table 4.4. There was a non-significant trend for difference in Fearfulness to predict successful socialization, and the high coefficient estimate for this relationship suggests that differences in Fearfulness could be strongly predictive of socialization success. A future study with a larger sample size may shed more light on this relationship, as the sample used here is smaller than advised for logistic regression [Tabachnick & Fidell, 2001].

What is clear from these results is that personality as measured here is not a powerful predictor of socialization success. One possible confound was that information about animal kinship and familiarity was lacking when making pairing decisions. Paired animals may have been previously housed directly next to or above/below each other, or they might have come from the same social group at a previous breeding facility. Either scenario would likely make the animals more tolerant of each other, and less likely to be separated due to aggression. These factors might mask the effects of personality in socialization outcome. Moreover, within the small number of pairs that could not be socialized due to aggression (N=9), five pairs included one of the same three individuals, who the center staff attempted to socialize multiple times. This suggests that these three individuals were especially difficult to socialize, and the variable that made them "difficult" was not captured by our personality test. We suggest further study of other "hard-to-pair" individuals to better understand the experiences and behaviors that might make them difficult to socialize.

Personality and social behaviors within pairs - Results

As described above, we recorded a total of 178 videotaped observation sessions for animals that were successfully paired. Summaries of behaviors observed are given in Table 4.5. In general, affiliative behaviors were common (animals spent a mean of 15.4% of their time engaging in affiliative behaviors.) and aggressive behaviors were rare. However, the most notable aspect of Table 4.5 is the amount of variation between pairs in behaviors observed (indicated by range). Contact and noncontact aggression were significantly correlated (*R* = 0.47, *df* = 176, *p*<.001), but neither type of aggression was correlated with total affiliative behaviors.

We performed a repeated-measures ANOVA to determine whether there were any changes in the frequencies of behaviors over the 8 weeks of observations. There were no significant changes in the frequency of noncontact aggression (*F*(1, 13) = 1.31, *p*=.27) or contact aggression (*F*(1, 13) = 1.89, *p*=.19) over weeks. There was a non-significant trend towards a decrease in total affiliative behaviors within pairs over weeks (*F*(1, 13) = 4.47, *p*=.051). Using post-hoc pairwise t-tests with a Bonferroni correction, however, we found that no two weeks were significantly different from each other. Thus, we considered this a minor trend that did not meaningfully impact our results or interpretation of the data. As there were no major changes in behaviors over time, we calculated behavioral averages for the full month which we used in the analyses below.

We compared behaviors observed during morning (before 12 PM) and afternoon (after 12 PM) video observation sessions using paired t-tests. We found no difference in total affiliative behaviors between morning and afternoon sessions (*t*(29) = -1.87, *p* = 0.07). There were also no differences in contact aggression (*t*(29) = 0.26, *p*=0.80) or noncontact aggression (*t*(29) = -1.51, *p* = 0.14). Thus, we did not differentiate between morning and afternoon sessions in subsequent analyses.

Relationship between personality and pair behaviors

The difference in personality scores within a pair predicted overall affiliative behaviors observed (Table 4.6a). There was a marginally significant relationship between personality difference and mean non-contact aggression observed (*p*=.07), and no significant relationship between total contact aggression and personality difference. In particular, larger differences in Cautiousness between pair members predicted less affiliative interaction, while greater differences in Fearfulness predicted more affiliative interaction. Greater differences in Aggressiveness between pair members significantly predicted fewer instances of non-contact aggression, and may be related (marginally significantly) to fewer instances of contact aggression and a greater total time spent in affiliative behaviors.

The mean of personality scores within a pair (i.e., how extreme the pair was in their scores overall) significantly predicted the mean instances of non-contact aggression observed, and marginally significantly predicted the instances of contact aggression (Table 4.6b). There was no relationship between the mean of scores and affiliative behaviors observed. The mean of Aggressiveness scores was a significant predictor of both contact and non-contact aggression, suggesting that pairs where both members scored high on "Aggressiveness" were more likely to engage in aggressive interactions. The mean of Confidence scores was also a significant predictor of contact aggression and a marginally significant predictor of non-contact aggression (*p*=.09).

Discussion:

We found that overall, personality was predictive of specific behaviors observed in pairs, but was not predictive of overall pair success. Pairs that engaged in more affiliative behaviors tended to be similar in their Cautiousness scores, but different in their Fearfulness scores (and potentially more different in Aggressiveness). Affiliative behaviors are associated with appeasement and reconciliation following aggression [de

Waal & Ren, 1988; de Waal, 2000]. Affiliative behaviors such as grooming and social contact repair the social relationship and reduce stress for both participants following aggressive interactions (de Waal & Van Schaik, 1988; Sapolsky, 2005). In our pair situation, if one individual was much more Fearful than the other, and one more Aggressive, then the more Fearful individual might experience stress. The more Fearful individual could assuage this stress by grooming its partner – decreasing stress for them both, and potentially reducing the chance that the partner would engage the Fearful individual in an aggressive interaction [Aureli & Van Schaik, 1989; Sapolsky, 2005]. On the other hand, our measure of Fearfulness is likely also tied to low dominance status. Past work has shown that two individuals who differ greatly in dominance status and/or stress responses are more likely to engage in aggressive interactions [Higley et al., 1996a]. Such interactions might be expected to be followed by affiliative reconciliatory behaviors, explaining the correlation of differences in Fearfulness with both affiliative behaviors and noncontact aggression seen here.

The findings that both Aggressiveness and Confidence are related to aggression (both contact and non-contact) are to be expected. In the close quarters of pair housing, two individuals with above-average tendencies towards aggressive behavior might be expected to fight. The component Confidence includes components such as “approach” and “quiet face” which are associated with dominant, not submissive, behavior. One past study that compared similar personality component scores with social behavior in rhesus macaques found that variance in Aggressiveness and Confidence was a better predictor of social behavior than was the group’s mean score on these factors [Capitanio, 2004]. This is counter to the findings here, which show that the overall scores, and not the differences between individuals in these scores, matter most, at least in a pair setting. A comparative study using paired rhesus macaques could determine whether this difference is due to the species in question or the housing conditions. It is possible that the effects of personality play out differently in small groups (as used in the Capitanio study) than in pairs.

A major finding here, as in the infant study in Chapter 2, is that our personality scores do predict behavior in a social context. This cross-context generalizability validates these as true measures of an individual's behavioral tendencies. These results suggest that for pair housing, individuals that differ in Fearfulness, are similar in Cautiousness, and are not both extreme in their Aggressiveness or Confidence scores would constitute pairs that are most likely to be successful. Such component pairings may minimize aggressive interactions and increase affiliative behaviors, resulting in better health outcomes for the animals. Further experimental research – particularly more manipulations of personality-tested paired animals – will help clarify the relationships between personality and pair behavior.

