Personality and social relationships in captive chimpanzees *(Pan troglodytes)*

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Table of Contents

Abstract

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This thesis explores the use of personality trait ratings of captive chimpanzees, and examines how such ratings might relate to social behaviour.

A number of previous studies have utilised trait rating scales to investigate the personality of nonhuman species. The present study explored the use of a constructivist method of generating personality trait terms to construct a rating instrument that adequately reflected perceived variation in chimpanzee personality. The repertory grid method developed by Kelly (1955) was used to generate relevant personality descriptors, and a sample of chimpanzees from seven different zoos were rated using this instrument. An analysis of the ratings produced four clear personality factors: Sociability, Dominance, Anxiety and Curiosity, which appear very similar to factors produced in previous work on primate personality. Ratings for one group of chimpanzees were compared over a three year period and high cross-temporal consistency was found for most of the items on the rating scale.

Personality factor scores of a sample of chimpanzees housed at Chester zoo were compared to a range of affinitive and agonistic behaviour patterns. Despite the small sample size, strong relationships were found between scores on each of the four factors and frequency and duration measures of time spent alone, time spent in proximity, grooming, play and agonistic interactions. However, the effects of age and sex on trait-behaviour relationships suggested that some of the variation between individuals reflects differences in individual adaptive strategies.

To examine the relationship between personality ratings and behaviour in more depth, information regarding the distribution, reciprocity and intensity of social interactions was obtained. Previous researchers (e.g. Hinde, 1976) have highlighted the importance of an understanding of the dynamics of social relationships and social structure in the study of individual differences. The present findings suggest that an understanding of such relationship parameters can clarify the description and interpretation of within-species differences.

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For C
For the chimpanzees
and for the two Poppies, in memory.

In reality, any attempt to express the inner nature of a thing is fruitless. What we perceive are effects, and a complete record of these effects ought to encompass this inner nature. We labour in vain to describe a person's character, but when we draw together their actions, their deeds, a picture of their character will emerge.

Johann Wolfgang von Goethe, Theory of Colour
(in Naydler, 1996: 33).

CHAPTER ONE

The concept and measurement of personality in nonhuman animals

1.1 Introduction

The study of individuality is fundamental to psychology. Yet the history of personality psychology, perhaps more than any other field within the discipline, has long been characterised by a state of tension. Ironically, for a field which today is one of psychology's more prolific research arenas, this tension is characterised by a profound disharmony among researchers regarding the very nature of their subject. While most subject areas experience an uneasy blend of different perspectives, emphases and methodologies, the greatest discord between personality researchers is focused on the nature of the concept of personality itself. This is also true of the study of nonhuman personality. This chapter will explore research into nonhuman personality in the context of a general critique of personality theory.

It is perhaps easier to identify the aims of personality research than to attempt a definition of the concept. Indeed, the latter enterprise has often produced a confusing array of positions, from Cattell's crisp denotation:

> ...that which permits a prediction of what a person will do in a given situation. (Cattell, 1950: 2, cited in Lamiell 1987: 5)

to Allport's more expansive translation:

> ...the dynamic organisation within the individual of those psychophysical systems that determine his characteristic behaviour and thought. (Allport, 1961: 28, cited in Lamiell 1987: 5)

Even though it may be true to say that "defining personality is itself a matter of personality" (Lamiell, 1987: 5), what unites this plurality of perspectives is a basic recognition of both the consistency and variability of behaviour. Research on human personality has variously sought to delineate the structure, function and behavioural correlates of personality in a scientific way. The application of the concept of personality to nonhuman animals has, in its time, focused on all of these issues. Theoretically, however, it has been influenced by many of the changing fashions in the human personality field. Researchers have borrowed theoretically and empirically from the field of personality psychology, and nonhuman personality research today clearly mirrors the dominant motifs of human personality work. In this chapter, the main studies of nonhuman personality research will be placed in their broader theoretical and methodological context, and their findings discussed in the framework of questions regarding the structure and function of personality.

1.2 The structure of personality

1.2.1 The physiological basis of emotional expression

The relationship of personality to behaviour is not a clear one. However, the foundations of work on nonhuman personality were phrased very clearly in terms of action. Darwin was perhaps the first writer to explicitly link nervous system activity with emotional expression. In *The Descent of Man* he stated:

> We have seen that the senses and intuitions, the various emotions and faculties, such as love, memory, attention, curiosity, imitation, reason &c., of which man boasts, may be found in an incipient, or even sometimes in a well developed condition, in the lower animals. (1871: p. 105)

In this work, Darwin suggested that nonhuman animals possessed the entire range of human subjective experience. A year later, in *The Expression of the Emotions in Man and Animals*, he documented gestures and facial expressions which he assumes are indicative of various subjective states: jealousy, rage, curiosity, disappointment. A key theme of Darwin's writing on emotion was his emphasis on the continuity of emotional expression and subjective feelings across taxa. In both humans and nonhumans, individual expressiveness was tied closely to variations in nervous system functioning, though the exact nature of this link was not understood fully at this time (Ekman, 1998).

The link between biology and personality was echoed almost seventy years later by Robert Yerkes. Yerkes drew parallels between personality traits of humans and chimpanzees, and suggested that, for the latter, personality should be seen as 'the unit of social organization.' Yerkes' concept of personality was as "the product of integration of all the psychobiological traits and capacities of the organism." (Yerkes, 1939: 30).

In an influential paper some years later, Hebb attempted to formalise the processes utilised by human observers in ascribing emotional states to chimpanzees (Hebb, 1946). Hebb based his efforts on human-chimpanzee interactions at the Yerkes Laboratory, and his conclusions regarding these interactions reflect many of the important themes that characterised the field of nonhuman (and human) personality research in ensuing years. In attempting to identify a causal basis for emotional expression, Hebb relied on a general theory of physiological arousal, as have many researchers since, most notably Eysenck (1967). As Claridge notes, Eysenck's explanations of personality dimensions in terms of nervous system excitation and inhibition drew on earlier research by Pavlov and Hull; indeed Pavlov himself had conducted some early work on individual differences in the temperament of dogs, proposing nervous system variation as the cause of these differences (Claridge, 1985). While it is true that in more recent years general models of arousal have been found wanting (Buss, 1991), personality research in nonhumans continues to be influenced by physiologically based theories of emotional variation.

1.2.2 Emotion, temperament and traits

In classical ethology, functional explanations of behaviour have focused more on group norms, rather than individual differences. From this perspective, variation between individuals has often been seen as an inconvenience, rather than as providing an additional source of information (Stevenson-Hinde, Stillwell-Barnes and Zunz, 1980a). If attention has been directed at intraspecific variation, this has usually highlighted individual variations in mating, foraging and other strategies (Slater, 1981); such variation, if conceptualised as the product rather than the material of natural selection, specifies the notion of optimality as extraneous (Wilson, Coleman, Clark and Biederman, 1993).

