ANIMAL BEHAVIOUR, 2008, 76, 455–465
doi:10.1016/j.anbehav.2008.01.024

Individual differences in infant temperament predict social relationships of yearling rhesus monkeys, *Macaca mulatta*

TAMARA A. R. WEINSTEIN* & JOHN P. CAPITANIO†
*Department of Psychology, University of California, Davis
†California National Primate Research Center

(Received 28 April 2007; initial acceptance 5 June 2007; final acceptance 4 January 2008; published online 20 June 2008; MS. number: A10758R)

Affiliative relationship formation in nonhuman primates is influenced by kinship, rank and sex, but these factors do not fully explain observed variation in primate social relations. Individual differences in temperament have a number of important behavioural and physiological correlates that might influence relationship formation. We observed 57 yearling rhesus macaques at the California National Primate Research Center for 10 weeks to determine whether individual differences in temperament relate to the number and quality of affiliative relationships formed with peers. Subjects' temperament characteristics had previously been quantified during a colony-wide biobehavioural assessment when subjects were 90–120 days of age. Yearlings that had scored high on equability (showed calmness and low levels of physical activity) as infants had fewer peer relationships than yearlings that had scored low on this dimension. In addition, yearlings preferentially affiliated with peers that had similar equability and adaptability scores (reflecting the degree of behavioural flexibility that subjects displayed during the biobehavioural assessment). Although kinship, rank and sex influenced relationship formation as expected, temperament remained a significant predictor of affiliative preferences even after controlling for these variables. Our findings suggest that temperament is a proximate determinant of variation in affiliative relationship formation in group-living primates.

Keywords: affiliation; juvenile; *Macaca mulatta*; personality; relationships; rhesus macaque; social behaviour; temperament

In nonhuman primates, affiliation, typically defined by such behaviours as proximity, contact, grooming and play, constitutes a central component of social living. Frequent affiliative interactions between specific individuals over a period of time give rise to affiliative relationships or 'friendships' (Hinde 1976), which may benefit individuals in a variety of ways. For example, male friends may protect females and their infants (Manson 1994; Palombit et al. 1997), males may gain increased opportunities to mate with their female friends (Hill 1990), and in the presence of friends, individuals may show an attenuated behavioural and physiological response to an acute stressor (Higley et al. 1992; Gust et al. 1994; Boccia et al. 1997; Beehner et al. 2005). Even outside the context of friendship, affiliative interactions are associated with important fitness-related consequences; grooming, for example, can be exchanged for agonistic support (Silk 1992; Hemelrijk 1994), food (de Waal 1989), protection against harassment (Silk 1982) and access to infants (Muroyama 1994; Henzi & Barrett 2002). Postconflict affiliation prevents further aggression from developing and reduces distress and uncertainty (Silk 2002). The tension-reducing effects of affiliation, particularly grooming, are evident even in the absence of prior agonistic encounters (Schino et al. 1988; Aureli et al. 1999). In fact, grooming bouts that occur neither following aggression nor in exchange for commodities are quite frequent, and probably function to establish and maintain cohesion amongst group members (Rowell et al. 1991; Borries et al. 1994; Cooper & Bernstein 2000).

Nonhuman primates begin forming affiliative relationships with their groupmates during juvenility, and such

Correspondence and present address: T. A. R. Weinstein, Department of Psychology, Simpson College, 701 North C Street, Indianola, IA 50125, U.S.A (email: tamara.weinstein@simpson.edu). J. P. Capitanio is at the California National Primate Research Center, University of California, One Shields Avenue, Davis, CA 95616, U.S.A.

0003–3472/08/$34.00/0

friendships can persist through adulthood. For juveniles, formation of peer relationships reflects a transition from affiliating primarily with the mother to becoming a fully integrated member of the group (Hinde & Spencer-Booth 1967). Crucial to the success of this integration is the mastery of myriad complex social skills, which arises out of juveniles' social interactions (Joffe 1997). For example, social play, a behaviour seen primarily in the juvenile period, has long-been considered important in this regard (Poirier & Smith 1974). Relationships formed during juvenility have been suggested to play a vital role in facilitating the acquisition and formalization of dominance rank during adolescence (de Waal & Luttrell 1985; Datta 1988). Moreover, relationship formation during juvenility may have long-term fitness consequences, because the degree of social integration during adulthood affects reproductive success independently of dominance rank or environmental condition (Silk et al. 2003).