Part 3: Relationship between Individual Personality and Social Behavior in a Group:

In addition to examining predictive power of personality in small groups of very young monkeys (Chapter 2) and in pairs of adult monkeys (Chapter 4 Part 2), we also sought to understand how personality predicts social behavior in larger groups of adult monkeys.

Group housing in Arizona

Monkeys at the WaNPRC breeding facility in Mesa, Arizona were housed in large indoor-outdoor runs. Runs were composed of indoor areas that were approximately 10 X

10 X 9 feet in dimension, connected by a run-through passage to an outdoor area approximately 10 X 30 X 20 feet in dimension. Animals had free access to the indoor and outdoor portions of their caging, except during daily cage cleaning, occasional cage repair and maintenance, or rare inclement weather events (such as extreme heat). Outdoor areas had multi-level perches and various enrichment structures including swings, ropes, beams, and wading pools. These enrichment structures were alternated between groups approximately every few months. Indoor areas were broken into several small rooms, each with multi-level perches, and contained hay or bedding. Animals received commercial monkey biscuits both indoors and outdoors twice daily, and *ad libitum* water from spigots throughout the structure. Monkeys also received enrichment of produce or seeds daily, as well as toys and tactile materials (cardboard, paper, and palm fronds).

Subjects were housed in either breeding groups, consisting of a single adult male and 14 – 20 adult females (Mean group size = 18.84) or in mother-infant groups, consisting of 9 – 12 adult females (Mean = 11.73) and their un-weaned infants (< 12 months old). Adult females ranged in age from 4.02 years to 22.07 years at the beginning of the observation period (May, 2013; Mean = 9.07; SD = 4.25 years).

Personality testing

All subjects housed in the Arizona breeding complex were personality tested as described in Part 1. Subjects were personality tested prior to moving to the Arizona facility (while housed in another facility in Alice, Texas). Adult females were held in individual cages during testing, as described in Part 1. However, adult males were tested while housed individually within their familiar group enclosure. Although males were restricted to the indoor portion of their enclosure during testing, this area was much larger than the temporary cages in which females were tested. This difference in enclosure size and familiarity appeared to affect the outcomes of male personality tests, as they were not comparable to the results from the pilot test described in Chapter 3. Given the unreliability of these measures for males, the bulk of our analyses below were for female macaques, and we do not assess the personality type of males in the breeding groups.

Focal observations - Methods

We used 5-minute focal sampling to describe individual social behavioral patterns. Each individual in a group was observed for 5 minutes, and we recorded the duration and frequency of all social behaviors (Table 4.3; Total N=141) that occurred in those 5 minutes, along with their recipient's ID. All individuals were identified by chest tattoos and patterns of dye-marking on the back and arms/legs. The identification system was highly effective, with 92.8% of all interaction partners identified. For affiliative social interactions, the rate of identification was even higher (96.4% identified). Fewer partners were identifiable in other social interactions, especially those that occurred at a distance, such as LENs or open mouth threats. Due to the difficulty of accurately recording data on these interactions, we did not include partner identity in analyses of such behaviors.

Each animal in the sample (N=141) received at least 45 minutes of focal observations total. Observation time and order occurred randomly throughout the day, between the hours of 7:30:00 A.M. and 6:05:00 P.M. Most observations occurred in the morning. Animals occasionally moved out of sight during the 5-minute observation period (i.e., the animal went outside when observing from inside, or vice versa). We recorded the duration of out-of-sight periods. If any focal subject was out-of-sight more than 120 seconds of their total 300 s (5 minute) observation period, the observation was deleted and the animal was observed again. On average, animals were out of sight a mean of 4.75 seconds per session (SD=6.75 sec). The time out-of-sight was subtracted from their overall observation time when calculating rates of behaviors. All observations occurred between April 2013 and October 2013. Data were recorded on an iPad using software developed by Adrienne Sussman and Arthur Davis.

Focal observations - Results

The frequencies of behaviors observed are given in Table 4.7. In comparison to the behaviors listed for animals housed in pairs at the PC (Table 4.5), Table 4.7 indicates that group-housed animals engage in aggressive interactions far less frequently than pair housed animals. In addition, though animals in both pair and group housing engaged in roughly equal total amounts of affiliative behaviors, animals in pair housing spent a larger percentage of their time grooming, and less time in social affiliative contact than did animals in group housing. As in Table 4.5, Table 4.7 demonstrates that individuals varied greatly in their rates of behaviors, as demonstrated by high standard errors and large ranges. There were some differences in behaviors between mother-infant groups and breeding groups, as well, discussed in Part 4.

We used OLS regression to determine whether personality predicted social behaviors observed during focal sampling. For each individual in the sample, we calculated the total duration of affiliative behaviors and the total instances of contact aggression, noncontact aggression, and fear grimaces that individual engaged in either as a focal subject or as a recipient. Affiliative behaviors included social contact, initiating or receiving grooming, social play, rump presenting, or mounting. Noncontact aggression included chasing, fleeing, or open mouth threats, and contact aggression included biting, lunging, and rough behavior. Only individuals with at least 15 minutes of observation time were included in the sample, and all behaviors of interest were standardized as rates per observation hour.

We found that personality did not significantly predict the duration of affiliative behaviors an individual engaged in, nor the amount of contact aggression (Table 4.8). There was a significant relationship between the personality measure "Fearfulness" and the amount of noncontact aggression an individual was involved in (either as participant or recipient), though overall personality did not significantly explain the variance in noncontact aggression (p=.09).

We also examined these relationships for individuals in mother-infant groups only (N=30 females) and breeding groups only (N=89 females). We found that in the context of mother-infant groups, no personality components were significantly related to any social behaviors (all *p*s >.05). However, in breeding groups, personality and social behavior were more strongly related (Table 4.9). In particular, personality significantly predicted affiliative behavior observed, with Cautiousness having a significant independent effect. Individuals with higher Cautiousness scores took part in significantly less affiliative behavior. There was also a non-significant trend for individuals higher in Fearfulness to exhibit less affiliative behavior (p=.07). Fearfulness was also a significant independent predictor of contact aggression in this group, with more fearful individuals involved in more contact aggression. However, there was no overall significant relationship between personality and contact or noncontact aggression in this subset of the sample.

Focal observations and Association index

We used a Simple Association Index to measure the strength of the affiliative relationships between individuals in our sample. While the Simple Association Index is problematic in field situations, it is recommended for studies of captive animals [Cairns & Schwager, 1987]. We calculated the association index for all pairs of individuals who were observed in the same group and interacted at least once. We then calculated the Simple Association Index as the total time the animals were observed engaging in affiliative interactions, divided by the total amount of time they were observed [Cairns & Schwager, 1987]. This gave the proportion of time the individuals spent together out of the total time they were observed. We then regressed this value against the personality score differences and means for each pair, to see whether certain combinations of personality were more likely to associate.