Modern studies of nonhuman personality have relied on a range of explanatory principles to elucidate behavioural differences between animals. While some researchers have relied on the concept of traits, others have emphasised the simpler functional characteristics of emotion and temperament (see Gosling, 2001 for a comprehensive review). The relationship between the three concepts remains uneasy, however, and their definition and use is often confused within the field. This may well reflect the genuine difficulty of addressing the proximate causes of complex behaviour. It may also point to a general unwillingness to appropriate such psychologically loaded concepts as personality and apply them to nonhumans. Perhaps for this reason, the concept of temperament, with its basis of physiologically derived emotional expression, has functioned as an important link between the more anecdotal accounts of Darwin and Hebb and later attempts to empirically verify individual differences.

1.2.3 Studies of temperament in nonhuman primates

Allport defined temperament as an individual's "emotional nature, including his susceptibility to emotional stimulation, his customary strength and speed of response, the quality of his prevailing mood, and all the peculiarities of fluctuation and intensity in mood." (1961: 34, cited in Carver and Scheier, 1992). Current researchers (e.g. Buss and Plomin, 1984) emphasise the genetic basis of temperament as inherited patterns of responding (Carver and Scheier, 1992). In their review of the concept of temperament in primates Clarke and Boinski (1995) have noted that temperament is more usually defined in terms of reactivity or response style in novel or potentially stressful situations. In humans, dimensions such as bold-shy and fearful-unfearful have been used to characterise responses to novel stimuli, and studies of nonhuman temperament have utilised similar dimensions (Clarke and Boinski, 1995).

Temperamental differences in humans and nonhumans have been linked to a number of physiological, hereditary and environmental factors.

For example, Suomi (1991) described two basic styles of responding in rhesus monkeys. Uptight animals are shy and fearful when presented with novel stimuli, and are classified as 'highly reactive'. Laidback individuals respond to novel stimuli in a more relaxed manner and are more flexible in adapting to novel or stressful situations. Differences in reactivity level, tested using Brazelton's (1973) Newborn Behavioural Assessment Scale, appear to be present in the first few weeks of life, and to be strongly related to physiological factors. In novel situations more reactive individuals show higher heart rate and less beat-to-beat variability over the course of the session. Less reactive animals show an initial increase in heart rate which stabilises throughout the session. Differences in reactivity level also appear to be stable over the life span for these animals, but their behavioural expression is to some extent dependent on environmental variables. Behavioural and physiological differences in the rhesus tested by Suomi were mainly apparent in challenging situations, and in particular when these situations were prolonged. When separated from parents or peers, for instance uptight infant monkeys showed withdrawn responses that persisted over the period of separation; laidback monkeys became adapted to the situation.

Both physiologically and behaviourally, reactivity levels appear to be stable over the life span and highly predictive of an individual's behaviour in similar situations across time (Suomi, 1991), although the actual form in which this individual variation is expressed may be situationally specific. When separated from parents or peers, highly reactive infants typically show withdrawal responses; when separation is experienced in adolescence, the individual becomes instead agitated, hyperactive and shows stereotyped responses (Suomi, 1991). By contrast, physiological measures of reactivity, such as cardiac activity and cortisol and adrenocorticotropin levels, remain consistent during an individual's lifetime (ibid.), suggesting the possibility of determining the existence and stability of at least some biobehavioural links.

Suomi (1987) and Higley and Suomi (1989) have attempted to further elucidate the relationships between environmental and genetic factors in temperamental differences. In a series of cross-fostering studies, infants categorised as either high or low reactivity were placed with 'foster' mothers of varying levels of reactivity and nurturance. The infants' early level of reactivity, determined by the Brazelton Newborn Behavioural Assessment Scale, was a much better predictor of their behaviour in subsequent separation experiences than either the foster mother's level of nurturance or reactivity (Suomi, 1987). At 8-9 months of age the infants were permanently separated from their foster mothers and placed into peer groups. Some of these groups contained an old male and female pair (called 'foster grandparents'). The male typically acted to break up fights and control aggression among the young males; the old female acted as surrogate mother for those infants who required her. Results showed that highly reactive infants who had experienced nurturant foster mothers quickly established relationships with the older animals and became the most dominant individuals in the group. In contrast, highly reactive infants who had been fostered by more punitive mothers avoided the older animals and became subordinate members of the hierarchy. Independent of foster mother style, less reactive animals did not establish close relations with the older pair and became intermediate in dominance status. It seems then that the effects of relatively stable levels of reactivity can be mitigated to a certain extent by rearing technique.

Other researchers have focused on the role of physiological arousal in producing stable 'styles' of responding. Chamove, Eysenck and Harlow (1972) rated juvenile macaques on a range of behaviours, including play, contact, exploration and fear behaviours. The animals were observed in dyads, and groups of three and four. A factor analysis of the ratings produced three factors: affiliative, hostile and fearful, which the authors compare with the extraversion, psychoticism and neuroticism factors found in humans. They suggest that the similarity between these factors may be due to similar anatomical structure and nervous system functioning across the primates.

1.2.4 The emotional basis of personality

The extent to which it is possible to generalise across species in terms of a wider range of emotional expression is a difficult issue. Despite this, personality differences have often been conceptualised in terms of emotional or motivational expression. Van Hooff, for instance, attempted to categorise an exhaustive range of primate behaviours in terms of their possible underlying motivation (van Hooff, 1962). He concluded that all behavioural responses can be classified as agonistic, which incorporates the two opposing tendencies to attack and flee, and attraction-repulsion, comprising the tendency to flee and social attraction (Figueredo, Cox and Rhine, 1995). A later analysis (van Hooff, 1973) addressed the question of behavioural motivation in the context of the problem of behavioural classification. Figueredo *et al.* (1995) consider the differences between ethological descriptions of behaviour; i.e. molecular descriptions (e.g. van Hooff, 1973) and more anecdotal, molar descriptions (e.g. Goodall, 1968). To a certain extent, however, both are dependent upon subjective ascription of emotional or motivational states; perhaps the difference lies more in the ability of the former to support those assumptions by explicit and empirical reference to the structural patterning of behavioural sequences.

One strand of nonhuman personality research has utilised the assumption by Plutchik that similar emotions may be found across a range of species (Plutchik, 1970, 1980, 1984, 1989), and that the adaptive function of emotion may be determined by considering its interaction with variables such as sex and age. These studies utilised a rating instrument called the Emotions Profile Index (EPI) developed by Kellerman and Plutchik (1968). According to Plutchik, there are eight basic 'primary emotions' which together constitute all possible emotional expression (Plutchik, 1965). The original form of the EPI consisted of sets of paired-trait words, such as cautious-affectionate, gloomy-resentful (Buirski, Plutchik and Kellerman, 1978). In the human version of the instrument, subjects choose one word from each pair which best describes themselves. The trait pairs are rated by reference to eight scoring categories (corresponding to the eight primary emotions). Various versions of the EPI have been adapted and applied to nonhumans for the purposes of describing personality differences between individuals.