Individuals display specific affiliative preferences in that they only establish relationships with certain groupmates; the number and qualities of such preferences vary from individual to individual. Studies investigating the proximate basis of this variation have found that animals often form relationships based upon kinship, sex and rank (Seyfarth 1977). For example, animals generally prefer to affiliate with kin over nonkin, with same-sex groupmates over those of the opposite sex, and with similarly ranked animals over distantly ranked animals (de Waal & Luttrell 1986; Ehardt & Bernstein 1987; Nakamichi 1996). The extent to which affiliative relationship formation fits these general patterns, however, often depends upon the specific behaviour in question (e.g. grooming relationships are often more kin biased than play relationships), and many exceptions to these patterns exist (Janus 1989; de Waal 1996; Nakamichi & Shizawa 2003). Studies typically overlook this 'unexplained' variation in affiliative preferences, however, in favour of stressing the abovementioned general patterns (although see Nakamichi & Shizawa 2003).

Unexplained variation in affiliative preferences probably arises from individual-specific characteristics that have yet to be examined in this context. Research in humans has suggested that personality may be an influential factor. For example, the human trait extraversion is related to the size and quality of an individual's social network (e.g. Asendorpf & Wilpers 1998). The study of personality has recently attracted increasing interest from animal behaviour researchers (Weinstein et al., in press). The term 'personality' refers to individual differences in behaviour that persist over time and across situations, and many consider it interchangeable with terms such as 'temperament', 'behavioural syndrome' or 'style' (Clarke & Boinski 1995; Gosling 2001; Sih et al. 2004). Individual variation in personality reflects stable differences in underlying affective, motivational, physiological and cognitive processes, which are influenced by both genetic and environmental factors (Champoux et al. 2002; van Oers et al. 2005). Personality is often assessed by measuring individuals' responses to novel or stressful stimuli, and studies of nonprimates typically classify these responses along a shy–bold continuum (Wilson et al. 1993; Verbeek et al. 1994). Individual variation along this continuum has been related to variation in aggressiveness, exploratory behaviour, response to predators, foraging behaviour, social learning and risk taking in birds, fish and insects (Sih et al. 2004). In addition to direct measures of behaviour, personality is often assessed using researchers' ratings on behaviourally defined trait adjectives (e.g. aggressive, curious, playful), which are conducted after having observed the animals either in a natural social setting or in a variety of experimenter-designed situations (Capitanio 2004; Weinstein et al., in press). These trait ratings are broad, qualitative descriptors of the individual's overall style of responses, and are usually investigated using factor analysis or principal component analysis to identify higher-order factors reflecting underlying latent traits (Itoh 2002). The resulting factors are strongly rooted in empirical data, show high reliability and longitudinal stability, are replicable with different samples, and relate to behavioural variation in both social and nonsocial situations (Weinstein et al., in press).

Although individual variation in personality in nonhuman primates has been associated with a number of important behavioural and physiological correlates, such as early rearing experience, dominance status, aggressive and affiliative behaviour, immune function, and personality characteristics of offspring (Weinstein et al., in press), few studies have examined the relationship between personality assessed at one time point and social outcomes at later time points. Exceptions include studies by Capitanio (1999), who found correlations between personality factors in adult male rhesus monkeys and behaviour recorded in several different social situations up to 4 years following the original personality assessments, and by Fairbanks et al. (2004), who found that individual differences in impulsivity during adolescence predicted adult dominance status in male vervet monkeys, *Cercopithecus aethiops*.

We are aware of no studies, however, that have examined the role of personality in affiliative relationship formation. Given that much variation in relationship formation remains unexplained, we investigated whether measures of infant temperament predict the quantity and quality of relationships that an individual forms during juvenility. We examined relationships of different behavioural content (e.g. proximity versus play relationships), complexity (relationships in one versus multiple content areas) and quality (i.e. reciprocated relationships). We were also interested in whether individuals may be attracted to groupmates with similar temperament characteristics.

METHODS

Subjects and Living Arrangements

Fifty-seven yearling rhesus macaques (29 males) were sampled across four half-acre (0.19 ha) outdoor corrals at the California National Primate Research Center (CNPRC). These corrals consist of large multimale, multifemale groups comprising all age/sex classes, and group sizes of the corrals in our study ranged from 96 to 146 animals