We found no significant relationships between personality differences or means and association index scores (Table 4.10). No aspects of personality were significant predictors, though there was a non-significant trend for the difference in Confidence scores within a pair to predict association (p=.07). The trend was for animals with more different Confidence scores to spend more time in affiliative associations.

Personality and number of relationships

We calculated the number of “strong” connections that each female had within her social group. Our rationale in categorizing relationships as “strong” or “weak” was to distinguish between “true” relationships and spurious artifacts of observational error while calculating an individual's total number of affiliative partners (social network "degree", [Wey et al., 2008]). Error was introduced to observations via both misidentification of individuals (behavioral recipients, not focal individuals), and misrepresentation of behaviors (i.e., two animals standing next to each other that were not really touching). To determine which relationships were "strong", we first summed the total amount of affiliative time each female spent with others in her group. The median total time spent in affiliative interactions with others over the course of observations was 28 seconds. We characterized all pairs whose total affiliative interactions were longer than 28 seconds as having "strong" relationships. We counted the number of partners with which each individual had a "strong" relationship. We then regressed an individual's personality component scores onto their relationship count to see whether some personality types were more likely to have many social relationships.

We found that there was no significant relationship between number of strong relationships and personality (R^2=0.04, $F(4, 130) = 1.31$, p=.27). None of the individual predictors had a significant relationship with the number of social relationships (ps >.05). There was a trend for more Confident individuals to have more relationships, but this did not reach significance (p=.09).

Discussion

While we found relatively strong relationships between personality and behaviors in pairs (Part 2) and in small infant social groups (Chapter 2), the relationships observed in large adult social groups were weaker. Only the personality component Fearfulness was a significant predictor of social behaviors in this context in our overall dataset. The finding that Fearfulness in adults also corresponds to greater rates of non-contact aggression suggests that Fearfulness may be closely related to dominance status in this species, as more Fearful individuals are the targets of more threats and dominance displays than less Fearful individuals.

In breeding groups, personality was a significant predictor of social behavior, while in mother-infant groups, it was not. In breeding groups, Cautiousness in particular was negatively related to affiliative behavior, while Fearfulness was related to contact aggression. The Cautiousness finding suggests that this behavioral component, which describes individuals who do not engage socially with a human observer, is translatable across contexts, and predicts that individuals will also not engage with conspecific social partners.

The finding that personality did not predict association index or number of social partners at all is inconsistent with several past studies of personality and social behavior in macaques. Most notably, Weinstein and Capitanio [2008] found that personality in rhesus macaques predicts the number of social ties and the choice of social partners. However, this study was conducted with young macaques. As our own work in infant macaques (Chapter 2) found more robust links between personality and social behavior than were found here in adults, it is possible that these relationships are stronger in younger animals. Group dynamics most likely become more complex as animals mature. It is also likely that female reproductive hormones have a strong effect on behavior in adult female macaques, which is absent in infants or young animals. When female macaques are in oestrus (as indicated observationally by sexual swellings) they are more likely to engage in reproductive behavior and grooming, though evidence is mixed as to the strength of this relationship [Bernstein, 1963; Bullock, Paris, Goy, 1972; Tokuda, Simons, & Jensen, 1968; Goldfoot, 1971]. This can result in changes in social behavior over the course of the reproductive cycle. Such changes would not be described by a "baseline" personality, as measured here. Thus, changes in female hormones throughout the cycle may mask the relationships between baseline personality and social behavior, or baseline personality and number of social partners. The idea that female reproductive hormones are important here is also consistent with our finding that the relationships between personality and social behavior differed dramatically between mother-infant and breeding groups. Pregnancy and postpartum hormones may have particularly strong affects on behavior. For example, one past study described how the presence of pregnant females can affect an entire group's social dynamic [Ha et al.,1999]. We did not measure reproductive hormones at all in this study, but future studies should include these as a variable when trying to understand the relationship between personality and social behavior.

In addition to the effects of female reproductive hormones, our study also did not fully account for the effects of dominance status in our analyses. While we expected dominance status to be correlated with personality, as in past primate studies [e.g., Anestis, 2005], other factors (such as kinship, age, and body condition) are also strong determinants of dominance status in macaques [e.g., Paul & Kuester, 1987; Morgan et al., 2000]. In fact, Gosling and others have suggested that "dominance" should be considered an independent, orthogonal personality trait in primates [Gosling & John, 1999]. Effects of dominance status might also explain why the links between temperament/personality and social behavior were stronger in infant groups than in adults. As discussed in Chapter 2, infants groups do not typically have complex dominance hierarchies. Future research might be able to tease apart these factors to fully understand the variables that affect social behavior.

A final limitation of these results is that our social groups here were quite large. Past studies that found strong relationships between personality and social behavior looked at individuals in small groups. For example, Capitanio examined social groups of 3 or 5 [1999; 2004]. Our own research suggests that these relationships seem to be stronger in smaller social groups, indicating that macaque behavior may simply become more complex as group size increases. While the relationship between personality and social behavior can be described linearly in pairs (Part 2) or in small groups [e.g., Capitanio, 2004], third-party effects may become a more important factor in large groups [e.g., Call, Aureli, de Waal, 2002; Silk 1999]. Thus, based on our results, we can say that personality appears to be somewhat generalizable to a complex social context, but predictive power weakens as the complexity of the social group increases.

Part 4: Group Personality Makeup and Social Behavior

In addition to understanding how an individual's personality score relates to her behavior in a social group, we also wanted to understand whether a social group's behavioral style could be predicted based on the personalities present within that group. We examined the link between mean personality scores in a group, variance in personality scores in a group, and the amount of aggression and affiliative behavior observed

Group aggression levels - Methods

We used all-occurrences sampling to measure the overall aggression levels of social groups at the Arizona breeding facility. As described in Part 3, we observed five breeding groups containing adult females and a single adult male, and three mother-infant groups, containing adult females and their un-weaned offspring. There were 94 adult animals housed permanently in breeding groups, and 30 housed in mother infant groups, with an additional 30 whose location changed over the observation period. All-occurrences sampling was chosen to observe group aggression levels, because aggressive behaviors occurred relatively infrequently. Each social group was observed for four 15-minute observation periods each month (1 hour/month), for a total of 6 hours per group. These observations occurred most frequently in the late afternoon, between 3 and 7 p.m., when animals had received food and enrichment for the day, and the weather was cooler. Out of 192 total observation sessions, 17 occurred before 12 P.M.

During the observation period, all behaviors marked in Table 4.3 were recorded using an iPad tablet, as well as whether the behavior was initiated/directed towards a male, female, or infant. Event recording software was developed by Adrienne Sussman and Arthur Davis.

In addition to aggressive behaviors, we also calculated the mean duration of affiliative behaviors in each group. To do this, we used the focal sampling measures described in Part 3 to calculate the mean duration of affiliative behavior for each observation month. We used the grand mean of the 6 months as the affiliative behavior "score" for each group.