Buirski, Kellerman, Plutchik, Weininger and Buirski (1973) used a specially adapted form of the EPI to rate baboons *(Papio anubis)*. For the purposes of this study the trait words were generated and defined by the observers as being applicable to baboon behaviour. The trait words were paired in all possible combinations and one word chosen from each pair to rate each particular animal. For each animal a score was calculated that reflected its position on each of the eight primary emotions. These personality scores were then compared to dominance and grooming behaviour. It was found that dominant animals were rated lowest on the trait term fearfulness, and highest on sullen, jealous, defiant, belligerent and destructive. These animals were groomed the most, and were groomed for longer than other animals. Less dominant baboons were rated as showing more fearfulness and more sociability.

A similar study was carried out using the 'chimpanzee form' of the EPI with animals at the Gombe Stream Research Centre (Buirski *et al*., 1978). Observers picked one pair from forty-five paired trait terms to describe each animal. The trait pairs represented all possible combinations of 10 trait terms defined by the observers as relevant to chimpanzee behaviour. Trait terms included dominant, sociable and irritable. Each trait term was assumed to represent one or more basic emotions; e.g. sociable implies the two emotions of trust and gregariousness: these assignations were decided by several judges. As with the earlier baboon study (Buirski *et al.*, 1973) inter-rater reliability was moderate to high; the lowest reliabilities were for male chimpanzees. The authors suggest that this may be due to the shifting dominance relationships in the group at the time.

Sex and dominance of the animals were compared to the personality ratings. Female chimpanzees were rated as more timid, trustful and depressed than males, who were rated as more distrustful, aggressive, sociable and impulsive. Dominant animals were rated as more distrustful and aggressive, less dominant individuals were considered to be timid, impulsive and trustful. This is similar to the personality profile for females. It appears from the results that dominance rank was only estimated for males, however, so the nature of the relationship between dominance, sex and personality ratings is perhaps not as clear as it might be.

In discussing the differences between profiles of males and females Buirski *et al.* (1973) propose that these may reflect social and ecological pressures. They suggest that the relative distrustfulness and aggression of the males may be associated with "the need to seek food over a wide and often unknown range of environments" (p. 128). This is an unusual conclusion to draw, since wild chimpanzees feed over a relatively moderate range within which most of the reliable food sources are known. In addition, it is not just the males who range over this area looking for food (although they do seem to range more widely and to travel further than females (Goodall, 1986)). Another sex difference appeared in scores on depression; the authors attribute the higher scores shown by females animals on depression as possibly due to their lower dominance status.

In considering the implications of findings like these, the difficulties associated with studies of emotion in nonhumans become apparent. While it does not seem unreasonable to assume homology of emotion across related genera, distinguishing behavioural correlates of even a small range of emotions is very difficult (and often achieved on the basis of face validity, c.f. Buirski *et al.*, 1973, 1978). In addition, functional explanations of the adaptiveness of various emotions remain speculative at best.

1.2.5 The concept of traits in individual differences research

As Clarke and Boinski (1995) note, the concept of temperament is most commonly applied to the reactivity of an animal in a nonsocial setting, specifically a novel situation. Consequently, many researchers have conceptualised differences between social animals in terms of personality rather than temperament. The relatively more complex nature of personality traits may well be more useful in classifying social responses than the reliance on one or two simple dimensions of reactivity, especially in related phyla (Mather and Anderson, 1993)

Traditionally, the notion that one could reliably differentiate between individuals has depended upon the notion that there exist stable underlying characteristics which form the basis for this variation. That is to say, many personality theories have postulated the existence of traits. According to trait accounts of personality, an individual's behaviour is, at least partially, a reflection of their position on a variety of underlying dimensions, assumed to be normally distributed throughout the population. Opinions have diverged, often fiercely, with regard to the exact nature, quantity and basis of these traits, but suffice it to say for now that nonhuman personality research has made free use of the trait concept.

Perhaps the most divisive issue within the field of personality psychology has been the distinction between nomothetic and idiographic approaches. As applied to the study of personality, the nomothetic approach is characterised by a number of basic assumptions. Firstly, it is assumed that there exists a universal or generic set of personality dimensions, or traits, according to which every individual can be measured. Secondly, the assumption is made that the nature and existence of these traits may be discovered empirically, and operationally (i.e. behaviourally) defined; and thirdly, that general laws may be discovered that specify the nature of the relationship between personality variables and behaviour (Lamiell, 1987). Proponents of the idiographic approach differ in their assumptions regarding the universality of 'common' traits. According to an idiographic perspective (e.g. Allport, 1961), an individual's personality consists of his/her position on both common traits and 'unique' traits; i.e. traits that do not necessarily apply to other people. Although there have been recent reconceptualisations of Allport's basic premises which have sought to unite the principles of nomothetic and idiographic approaches (e.g. Lamiell's 'idiothetic' approach, 1981, 1982, 1986) personality psychology today remains characterised by the nomothetic assumptions of individual differences research.

1.3 Trait-based approaches to nonhuman personality

1.3.1 The issue of consistency

Contemporary studies of nonhuman personality have, often implicitly, been conducted within the individual differences framework. This is apparent in some of the main aims of the field:

1. To discover, for a particular species, and by mathematical and statistical means, the underlying taxonomy by which the personality of individuals may be defined
2. To ascertain the relations between any such personality variables and categories of observed behaviour

3. To determine the relationship between an objective, empirically determined taxonomy of personality variables and more subjective, intuitive personality characterisations made by observers.

Whilst researchers in the field of nonhuman personality have remained undecided about the existence and nature of a taxonomy of traits in their subjects, attempts to validate the applicability of personality nomenclature to nonhumans have often relied upon their implicit use. In both the subjective impressions of observers and the observation of behaviour a certain amount of consistency is assumed. Experienced observers are often confident about their ability to predict an individual's likely behaviour; indeed underlying any observational method lies the assumption that the behaviour of most individuals is reasonably consistent for most of the time. Within personality psychology, the issue of behavioural consistency has been hotly contested. Since its resolution has import for a field which has utilised many of the norms of human personality psychology I shall briefly outline it here.

Two types of consistency are implied by the use of the trait concept. Firstly, behaviour is assumed to be temporally consistent, and secondly to be consistent across a range of situations. These assumptions were called into question by the work of Mischel (1968). Mischel suggested that correlations between behaviours that were assumed to be indicative of the same trait typically fell in the range of .20 to .30. For instance in a study conducted by Sears (1963) nursery school children were rated on five 'dependent' behaviours, e.g. 'negative attention-seeking' and 'nonaggressive touching or holding'. The majority of the correlations between these different behaviours were quite low even though they were supposed to measure the same underlying trait. In attempting to explain this, later investigators (c.f. Bem and Allen, 1974; Bem and Funder, 1978) suggested that the problem lay with the incompatibility of objective, nomothetic analyses of personality and more subjective, idiographic assessments. As Allport had suggested many years before, the assumption that everyone possessed the same set of traits, and that these would be apparent in the same situations, may well be unfounded (Lamiell, 1987). If it is conceived that traits consist of stable underlying characteristics of a person then their measurement becomes necessarily dependent upon their accurate expression through self-reports or behavioural ratings. If the relationship between traits and behaviour is unclear then such instruments may only be partially predictive at best.