Statistical analyses and Results:

We used a repeated measures ANOVA to test for any change in overall aggression within groups over the months of observations. We found no significant difference between months ($F(4, 29) = 0.33$, $p=.85$). Thus, we combined all data for each group for subsequent analyses.

Groups varied in the levels of aggression observed during all occurrences observations (see Figure 4.1). There was no significant difference between breeding groups and mother-infant groups in the amount of contact aggression observed (Mann-Whitney $U=11$, df = 7, $p = .39$). However, mother-infant groups did have significantly less noncontact aggression (Mann Whitney $U=15$, df = 7, $p = .04$).

We examined the relationship between the personality make-up of the social groups and the aggression observed during all occurrences observations. We calculated the mean and variance of personality scores present in each group. We used pairwise Pearson's correlations to look for any relationships between aggression and the personality makeup of the group. We performed the same analyses with mean group affiliative behavior as the outcome variable, as well.

The results of these correlations suggest that the variances of personality components present within groups are significantly related to group behaviors (Table 4.11). In particular, the variance in Aggressiveness in the group positively correlates with rates of aggressive behaviors in the group. Increased variance in Cautiousness and Aggressiveness both also predicted higher rates of affiliative behaviors in the groups. Power for these analyses was very low (Table 4.11), so these results should be considered preliminary.

Discussion:

When compared to past observational studies of pigtailed macaque social behaviors, the frequencies of behaviors we observed were comparable. Alloway [2007] observed behaviors in captive pigtailed macaques housed in smaller, indoor social groups at the WaNPRC in Seattle. Like us, they also observed that behaviors within groups did not differ over weeks. They also observed roughly comparable rates of all occurrences aggression, though in their sample, contact aggression rates were slightly higher, and non-contact aggression rates were lower. They observed a bite rate of 0.06 bites per hour per group, compared to our rate of 0.02, and their rates of rough behavior (in that study, measured as "grab", "hit", "push", or "shake") totaled 0.26 instances per hour per group, compared to our rate of 0.08. They also observed a higher rate of chases (0.08 chases/ hour/group vs. 0.05 in our study). On the other hand, they observed fewer open mouth threats (0.17/hour/group compared to our 0.34/hour/group), fewer yawns (0.21/hour/group compared to 1.02/hour/group) and fewer lunges (0.06/hour/group compared to 0.16/hour/group). Considering that their study examined just 9 groups and ours just 8, this might be due to sampling error; it also might reflect changes in behavior due to housing differences. For example, the animals in our study were housed in considerably larger spaces, which might affect behavior. Past work has shown that higher densities within housing are strongly correlated with more frequent and severe aggression [Erwin & Erwin, 1976].

While the rates of behaviors we observed were species-typical, several findings of this study differed from other reports in the literature. For one, the similarity between mother-infant groups and breeding groups in our study went against a large body of research suggesting male presence reduces aggression in macaque groups [Sackett, Oswald & Erwin, 1975; Ha et al., 2011; Dazey et al., 1977; Flack et al., 2005; Flack et al., 2006]. However, none of these studies included groups composed only of females with young infants. The all-female groups in other studies generally included a mixture of adult females, with or without infants, and in varying stages of their reproductive cycles. Other past work demonstrates that female reproductive status (especially pregnancy) is a driver of female-female aggression [Ha et al., 1999]. The reported impact of the presence of a sire may not apply to all-female groups composed ONLY of mothers with infants.

The main finding of this section is that variance of personalities present within a group is significantly related to both rates of aggression and rates of affiliative behavior within those groups. Variance in Aggressiveness was the variable most related to group behavior, and variance in Cautiousness was also predictive. This result is consistent with findings by Capitanio, who demonstrated that variance in personality traits was more important than mean trait scores for predicting social behaviors in small groups of male rhesus macaques [Capitanio, 2004]. The finding here that variance in Aggressiveness predicts both increased aggression and increased affiliative behavior is not surprising, as aggressive behavior in macaques is often followed by bouts of affiliative reconciliation behaviors.. These findings suggest that groups whose members are more similar in Aggressiveness (i.e., have a lower variance) will show less aggressive behavior. This result is consistent with some computer models of primate social behavior [Puga-Gonzalez, Hildenbrandt, Hemelrijk, 2009], but should be validated with experimental manipulations of group membership.

While our results suggest a relationship between personality and social behavior, their interpretation should be limited. Besides the small sample size and resultant low power noted in Table 4.11, our groups were also fairly newly formed. Newly formed macaque groups are known to undergo periods of more intense female-female conflict [Bernstein, Gordon, & Rose, 1974], which can affect behavior for more than a year after group formation [Ha et al., 1999]. It is unclear whether this factor would exaggerate differences between groups in aggression rates, or mask them. Repeating this observation with the same groups at a later date would help address this potential confound.

In addition to the measures used here, it is also likely that the personality of the male in the breeding groups is a significant predictor of group social behavior. There is robust evidence that the male in a social group plays an active role in determining the amount of aggression in the group, and it may be that his personality determines his "policing" style [Flack et al., 2005; Flack et al., 2006; McCowan et al., 2011]. Given the small sample size (5 breeding groups) and differing conditions for male personality tests (described in Part 3), we were unable to use male personality as a predictive variable in this analysis. We recommend performing personality tests on males held (temporarily) in smaller cages, and see whether those tests are more predictive of overall group social behaviors.

Finally, the much weaker relationship between individual personality and behavior in large groups (Part 3), combined with the relatively strong relationship in pairs (Part 2), suggests that these dynamics may be dependent on group size. The dynamics of social behavior in adult macaques are much more complex in large groups, and perhaps after some threshold size, they are no longer explained by personality alone. Factors such as dominance status (which may be related, but not completely explained by the personality components measured, as described above), age, parity, and female ovulation all play roles in explaining the group's dynamics. These factors may interact with, or simply be more important than personality in explaining individuals,' and as a result, the group's behavior. Future studies should examine relationships between group dynamics and personality mixtures in smaller groups. It is likely that relationships are stronger in small groups, and become weaker as group size increases. .

Conclusions:

The results of our analyses demonstrate that the adult personality can generalize to a social context, with scores for all four personality components predicting aspects of behaviors observed in pair video sessions. However, personality did not predict which pairs would be successfully socialized and which would not, possibly because other, unmeasured factors in determining which animals to pair were used.

Personality was less successful at predicting social behavior in large groups. Personality (particularly Cautiousness) was predictive of affiliative behaviors in breeding groups, but not in mother-infant groups Fearfulness scores were related to non-contact aggression received by an individual in a large social group, and to contact aggression in breeding groups. We also were unable to identify any significant association patterns based on personality scores. Finally, the overall mean personality scores within a group did not predict the frequency of aggression observed in that group, but the variance in scores did. Higher variance in Aggressiveness was associated with greater rates of contact aggression and affiliative behaviors, and higher variance in Cautiousness was also associated with greater rates of affiliative behaviors.