1.3.2 Implicit versus explicit theories of personality

The problem of the trait-behaviour relationship may be conceptualised within the larger issue of behavioural interpretation. Since personality studies of nonhumans cannot make use of self-reports (a popular method of personality assessment in human psychology) researchers have utilised observer ratings. Typically, animals are rated on a number of trait terms or behavioural characteristics by experienced observers. These are sometimes supplemented or substituted by recordings of behaviour. Ratings are analysed in order to produce a smaller number of 'higher-level' dimensions. The aim of the majority of these studies is to quantify subjective impressions of individuals and determine whether these impressions bear any relation to the objectively observed behaviour of the animals.

Relatively early on in the history of personality psychology, the validity of subjective impressions of personality had been questioned. Work by Passini and Norman (1966), D'Andrade (1974), Schweder (1975) and others indicated that trait ratings can be heavily influenced by raters' assumptions about which traits should, or are likely to, co-occur. From this perspective, ratings do not reflect actual differences between individuals, rather they are indicative of raters' implicit personality theories (Bruner and Tagiuri, 1954). Given the tension between implicit and explicit personality theories, it seems likely that an adequate conceptualisation of personality measurement must embrace both approaches. As Hampson (1988) and others have noted, ratings of traits or behaviour are necessarily based upon theoretical interpretation.

The same point was essentially made by Hebb (1946), and has in a sense motivated much of the current work on nonhuman personality. Many researchers have commented on the ease and propensity with which observers form subjective impressions of personality characteristics of their subjects, and the concurrent tendency to assume that these impressions are ill-founded or anthropomorphic. However, if subjective ratings are seen as simply an expression of a familiarity with the usual behaviour patterns of the animals, then they may well serve as useful ways in which to organise this knowledge. There is another reason why the traditional favouring of objective descriptions over subjective ones may be problematic. As many authors have noted (e.g. van Hooff, 1973; Harré and Reynolds, 1984), it remains impossible to produce 'pure' objective descriptions of behaviour. Even apparently impartial behavioural categories, such as 'avoid' or 'approach' are based upon assumptions regarding the intentions or goals of the animal. It may therefore be more useful to view any behavioural interpretations as being 'filtered' through the interpretive system of the observer (Stevenson-Hinde *et al.*, 1980a).

It remains important nevertheless to determine to what degree trait concepts of personality can be usefully applied to nonhumans. Studies of nonhuman personality, whilst borrowing heavily from trait structures used in human personality work, have attempted to explore the relationship between behaviour patterns and trait ratings.

For example, Stevenson-Hinde and Zunz (1978) rated rhesus monkeys on a number of behaviourally defined adjectives (e.g., confident, dominant, sociable). The adjectives were chosen by an experienced observer, but reference was made to earlier work on temperament by Sheldon (1942). The animals were rated for two successive years and the following year were rated on an amended version of the adjective set. Correlations between observer ratings were significant on 19 of the original 33 adjectives, and on 23 of the amended 29 item list. Those items that showed inter-rater reliability were subjected to a principal components analysis. The first two components, conceptualised in terms of dimensions, were confident-fearful and active-slow. These two components appeared in analyses over the three years the animals were rated. In the third year, when the amended adjective list was used, a further component appeared: sociable-solitary. Composite scores on each component were calculated for each animal to determine any age or sex differences. Adult males were found to score higher than adult females and 1-5 year olds on the confident-fearful component, higher than adult females on the active-slow component and lower than adult females and 1-5 year olds on sociable-solitary (i.e. adult males were more confident, more active and more solitary). There was also a significant correlation between mothers and their infants in scores on the confident-fearful and sociable-solitary components. In terms of the temporal stability of the traits, individuals' scores over the three years were very consistent (average correlation coefficient for confident-fearful was .92, and for active-slow was .69).

The Stevenson-Hinde and Zunz (1978) rating instrument has also been utilised for the purpose of rating apes. Gold and Maple (1994) used a modified version of Stevenson-Hinde and Zunz' original 23 item adjective list to obtain ratings for 298 captive gorillas. Four factors were found: extraverted, dominant, fearful and understanding. These are similar to some of the original Stevenson-Hinde and Zunz factors of confident-fearful, sociable-solitary and active-slow.

In a later study (Stevenson-Hinde *et al.*, 1980a) ratings of rhesus monkeys on the same adjective list were correlated with a range of behavioural measures. Ratings on the trait aggressive were correlated with the total number of hits, threats and chases directed towards other group members. Scores on effective were correlated with total occurrences of displacement of others and avoidance by others; excitable with the sum of displays and threats directed outside the enclosure; fearful with total number of fear grins and avoidance of others; and playful with the sum of occurrences of playful behaviour (Stevenson-Hinde *et al.*, 1980a). In addition ratings on the sociable factor were correlated with the total number of individuals a given animal was in contact with over a sampling period. Correlations between all ratings and their associated behaviours ranged from .45 to .73.

One problem with any attempt to examine trait-behaviour relationships is the difficulty of deciding which behaviours might be indicative of a particular underlying trait. Stevenson-Hinde *et al.* (1980a) obtained summary scores for each animal based upon the items that loaded most heavily on each component. These scores reflected an individual's position on three dimensions: confident, excitable and sociable. Scores for mothers and their infants were significantly correlated for confident (.48) and sociable (.60) but not for excitable (.26), and ratings of mothers on all three dimensions at the time of birth were significantly correlated with ratings taken when infants were just over a year old. Mothers and infants were rated on a number of behavioural measures, including frequency of contacts and frequency of play initiated by the infant to individuals other than the mother. Correlations between such behavioural ratings and scores on the three dimensions varied with age of the infant. Infants rated as highly sociable at 58-85 weeks showed high levels of contact behaviour at 8 weeks but not at 16 or 52 weeks. At 52 weeks sociable scores correlated instead with frequency of approaching others. In species with complex social behaviour it can therefore be difficult to make simple predictions regarding trait-behaviour correlations. In general, however, the literature suggests that personality ratings of animals do in fact tend to correlate in expected ways with behavioural measures (Gosling, 2001).

1.4 The relation of trait ratings to life-history variables

In social species like primates, it is likely that a range of life history variables such as age, sex and dominance status may be linked to trait ratings of personality. It may also be true that any commonalities found between different species may be more related to these life history variables than to species-specific behaviour (Clarke and Boinski, 1995). It may therefore be possible, by comparing trait patterns across related species, to determine the developmental and social factors responsible for personality differences within groups.

A range of studies have attempted to explore the relationship between personality ratings and life history variables. Using the rating scale developed by Stevenson-Hinde *et al.* (1980a), Bolig, Price, O'Neill and Suomi (1992) rated the personality of rhesus macaques. Animals were also classified as high, medium or low reactivity and trait ratings were compared with reactivity level, dominance rank, age and gender. A close relationship was found between levels of reactivity and personality ratings, with highly reactive animals rated as most excitable, fearful, insecure, tense and irritable, and the least confident, curious, equable and understanding. Significant differences were found between males and females on reactivity level and trait ratings. Females were rated as more highly reactive than males, and as more excitable, while males were rated as more solitary. The traits confident and fearful were related both to dominance rank (measured as high, moderate or low position on a matriline) and reactivity level, with highly reactive, low dominance animals rated as least confident and most fearful. In a discriminant function analysis, it was found that as little as three personality traits were sufficient to reliably discriminate all the animals in terms of reactivity level. As Bolig *et al.* (1992) note, such convergent validity suggests the usefulness of subjective impressions of personality.

Caine, Earle and Reite (1983) used a modified version of the earlier Stevenson-Hinde and Zunz (1978) rating instrument to rate adolescent pig-tailed monkeys. Personality scores were correlated with dominance rank and separation experience. Dominant animals were rated highly on the traits confident, effective, aggressive, solitary, and opportunistic. Middle-ranking animals were rated as more tense than high or low ranking individuals and as more dependable. Low-ranking animals were more apprehensive, fearful, insecure, dependable, popular and dependent. The authors attribute the rather peculiar popular and dependable ratings for these animals to the possibility that lower-ranking animals are seen as relatively non-threatening. Independent of dominance rank or age, individuals who had experienced a ten-day maternal separation were rated as less sociable than controls. As the authors note, this inverse relationship between early separation and sociability scores has been found in at least one other study on rhesus macaques (Spencer-Booth and Hinde, 1971), but not in others (Stevenson-Hinde *et al.*, 1980a). It is likely however that, at least in macaques, the relationship between separation and sociability is affected by other important variables, such as reactivity level and subsequent socialisation experiences (c.f. Suomi, 1987, 1991; and Higley and Suomi, 1989).

McGuire, Raleigh and Pollack (1994) attempted to explore the relationship between trait ratings and behavioural and life history variables. Twenty personality constructs were defined by experienced observers who subsequently rated vervet monkeys over three separate time periods. Principal components analysis extracted three factors: socially competent, playful/curious and opportunistic. Individuals rated highly on the social competence factor were observed to be less solitary, less likely to show submissive behaviour and more likely to show grooming, vigilant and aggressive behaviour. High scores on the curious factor were related to high levels of activity, play and exploratory behaviour, and inversely linked to solitary behaviour. High scorers on the opportunistic factor were more likely to initiate aggression than low scorers. Clear patterns were also found for dominance status, with dominant individuals rated as more socially competent. Changes in dominance status seemed to be linked to changes in scores on the social competence and opportunistic factors. The direction of these changes is not completely clear, but there does seem to be a pattern whereby animals that gained status experienced an increase in scores on the socially competent and opportunistic factors (McGuire *et al.*, 1994).

A study by Murray (1995) used trait terms developed by Stevenson-Hinde and Zunz (1978) to rate captive gorillas, chimpanzees and bonobos. A principal components analysis produced three dimensions: confident-apprehensive, sociable-solitary, and excitable-slow. Summary scores on these components related to a number of environmental variables. For example, group size was significantly related to scores on sociable-solitary and excitable-slow for chimpanzees; with those animals housed in larger groups being rated as more sociable and more excitable. While there were no sex or age differences in scores on confident-apprehensive, there were differences on the other two dimensions. Both male and female immature chimpanzees were rated as significantly more sociable than adults. However, adults were rated higher on excitability than immatures, although this was only significant for females (Murray, 1995; see also Murray, 1998).

Murray's examination of social behaviour in this sample is a good example of the difficulty of predicting trait — behaviour relationships. Sociability scores were expected to correlate strongly with all measures of affinitive behaviour, including play and grooming. However, only initiation of grooming correlated significantly with sociability (with animals rated as more sociable initiating more grooming). Rate of grooming and being groomed, and the number of close associates groomed were not related to sociability scores. Conversely, sociability scores were positively correlated with rates of play, number of play partners and responsibility for initiating play. However, the highest scorers on the sociable-solitary dimension are juveniles, suggesting that the close relationship between sociable scores and play is age-specific. What is clear is that simple frequency measures of behaviour may not be the clearest expression of personality ratings, and that characteristics such as the closeness or quality of social relationships may be more important (see Chapter 4).

More recent attempts to investigate the structure of nonhuman primate personality have utilised a five-factor model of personality. The issue of how many factors are sufficient to explain human personality has long been a contentious issue, but a number of studies have shown that five factors (the 'Big Five') may be universal (John, 1990), although some researchers insist on fewer factors (Eysenck, 1952) or on more (Cattell, 1950). The Big Five factors have been defined as Neuroticism, Agreeableness, Extraversion, Openness to Experience and Conscientiousness. Using Goldberg's (1990) taxonomy of trait terms, King and Figueredo (1997) obtained ratings for 100 captive chimpanzees from a number of zoos. A factor analysis of the ratings produced six factors, five of which were interpreted as representing the Big Five. The additional factor, which accounted for most of the variance (20.8%) was labelled Dominance. Items loading on this factor included dominant, submissive, fearful, intelligent and persistent. It is clearly this factor which specifies the behaviours which are most salient for the observers. It is interesting to note that despite some discrepancies in the expected pattern of factor loadings, the factor loadings in general resemble those found in studies of the Big Five in humans. Where there are discrepancies, the authors attribute these to the difficulty of applying typical definitions of trait terms to chimpanzees. Terms such as lazy or sympathetic for instance, acquire their particular meaning by reference to human social standards, and may not necessarily be appropriately applied to chimpanzees.

Although the implication of similarities between human and nonhuman personality structure is persuasive when considered on the basis of factor analytic work, the generic use of adjectives derived from the human domain remains problematic. One of the criticisms levelled at subjective personality ratings is that the correlations between items are based upon their perceived semantic similarity (D'Andrade, 1974; Schweder, 1975). If the same items are used to rate humans and nonhumans then any similarities in the resulting factor structure may simply be a product of the raters' implicit personality theory. King and Figueredo, and others, present high inter-rater correlations as evidence towards the validity of the personality ratings made by their observers. They also suggest that the existence of a dominance factor suggests that raters were not simply using implicit theories of human personality when assigning ratings (King and Figueredo, 1997). It remains the case, however, that the study utilised descriptive adjectives from human personality work. Although care was taken to assign more appropriate definitions to these terms, this does not necessarily mean that they are the most relevant descriptions of chimpanzee personality.