We conclude, from this evidence, that personality measured in a nonsocial context does successfully predict behavior in a social context. However, the evidence from these studies suggests that as group size grows, the role of personality in predicting behavior diminishes. Overall, these results are sufficient to support our hypothesis that personality is the individual-level characteristic that leads to group-level differences, but we believe further research is necessary to fully understand these relationships.

Table 4.1: Description of variables included in the adapted personality test. For every 30 second cycle of the 4 – minute observation period, location and movement were point sampled at 10 seconds, facial expression was point sampled at 20 seconds, and all other variables were measured as one-zero at 30 seconds. Facial expressions were recorded as directed towards the tester, a conspecific, or neither.

Behavior	Definition
Facial Expression – point sample at 20 s (+30 s)	
Calm/Quiet	Attention is to tester's face/eyes (judged by eye direction), with no other facial expression
Ignore	Calm facial expression, attention not to tester. Includes looking in another direction, looking at clipboard/hands, and looking at conspecific
Hard stare	Prolonged eye contact (at least 3 sec), brow forward (threat)
Fear grimace	Corners of mouth drawn back exposing teeth (closed)
Open mouth threat	Mouth open, can display teeth, attention to target (threat)
Rapid glance	Eyes shifting rapidly between targets
Lipsmack	Lips rapidly pucker and open, tongue may move in and out of mouth
LEN	Lips extended, ears back, neck forward
Yawn	Head back, mouth opens slowly exposing teeth
Vocalizations – one-zero sample every 30 s	
Coo	Softer, clear call made with pursed lips. It contains harmonic elements.
Shriek	Long, high-pitched sound, which originates in response to threat. Loud noise, made with open mouth.
Bark	Gruff, short, loud call, often repeated.
Grunt	Softer, exhaling pant-like sound, softer than a bark.
Social Behavior– one-zero sample every 30 s	
Cage shake	Holding on to cage or platform and rapidly moving arms, moving the cage back and forth
Reach	Neutral/ submissive body, arm extended forward (soliciting treat)
Grab	Arm extended forward, with fingers attempting to grab or claw (agonistic)
Present rump	Raised rump faces target (tester or conspecific), looking over shoulder towards target
Present side	Attention to target, arm extended over head, side pressed on/near cage wall
Lunge	Rapid and abrupt motion towards the front of the cage
Self/undirected behaviors– one-zero sample every 30 s	
Manipulate self	Picking at or manipulating fur with fingers or toes, including grooming, plucking hairs, rubbing, etc.
Scratch	Moving fingers or toes rapidly back and forth through fur
Urinate	Urinating or defecating

Eat/Drink	Eating food, drinking from lixit, chewing on/ingesting foreign object (e.g., bedding, hairs)
Grind teeth	Any manipulation of the teeth (side to side or in chewing motion) in the absence of food/objects
Body shake	Rapidly moving body and head side to side, while remaining stationary (holding on to cage or platform with hands and feet)
Manipulate Object	Any unspecified manipulation of toys, cage, door, locks, etc. Includes manipulating biscuits without eating
Location in Cage – Point sample at 10 s (+30s)	
Front	Majority of body (at least 2/3) is in the front half of the cage
Middle	Body position is directly in the middle of the cage, impossible to judge front or back
Back	Majority of body (at least 2/3) is in the back half of the cage
Movement – Point sample at 10 s (+30 s)	
Move/ Lean away	Retreating or shoulders and head are actively directed away from the tester
Approach/ Lean towards	Approaching or shoulders and head are actively directed towards the tester
Shift	Shifting weight rapidly back and forth or side to side, without moving location in cage. Slower motion than body shake
Lunge	Rapid and abrupt motion towards the front of the cage
Crouch	Elbows touching the cage floor, shoulders lowered
Inactive	No body motion
Locomote	Moving through cage in a non-stereotypic manner, not moving directly “away from” or “towards” tester
Abnormal/Other	Covers stereotypic movements or any other motion not covered by the above categories

Table 4.2: Results of PCA for pigtailed macaques, using the adapted personality test, specifying 4 components and rotated with Varimax rotation. Variables that contribute with a loading of > |0.40| are shown in bold [Joliffe, 2002]. PC is principal component.

Behaviors	PC 1 Aggressiveness	PC 2 Confidence	PC 3 Cautiousness	PC 4 Fearfulness
Lunge (total)	**.86**	-.04	-.06	-.01
Lunge (instantaneous)	**.61**	-.06	-.03	.01
Open mouth	**.71**	.02	.19	-.14
Cage Shake	**.64**	.08	-.09	-.05
Grunt	**.48**	-.22	.07	.21
Quiet face	-.09	**.72**	.05	-.04
LEN to observer	.02	**-.67**	-.06	-.02
LEN to conspecific	-.18	**-.58**	-.29	-.17
Manipulate Object	-.10	**.52**	-.29	-.04
Front of Cage	-.08	**.64**	**-.60**	-.16
Back of Cage	.03	**-.60**	**.59**	.21
Inactive	.06	.04	**.78**	-.03
Approach	.36	.11	**-.58**	-.08
Yawn	.18	.09	**.58**	-.11
Mouth (eat/grind)	.12	.09	**.63**	-.07
Shriek	-.02	-.04	.02	**.95**
Grimace	-.05	.03	-.05	**.93**
Eigenvalue	2.60	2.45	2.38	1.97
Variance Explained	15.32%	14.39%	14.01%	11.57%
Total var. explained	15.32%	29.71%	43.72%	55.29%

Table 4.3: Variables measured in social behavior observations. Behaviors in bold were measured during group aggression observations.

Behavior	**Definition**
Bite	To grasp the hair/skin/limb of another individual with the teeth; may be accompanied by head shaking.
Chase	Focal animal pursues another individual past the location that individual occupied at the start of the interaction; accompanied by Flee behavior by recipient
Displace	Focal animal approaches another, who departs its location; focal animal then assumes that individual's location.
Lunge	Sudden forward charge towards the recipient that does not exceed the recipient's starting location.
Open-mouth threat	Mouth open without showing teeth, usually accompanied by thrusting head toward another individual. Eyebrows raised and ears pulled back; the mouth corners and lips are tensed, forming a rounded opening
Rough behavior	Agonistic interaction involving slight physical contact and usually no facial or vocal components: includes grabbing, kicking, pulling, pushing, poking, slapping, pulling hair, or shoving
Yawn	To open the mouth widely, baring the teeth while tilting the head back.
Avoid	Focal animal locomotes away from an approaching animal (moves aside without physical interaction)
Fear-grimace	Lips pulled back bearing teeth, in "smile"
Flee	Rapid withdrawal following aggressive behavior by another individual; may be accompanied by Chase
Rump Present	Orientation of the hindquarters toward another individual, usually accompanied by lowering the forelimbs, lifting the tail, and looking over the shoulder
Approach	One individual moves into proximity (within 1 m) of another, NOT accompanied by avoid or chase
Groom-initiate	Using fingers to sort through another individual's hair
Groom-receive	Laying or sitting next to an individual who is sorting through the hair of the stationary individual
Lipsmack	Quick movement of the jaw pressing the lips together
Contact	Individual is making physical sustained contact (>2 sec.) with another individual with any part of the body.
LEN	Lips forward, ears back, neck extended
Social Play	Physical contact/interaction without visual threats or vocalizations. Includes play-fighting
Mount	One individual interacts with another from behind, touching front of body to back of another's body; including but not limited to hip touch, foot clasp, thrusting

Table 4.4 – Results of logistic regression, predicting socialization success from either differences in personality scores or sum of personality scores.