The case for similarity between human and animal personality structure is strengthened considerably if criterion-related validity can be shown for existing rating scales; that is, if trait ratings allow prediction of scores on other measures. For instance, it has been suggested that personality characteristics may be linked to mood states (e.g. Watson and Tellegen, 1985), in particular, the Big Five dimensions (John, 1990). The only study to date comparing personality ratings with mood states in nonhumans has been carried out using a sample of captive chimpanzees (King, 1999). King and Figueredo (1994) investigated the relationship between observer ratings of personality and happiness (or 'subjective well-being') in a large sample of captive chimpanzees. In humans, scores on Extraversion are positively correlated with subjective well-being, and scores on Neuroticism are negatively related to subjective well-being (e.g. McCrae and Costa, 1991, cited in King, 1999), and indeed earlier work (e.g. Watson and Tellegen, 1985) suggested that the two factors of positive affect and negative affect are sufficient to account for variance in mood (Kline, 1993a).

To obtain scores for subjective well-being in chimpanzees, King and Figueredo (1994) asked observers to assess, for each of 83 chimpanzees, the relative amount of time each individual experienced positive and negative affect, the amount of positive feeling each animal experienced as a result of social interactions with other chimpanzees, and their effectiveness in achieving social goals. In addition, raters were also asked to imagine being each chimpanzee for a week, and to rate the desirability of such a state for each animal. Multiple regression analysis indicated that, in chimpanzees as in humans, Extraversion and Conscientiousness scores are positively related to subjective well-being, while Neuroticism scores are negatively related to subjective well-being. However, the positive relationship between Agreeableness scores and subjective well-being found in humans was not present in the chimpanzee data, with no relation found between Agreeableness and subjective well-being (King, 1999).

The patterns of relationship between personality and subjective well-being found in this study provide important support for the cross-species generality of personality structure. In addition, the high inter-rater reliabilities in this study (>.75) suggest that aspects of chimpanzee subjective well-being can be adequately rated. An interesting aspect of this study is the focus upon more global estimates of subjective well-being: the rating questions focused upon general estimates of the animals' usual patterns of responding. More transient aspects of affective states may be more difficult to assess; due to the intra-individual variability in mood states (and the inter-individual variation in such variability) only repeated measurements of mood are useful (Kline, 1993a). The extent to which more transient mood states can be effectively rated in nonhumans, and their relation to more stable aspects of personality remains to be answered.

Additional work on the construct validity of nonhuman personality ratings comes from a study that examined the construct of psychopathy in captive chimpanzees. In humans, psychopathic personality is characterised by low empathy, high aggressiveness, lack of guilt, dishonesty, risk-taking and a difficulty in forming intimate attachments. In addition, ratings on some of the Big Five factors are associated with psychopathy (i.e. high Extraversion, low Agreeableness and high Conscientiousness are associated with psychopathy) (Lilienfeld, Gershon, Duke, Marino and de Waal, 1999). Lilienfeld *et al.* (1999) developed a measure of chimpanzee psychopathy (the CPM) and compared observer ratings on the CPM with personality ratings and several behavioural measures on a small sample of captive chimpanzees (N = 34). Scores on psychopathy correlated positively with Extraversion (.60, p< .01), and Neuroticism (.28, n.s.), and negatively with Agreeableness (-.42,

$p < .05$). A number of predicted relationships between CPM scores and behaviour were significant; CPM correlated positively with silent bluff displays, play, sexual mounting, low-intensity agonism, teasing and daring actions; and correlated negatively with repetitive movement, detachment and generosity (Lilienfeld *et al.*, 1999). Although previously only applied to humans, the construct of psychopathy may be usefully applied to other social primates; in particular, the frequency of more subtle aspects of social interaction such as deception and manipulation, which may be present in chimpanzees (e.g. Whiten and Byrne, 1988) could be interpreted as indications of psychopathy (Lilienfeld *et al.*, 1999), though we must be careful of interpreting such behaviours from an anthropocentric perspective.

Further evidence for the cross-species generality of the Big Five personality structure comes from studies of non-primates. Gosling (1998) rated spotted hyenas *(Crocuta crocuta)* on trait terms chosen by observers experienced in hyena behaviour. Adjectives were initially drawn from studies of human and nonhuman personality, with the final selection of 44 trait terms chosen to reflect all aspects of hyena behaviour or demeanour. Four observers rated 34 hyenas on all of the items. Inter-rater reliability was reasonably high (mean alpha reliability .71). A principal components analysis of the ratings produced five factors: assertiveness, excitability, human-directed agreeableness, sociability, and curiosity. There seems to be some similarity between some of these factors and the Big Five structure: excitability could be seen as Neuroticism, curiosity as Openness to experience, sociability and human-directed agreeableness as similar to human Agreeableness, assertiveness may be seen as a combination of human Extraversion and low Agreeableness (Gosling, 1998).

An interesting aspect of this study is the author's attempt to separate the effects of dominance, sex and age from personality per se. Correlations between factor scores on each of the five factors and dominance status were only significant for the assertiveness factor (.84). Similarly, only assertiveness correlated significantly with sex (.60), with females rated as more assertive than males. Age did not correlate significantly with any of the five personality factors. In order to facilitate a comparison with the dimensions found in similar studies, some of the terms used to rate the hyenas were drawn from previous studies on nonhuman personality. When the factor structure based upon these terms was compared to that based on only 'hyena' adjectives several similarities were found. For example, the hyena assertiveness scale correlated .85 with the confidence dimension found by Stevenson-Hinde and Zunz (1978) for rhesus macaques. Assertiveness also correlated highly with Bolig et *al.'s* (1992) aggressiveness scale (.86) and Gold and Maple's (1994) dominance scale (.94). It seems clear then that there may be considerable overlap between the dimensions elicited in personality ratings across different species, even using different rating scales.

The utility of employing generic terms in order to examine similarities between species is evident but has to be tempered with the necessity of accommodating specific aspects of a species' behaviour or temperament (Gosling, 2001). This balance has rarely been achieved in studies of nonhuman personality. For instance, Figueredo *et al.* (1995) attempted to compare the personality of stumptail macaques *(Macaca arctoides)* and zebra finches *(Poephila guttata)*. A modified version of Stevenson-Hinde and Zunz' (1978) scale was used to rate both species, the definitions of each term being the same in both cases. Items were assigned to each factor a priori, based upon the Stevenson-Hinde and Zunz (1978) factors. Using generalisability analysis, construct validity, inter-rater reliability and temporal stability of the factors was examined. The Stevenson-Hinde and Zunz factor structure was found to fit trait ratings for both species, and inter-rater reliability was high. As the authors note, however, the influence of implicit personality theory on the results is more difficult to examine, and may not interact with ratings in a predictable way.

1.5 What do trait ratings actually measure?

Despite the range of theoretical and empirical approaches used to investigate nonhuman personality, a clear aim of many of these studies has been the attempt to establish the existence of construct validity. That is, the tension between implicit and explicit personality theories that has characterised human personality work has served to structure much of the work on nonhuman animals. This is in spite of the fact that personality studies on nonhumans have been seen to be at least as productive as human personality research in a number of ways. Firstly, quantitative analysis of observer trait ratings indicates that the personality of many species may be usefully conceptualised in terms of a trait structure, similar in some ways to the trait structures identified in human personality work. This is perhaps more impressive in light of the range of species studied: e.g. wolves (MacDonald, 1983), piglets (Forkman, Furuhaug and Jensen, 1995), cats (Feaver, Mendl and Bateson, 1986) and octopuses (Mather and Anderson, 1993). Secondly, many studies have indicated moderate to high levels of inter-rater reliability, and some work (e.g. Stevenson-Hinde *et al.*, 1980a; Stevenson-Hinde, Stillwell-Barnes and Zunz, 1980b) has shown that personality ratings are stable over time. Thirdly, when attempts have been made to compare trait ratings with life history variables or behavioural factors, such as dominance, sex and age, reasonably informative relationships have been identified. It is, however, in this last domain that the most problematic issues lie, for it is the demonstration of the validity of subjective personality impressions that has remained the *sine qua non* of both human and nonhuman personality work. In this section, I will try to address some of the problems encountered in elucidating the nature of the trait-behaviour relationship.

1.6 The basis of subjective personality ratings

> ...basic research must be addressed ultimately to questions concerning (a) the grounds on and reasoning processes by which individuals frame those meaningful ideas that constitute their own knowledge, broadly defined, and (b) the nature of the relationships between such knowledge and overt action. In effect, this view asserts that personality psychology's core concern is subjective or personal knowledge. (Lamiell, 1987: 21)

One of the aspects that characterises many human and nonhuman personality studies is the tendency to instruct those conducting ratings to base their evaluations on their 'overall impressions' of the individuals, rather than on any explicit summation of behaviour. This is not surprising, given the widespread assumption that the personality of an individual is expressed not just in specific behaviours, but in a range of other personal characteristics: mood or temperament, 'cognitive style', emotional reactions, motivations and goals, even general demeanour or posture. Are personality ratings simply expressions of the sum of knowledge an observer has acquired about these facets of individual character, or do they represent a more subtle reasoning process?

In addressing this question it is useful to consider the circumstances under which observers have difficulty rating individual animals. Although many studies have found reasonable inter-rater reliability and temporal stability in personality ratings, some animals remain difficult to categorise. Martau, Caine and Candland (1985) found that inter-rater reliability was particularly low for monkeys undergoing status changes throughout the rating period. The observer correlations in Bolig *et al.*'s (1992) study of rhesus macaques were low for seven animals, four of which were adolescents or young adults. Of these four, three were undergoing peripheralisation. Another two animals were juvenile females experiencing social and physical change due to the birth of their first offspring. Clearly then, observers seem sensitive to salient social and environmental factors that affect the animal's personality. What seems apparent, however, is that traditional trait ratings may in some cases be unable to capture the dynamic quality of personality change.

One conclusion that may be drawn from an identification of such difficulties is that subjective ratings reflect the inadequacy of implicit personality theories. If raters do not concur on their interpretation of the same set of behaviour, we would usually assume a lack of objectivity. From a nomothetic standpoint, the existence of traits, as underlying explanatory concepts, should be evident from their behavioural referents. As long as trait-behaviour relationships are reasonably clear, then individuals should be observed to be fairly consistent. It is not surprising then that the standard rating procedures are unable to cope with a perceived lack of consistency:

> Kambi is an animal who has been in the colony as long as Bimba, but the caretaking staff refuse in general to explain her occasional aggressions. Something necessary to a diagnosis is missing. There is a lack of the consistency in over-all behaviour that leads to agreement in Bimba's or Pati's

> case. The staff simply regard Kambi as a 'screwball,' a moody psychopathic whose behaviour is past accounting for. (Hebb, 1946: 93)

According to Hebb, the most important prerequisite for adequate classification is an ability to readily interpret and classify behaviour patterns:

> The names [of emotions] are applied only when familiarity with the animal reveals a long-term pattern of behaviour *with which the observer is already familiar* in man and some evidence of validity in the categorization is found in its practical value in predicting the outcome of a behavioural sequence. (Hebb, 1946: 93, emphasis in original)

If behaviour is not consistent (e.g. if the animal is undergoing status changes) then interpretation of current behaviour is difficult and prediction of future acts impossible. As Shotter (1984) notes, the significance of an act can only be uncovered in terms of the future acts it implies. Yet to obtain construct validity, to show that trait ratings are not purely subjective, some correspondence with behaviour needs to be shown.

1.7 The problem of context

Within human personality research, attempts to validate trait ratings have long focused on the problem of determining the exact nature of trait-behaviour correspondences. In order to ascertain the accuracy of trait ratings, the 'relevant' behaviours must be observed. There must therefore be some sensible (preferably empirical) method of deciding which behaviours are indicative of which traits. We have seen, however, that personality ratings usually do not encompass specific knowledge concerning correlations between behaviours, and that raters often find it difficult to articulate the basis upon which personality assessments are made.

It may be, however, that the material of subjective interpretation is in fact more relevant to understanding the behaviour of complex social species, compared to traditional methods of measuring the frequency or duration of single behavioural units. Since personality assessments only really apply to social species (an individual's position on a trait or traits is defined with reference to social norms), it is likely that the information observers use consists of patterns of responding in social interactions and relationships. That is, personality may be properly considered to be a 'style of responding' rather than the sum of an individual's actions over time. This notion of behavioural style relates more to the individual's propensity to respond in a particular way. Thus when observers are making personality judgements about nonhumans they are making assumptions about a whole range of 'unobservables'. They are taking into account the animal's emotional reactions, its possible future behaviour, and possibly also the animal's interpretations of particular situations.

Simple correspondences between ratings and behaviours are therefore unlikely to yield more than suggestive patterns of relationship. For the purposes of distinguishing between individuals we may have to refer more to the social context of action rather than individual behavioural responses (c.f. Harré and Secord, 1972). In addition, it may be necessary to examine in more detail relatively amorphous concepts that structure observer impressions, for instance the 'quality' of an individual's social interactions (Stevenson-Hinde and Hinde, 1986).

As Clark and Ehlinger (1987) note, individual differences in behaviour can often be linked to variation in the strategies individuals use over changing social and environmental conditions. Thus, developmental influences on behaviour patterns may be an important source of individual variation. It is perhaps easier, however, to determine the functional significance of such variation, based as it is upon maturational or genetic factors. More difficult is establishing the relative influence of more proximate factors. In particular, it may prove impossible to fully disentangle the sources of variation within species that form close social relationships.