	Variable	Odds Ratio	SE	p
Analysis 1 – Score differences	Aggressiveness	-0.22	0.43	.73
	Confidence	-0.12	0.64	.77
	Cautiousness	-0.31	0.43	.51
	Fearfulness	2.71	1.54	.08
Analysis 2 – Score means	Aggressiveness	1.14	0.90	.20
	Confidence	0.50	0.40	.21
	Cautiousness	0.82	0.64	.20
	Fearfulness	-1.39	1.22	.25

Table 4.5 - Frequency and duration of behaviors observed in video-recorded observations of pair-housed animals.

Behavior	Mean	SE	Range	Mean percentage time
Affiliative behaviors – duration in seconds				
Contact	72.80	17.22	0 – 2133	2.0%
Groom	437.29	47.61	0 – 3266	12.1%
Play	22.94	6.68	0 -707	0.6%
Rump	13.15	1.64	0 – 117	0.4%
Mount	7.11	1.29	0 – 99	0.2%
Total Affiliative	553.28	51.81	0 - 3316	15.4%
Fear/ Aggressive behaviors – frequency per hour				
Fear	0.28	0.09	0 - 12	n/a
Rough	0.08	0.02	0 – 2	
Bite	0.02	0.01	0 – 1	
Lunge	0.16	0.07	0 – 8	
Open	0.34	0.12	0 – 17	
Yawn	1.02	0.19	0 – 24	
Flee	0.05	0.04	0 – 6	
Total Contact	0.26	0.08	0 – 8	
Total Noncontact	1.41	0.24	0 - 24	

Table 4.6 – Results of linear regressions of a) *difference* in pair personality scores and b) mean of pair personality scores. In both tables, outcome variables are minutes of affiliative behavior, and frequencies of contact and non-contact aggression, calculated from video recordings of pairs.

4.6 a	Mean minutes of Affiliative Behavior			Mean Contact Aggression			Mean Non-contact aggression		
Difference of scores:	B	*SE B*	*p*	B	*SE B*	*p*	B	*SE B*	*p*
Aggressiveness	2.25	1.18	.07	-0.21	0.11	.08	-0.43	0.16	.01 **
Confidence	-0.16	1.19	.89	0.03	0.11	.76	-0.03	0.16	.84
Cautiousness	-2.91	1.42	.05 *	0.05	0.14	.70	0.06	0.19	.74
Fearfulness	20.23	6.03	.003 **	-0.25	0.59	.68	-0.03	0.79	.97
R^2	0.36			0.17			0.29		
F(4, 24)	3.34 (p=.03*)			1.24 (.32)			2.46 (p=.07)		

4.6 b	Mean minutes of Affiliative Behavior			Mean Contact Aggression			Mean Non-contact aggression		
Mean of scores:	B	*SE B*	*p*	B	*SE B*	*p*	B	*SE B*	*p*
Aggressiveness	-2.98	3.26	.37	0.06	0.02	.02*	0.94	0.35	.01 **
Confidence	0.92	2.50	.71	0.04	0.02	.05*	0.47	0.27	.09
Cautiousness	1.43	3.10	.65	-0.02	0.02	.34	-0.48	0.34	.17
Fearfulness	8.57	12.88	.51	-0.13	0.10	.19	-1.36	1.40	.34
R^2	0.12			0.29			0.33		
F(4, 24)	0.79 (p=.54)			2.50 (.07)			2.99 (p=.04 *)		

Table 4.7 - Frequency and duration of behaviors observed in focal observations of large social groups. Rates are calculated per observation hour, for easier comparison with Table 4.4. Based on 1166 5-minute observation sessions.

Behavior	Mean	SE	Range	Mean percentage time
Affiliative behaviors – duration in seconds				
Contact	19.72	3.47	0 – 536	6.57%
Groom	19.87	5.62	0 – 880	6.62%
Play	0.06	0.08	0 -23	0.02%
Rump	2.33	1.25	0 – 405	0.78%
Mount	0.77	0.34	0 – 53	0.26%
Total Affiliative	42.76	7.21	0 - 1079	14.25%
Fear/ Aggressive behaviors – frequency per five minutes				Frequency predicted per hour
Fear	0.07	0.03	0 – 7	0.80
Rough	0.05	0.02	0 – 3	0.61
Bite	0.005	0.08	0 – 1	0.062
Lunge	0.03	0.02	0 – 4	0.39
Open	0.07	0.04	0 – 8	0.85
Yawn	0.10	0.04	0 – 6	1.24
Flee/Chase	0.08	0.04	0 – 9	0.91
Total Contact	0.09	0.03	0 – 5	1.06
Total Noncontact	0.25	0.07	0 - 13	3.01

Table 4.8– Results of regression of individual personality scores on social behavior measured through focal observations.

	Affiliative Behavior (duration/ observation hour)			Contact Aggression (Frequency / obs. Hour)			Noncontact Aggression (Frequency / obs. Hour)		
Variable	B	*SE B*	*p*	B	*SE B*	*p*	B	*SE B*	*p*
Aggressiveness	0.81	0.74	.28	-0.05	0.17	.79	-0.24	0.33	.47
Confidence	0.65	1.26	.61	-0.36	0.29	.22	-0.44	0.56	.43
Cautiousness	-0.68	1.04	.52	-0.31	0.24	.20	-0.50	0.46	.28
Fearfulness	0.68	0.52	.20	0.10	0.12	.39	0.46	0.23	.05 *
R^2	0.02			0.05			0.06		
F(4, 131)	0.83 (p=.51)			1.82 (.13)			2.07 (p=.09)		

Table 4.9: Results of regression of individual personality scores on social behavior measured through focal observations **for females in breeding groups only** (N=89).

	Affiliative Behavior (duration/ observation hour)			Contact Aggression (Frequency / obs. Hour)			Noncontact Aggression (Frequency / obs. Hour)		
Variable	B	*SE B*	*p*	B	*SE B*	*p*	B	*SE B*	*p*
Aggressiveness	0.79	0.50	.12	-0.001	0.002	.97	-0.005	0.005	.37
Confidence	1.29	0.86	.14	-0.004	0.003	.25	-0.01	0.009	.16
Cautiousness	-1.57	0.69	.03*	0.001	0.002	.83	-0.001	0.008	.93
Fearfulness	-1.13	0.61	.07	0.004	0.002	.04*	-0.001	0.007	.87
R^2	0.12			0.06			0.04		
F(4, 83)	2.80 (p=.03)*			1.39 (.24)			0.80 (p=.53)		

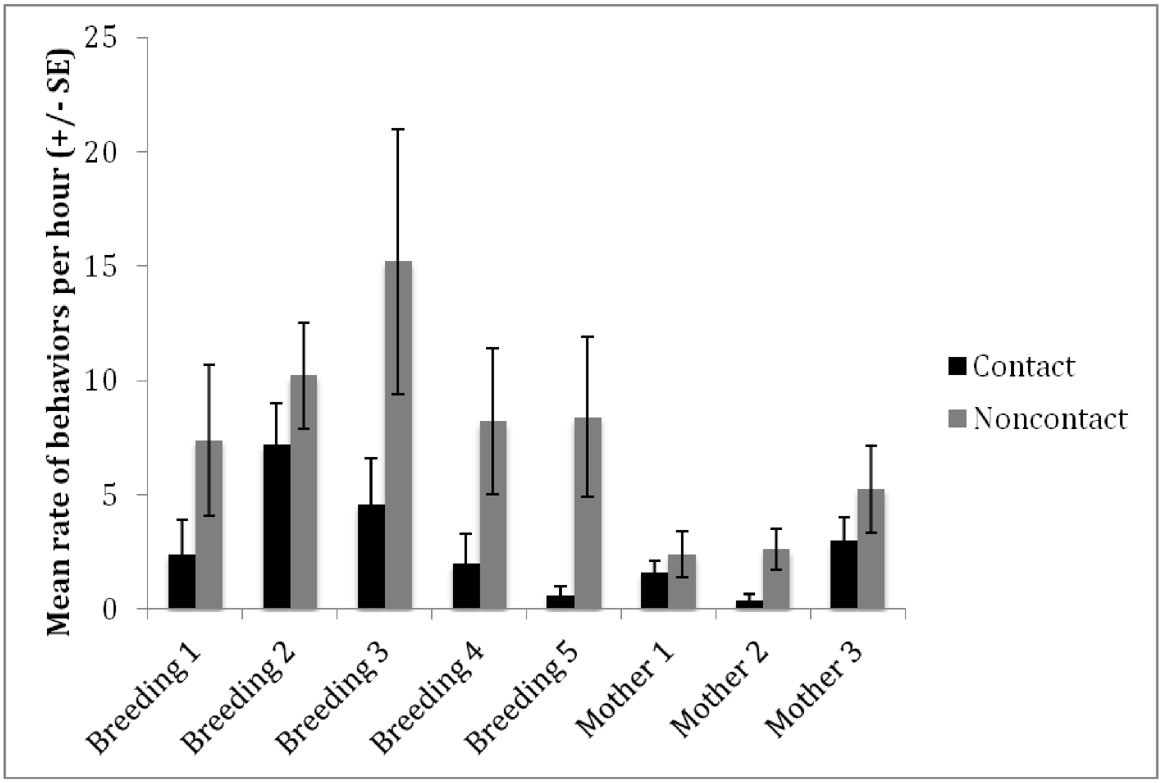
Table 4.10: Regression of personality component scores on simple association index scores.

		Association Index		
		B	**SE B**	**p**
Model 1 – differences in pair scores	Aggressiveness	-0.003	0.003	.20
	Confidence	0.01	0.005	.07
	Cautiousness	0.002	0.004	.70
	Fearfulness	-0.004	0.003	.86
	R^2	0.01		
	F(4, 554)	1.39 (p=.24)		
Model 2 – means of pair scores	Aggressiveness	-0.001	0.002	.60
	Confidence	-0.003	0.004	.41
	Cautiousness	-0.001	0.003	.77
	Fearfulness	-0.001	0.002	.56
	R^2	0.004		
	F(4, 554)	0.50 (p=.73)		

Table 4.11 -- Results of Pearson's correlations of mean and variance of personality scores within a group with all-occurrences aggression and mean duration of affiliative behavior in that group. Power is given as 1-β, and significant results are indicated by *.

		Mean Contact Aggression			Mean Noncontact Aggression			Mean Affiliative Behavior		
	Personality component	R	p	1-β	R	p	1-β	R	p	1-β
Group Mean Score	Aggressiveness	0.48	.23	0.20	0.18	.67	0.06	0.49	.21	0.21
	Confidence	0.28	.50	0.08	0.53	.17	0.25	0.23	.59	0.07
	Cautiousness	-0.25	.54	0.07	0.08	.85	0.04	-0.45	.26	0.18
	Fearfulness	-0.38	.35	0.13	-0.51	.19	0.23	-0.57	.14	0.29
Group Variance in Scores	Aggressiveness	0.71	.05 *	0.51	0.32	.44	0.10	0.71	.05*	0.51
	Confidence	0.41	.32	0.15	0.15	.72	0.05	0.66	.08	0.42
	Cautiousness	0.61	.11	0.34	0.39	.34	0.14	0.70	.05*	0.49
	Fearfulness	-0.29	.48	0.09	-0.40	.33	0.14	-0.54	.16	0.26

Figure 4.1 – Comparison of all-occurrences rates of contact and noncontact aggression between five breeding groups (adult male and females only) and three mother-infant groups (mothers and infants only).



Chapter 5: Conclusions

In the previous chapters, we demonstrated that individual behavioral differences (i.e., temperament or personality) are identifiable in both infant and adult macaques. In infants and adults, these individual differences follow predictable developmental patterns of change. In addition, adult personality scores differ between species in ways that parallel known species-typical differences in social behavior.

Infant temperament scores were predictive of behaviors in small social groups, and adult personality scores predicted behaviors observed among pairs of adults. Adult personality was also predictive of some social behavior in large groups of adults, and group personality make-up was related to a group's average aggressive and affiliative behaviors.

Throughout the preceding chapters, we explored interpretations of specific results in detail. Here, we offer some broader implications of these results and suggest future areas of research.

Major Finding 1 – Personality stability and change

One of the major findings of our work, discussed in Chapters 2 and 3, is that temperament and personality follow predictable patterns of change with age. At the same time, we showed that individuals' personality scores are fairly stable over shorter periods, with reliability scores similar to those reported elsewhere in the literature.

This pattern of short-term reliability coupled with long-term change closely mirrors what is seen in the human literature. Human developmental researchers have shown that infants and children tend to become less extreme in their temperament scores over time [Kagan, 1997], and we found the same result in infant pigtailed macaques.

Personality in humans also changes predictably throughout adulthood, with changes decreasing with age [McCrae et al., 2000; Roberts & DelVecchio, 2000; Helson et al, 2002; Terracciano et al., 2005; Roberts et al., 2006] - again paralleling our result in pigtailed adults. Finally, in human studies, these changes in adulthood tend to be less extreme than the changes observed earlier in life – a finding that is also consistent with the dramatic changes observed in our infant studies and the more subtle changes in our adult personality studies.

These predictable developmental changes may be attributed to a number of factors. For example, they might be caused by changes in reproductive hormones throughout the lifetime, in expression of genes in adulthood, or simply due to experiences that typically occur in adulthood. In our macaques, for example, "typical" experiences might include reproducing, changes of the dominant male in a group, or moving to the lab environment (discussed in Chapter 3). Understanding the physiological causes of these lifetime personality changes is an area that requires future research.

Overall, the finding that temperament and personality develop similarly in macaques as in humans suggests a new area for animal behavior research. Very few animal studies take age into account when calculating personality scores (see, for example, [Bell et al., 2009]), and when they do, they often only distinguish between large categories, such as infants, adolescents, and adults. Studies that do look at developmental changes over long time periods have not always been consistent with the results show here [Stevenson-Hinde et al., 1980]. Further research is needed to understand these discrepancies in study results, and perhaps pinpoint some of the developmental events that lead to changes in temperament or personality. Comparative research would be an ideal avenue to better understand these developmental changes, so we encourage other researchers to further their study of the relationships between personality and age in other species. Our results also suggest that including age as a variable in studies of personality may be important, since personality and age appear to be related.

Major Finding 2 – Personality Across Contexts

Another major implication of our findings is that individual differences can be consistent across contexts. In particular, we found that infant temperament and adult personality scores that were measured in the context of an animal-human interaction within a familiar home environment were also predictive of social interactions with conspecific in a different environment.

Several other animal studies have demonstrated generalizability across contexts. For example, Capitanio found that personality in adult rhesus macaques predicts stress responses to an unstable social situation and response to a threatening human tester [Capitanio, 1999]. On the other hand, several studies found varied responses across contexts in great apes, bighorn ewes, and great tits [Uher, Asendorpf, & Call, 2008; Reale, Gallant, Leblanc, & Festa-Bianchet, 2000; Carere et al., 2005]. Most published personality work does not compare personality scores with behaviors measured in a different context at all, making it difficult to understand overall which types of traits tend to generalize across contexts and which do not. Better understanding of the generalizability of personality traits may help us understand both their physiological underpinnings and their adaptiveness.

In our results, Boldness and Reactivity in infants were approximately equal predictors of infant social behavior, but among adult personality components, Aggressiveness was a better predictor than other components. This suggests that infant temperament is more generalizable across contexts than adult personality, perhaps because infant behavior is more closely tied to physiological processes, while adult behavior is also influenced by external factors like dominance status of social partners and individual experiences. Understanding these differences between infant and adult behaviors would be a fascinating avenue of study. A first step in this direction would be to quantify the links between genetic or hormonal correlates of temperament/personality, and the strength of their links to behaviors in younger vs. older animals. Our prediction is that all links between biology, individual differences (measured in a nonsocial context, as they are here), and social behavior will be stronger in infants and young animals than in older animals. However, these relationships might vary depending on the group size, the experiences of the animals in a group, and the species.

We highly recommend, based on our results for infants and adults, that other researchers measure temperament/personality in a non-social context. We believe that our methods were reliable, repeatable, and simple, compared to other methods reported in the literature. For both infant temperament and adult personality, our measurements were highly reliable between observers, and were very time-efficient. More importantly, measuring personality in a different context from the animal's natural context allows for more research into the impact of the social setting on behavior. We believe more research with these methods will shed light on the interplay between genes, physiological processes, and social behavior in social animals.

Major Finding 3 – Personality and group differences

A third important finding of our research was that individual differences (temperament or personality) predicted social behaviors strongly in small groups (Chapter 2) or pairs (Chapter 4), but more weakly in large social groups (Chapter 4). We believe that hormonally induced changes in behavior throughout the female reproductive cycle may be a major part of this discrepancy. Female-female interactions in large groups may be impossible to predict fully without factoring in these hormonal effects. Moreover, the dominant male's personality may be a driving force in determining group dynamics, as discussed in Chapter 4. We recommend continued study of personality and group social behavior, with these and other factors incorporated, to better understand these relationships.

While these confounds (female reproductive hormones and male personality) alone may account for the weak relationship between personality and social behavior in large groups, our results also suggest that the relationship between personality and social behavior is stronger in smaller groups. We recommend that researchers test the relationships between personality and social behavior in single-sex adult groups with 3-10 group members (accounting for the effects of adult female hormones, as mentioned). Such a study would help identify the point between pairs and large groups at which the predictive power of personality weakens. Pinpointing this relationship between group size, personality, and social behavior would give a crucial piece of information, allowing us to more accurately model the relationship between personality and social behavior in groups.

Major Finding 4 – Personality and species differences

We found that species differ in their average personality trait scores, in ways that are consistent with their species-typical social behaviors. We also found that the variance in personalities present in a group does significantly predict that groups' social behavior, and that personality predicts an individual's behavior in a social group (though it is less predictive in large groups). Together, these results support the idea that personality might be the basis for the evolution of species social differences. Our findings fit with several other empirical, theoretical, and modeling studies supporting the idea that individual personality is the factor that predicts the behavioral dynamics of a group [Dall et al., 2004, Capitanio, 2004; Sih & Watters, 2005; Hemelrijk & Wantia, 2005; Puga-Gonzalez, Hildenbrandt, Hemelrijk, 2009].

Because natural selection acts on the individual, not the group level, the evolution of social behavioral differences between species is not well understood. As described in Chapter 1, most explanations for the evolution of species social differences focus on the adaptive value of the species-typical social behavior, without much emphasis on which individual-level traits are selected for in each species. While group social behavior can be adaptive, some selective force must also be acting on individuals to create those adaptive group-level traits. The results presented here suggest that individual differences, or personality, might be the individual-level trait that is selected to result in differing group dynamics. In light of this mounting evidence, we believe that it would be appropriate to revisit older studies of the adaptive value of group differences in a "personality framework".

As several recent studies have shown, different personality traits can be advantageous to an individual in different environmental conditions, and the mixture of personality types in a population might represent an evolutionary stable state (ESS; e.g., [Dingemanse et al., 2004]). This type of framework should be tested in the macaques, as well. For example, rather than trying to understand the differences between rhesus and pigtailed macaques by understanding why their existing group structure is adaptive, it would be interesting to examine the average distribution of personality scores in each species. If the personality scores present represented an ESS, as in great tits [Dingemanse et al., 2004], and personality predicts social behavior, then it is possible that the social dynamics observed might be a result of selection on personality, rather than an adaptation in themselves. We encourage other researchers to continue study in this area, as this may be one of the major ways in which the study of personality in animals can impact our understanding of the evolution of social behavior.

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