Hinde and Spencer-Booth (1971) observed 31 rhesus mother-infant pairs in order to determine possible sources of individual variation. Pairs were assessed on a number of measures relating to the proportion of time that the infant spent off the mother, and the extent to which both partners were responsible for ventro-ventral contact. The effects of the sex of the infant and dominance and parity of mothers were also considered. It was found that individual differences were best characterised as properties of the relationship between the individuals, and that behavioural differences were closely linked to the changing aspects of the mother-infant relationship. For example, proportion of time the infant spent off the mother varied according to the frequency with which the mother rejected the infant when it attempted to make contact with her. Some characteristics of the infant also contributed to this measurement however. Specifically, those infants that spent more time off their mothers made less effort to maintain maternal proximity. So individual differences between mother-infant pairs for this measure depend upon both mother and infant characteristics, and on the nature of the mother-infant relationship itself. In addition, the relative importance of these characteristics for the overall behaviour of the dyad varied according to age of the infant. Before 12 weeks, maternal differences seemed to be more influential in determining dyadic interactions. After this time, however, infant differences assumed greater significance. For the mother-infant relationship, then, and certainly for other social relationships within primate species, it may be misleading to expect clear differences between individuals to emerge on the basis of single behavioural measures. What is clear is that, for both subjective and objective ratings, a particular behavioural act only acquires meaning and significance when considered within the social and environmental context in which it is performed. As Hinde and Spencer-Booth (1971) note, the structure of an individual's social relationships must be explicated before one can begin to establish the effects of individual differences. Indeed, in species with complex social structures, it is likely that personality is a function of relationships, rather than an aspect of the individual.

1.8 The function of traits

We arrive then at a consideration of what the trait concept, as used in explicit and implicit personality theories, actually signifies. If traits fail to show a one-to-one correspondence with behaviour, and do not subsume clusters of similar behaviours, then what is their taxonomic purpose? A form of this question characterised the important debate within human personality research concerning the relative roles of traits and situations in contributing to behaviour (e.g. Mischel, 1968). From a functional perspective, traits are assumed to be causal, underlying entities which structure behaviour. For example, McGuire *et al.* (1994) found that higher ranking vervets were rated highly on traits constituting a social competence factor. They suggest that a high level of social competence determines status:

> ...it is more likely that high scores on the social competence factor predisposes an individual to attain high social rank. Confident, alert and unanxious individuals may be particularly adept at evaluating social situations, acting forcefully and effectively, and generating support from other group members when dominance relationships are being established. (1994: 11)

In a similar vein, Sapolsky (1990) argued that dominant baboons showing a low reactive behavioural style were able to distinguish between real and apparent sources of threat better than highly reactive animals (cited in Clarke and Boinski, 1995).

In support of a causal view of personality style, there does seem to be evidence for an innate basis for reactivity level (e.g. Suomi, 1991) and for the heritability of at least some of the 'Big Five' traits (Bouchard, 1994). However, the assumption that traits are causal has been questioned by some researchers. Within the human personality field, the act frequency approach of Buss and Craik, for example, presents an essentially non-causal view of traits (Buss and Craik, 1983). According to this view, traits are simply labels that summarise a range of behavioural acts; they do not necessarily possess any causal properties (Carver and Scheier, 1992).

Essentially the same point has been made by Harré (1998). He takes issue with the tendency to invoke the trait concept as both a higher-order disposition *and* an explanatory concept. He points out that a disposition is an observable property of an object, whereas an explanatory principle is unobservable. According to Harré, higher-order dispositions are always classificatory, not explanatory. Traits are thus clusters of the terms people use to describe themselves and others on questionnaires.

There is another, more serious, problem with the conception of traits as causal factors. This conception is dependent to a large degree upon nomothetic assumptions. In a nomothetic approach to personality, traits are assumed to be generic; that is, the personality of everybody can be conceptualised in terms of a limited number of common traits. The goal of nomothetic research is to determine this common trait structure, and to explicate its expression in behaviour. It is the nomothetic view of personality that really engendered the tension between implicit and explicit personality theories. If one assumes the existence of an underlying trait structure then it becomes important to gain accurate, objective measurements of it, and to distinguish these from more subjective measurements, which may 'cloud' the 'real' structure with subjective 'noise'.

As discussed above, much of the work on nonhuman personality has depended upon the nomothetic assumptions that characterise human personality research, and has utilised various human trait theories. The exceptions may be those studies which have utilised factor analysis and similar techniques to explore personality dimensions. Many researchers assume that such methods are essentially atheoretical, in that they allow analysis of rating data without any obvious recourse to a particular theory of personality. Stevenson-Hinde and Zunz (1978) for example, advocate their own use of principal components analysis to study subjective assessment of rhesus by contrasting it with the work on personality in baboons carried out by Buirski *et al*. (1973), which was based upon Plutchik's (1970) theory of emotion. On a purely practical level, however, factor analytic approaches are not purely empirical. The interpretation of trait loadings remains subjective, and is often based upon covert knowledge about the meaning and significance of certain behaviours. Also, such studies remain attached to the existence of explanatory, trait-like structures to explain individual variation. Thus, echoing the concerns of human personality research, students of nonhuman personality have stressed the importance of distinguishing between implicit and explicit theories of personality in order to access the 'true' causes of behaviour (e.g. Figueredo *et al.*, 1995).

There are, however, alternatives to the nomothetic position which may yet prove useful in providing new perspectives for both human and nonhuman personality studies. The work of Lamiell (e.g. Lamiell, 1981, 1982; Lamiell, Trierweiler and Foss, 1983) and other researchers using a more idiographic (or 'idiothetic') approach highlights some of the problems with nomothetic assumptions. According to Lamiell, the study of individual differences, based as it is upon the nomothetic paradigm, is simply not able to provide information about the consistency or nature of a particular individual's behaviour because it "focuses attention on the spaces *between* individuals" (Lamiell, 1987: 6, emphasis in original). In other words, from a nomothetic perspective, the personality of an individual is defined with relation to the personality of others (i.e. using normative measurement). This is assumed on the basis of the generic nature of traits; that traits are universal properties underlying the behaviour of everyone. Lamiell takes issue with this assumption, and discusses evidence that in fact personality ratings are not made upon the basis of comparison between individuals. He suggests that ratings reflect the rater's assessment of an individual's behaviour with reference to the possible behaviour of that person, not by reference to the behaviour of others. This rejection of the nomothetic approach has important consequences for the key issue of consistency, often taken as evidence that traits are operating to determine behaviour.

The idiographic approach to personality thus challenges the crucial point of traditional individual differences research: that normative trait ratings allow one to ascertain behavioural stability, and to predict future behavioural acts. This is an important challenge to the utility of trait ratings, but does not necessarily leave personality research without a foundation. Instead, researchers such as Lamiell propose the use of an alternative form of measurement: interactive measurement. This was a type of measurement described by Cattell (1944). Cattell distinguished three different forms of psychological measurement: normative, which defines a person's score in relation to the scores of others, ipsative, which defines the score in the context of other scores obtained from the same person, and interactive, defined as:

> measurement in terms of the actual physical and biological effects of behaviour, usually, in test situations, within a restricted framework defined by the test. It recognizes the oneness of the organism-environment and pays tribute to the oft-forgotten fact that a trait is never resident only in the organism but is a relation between the organism and the environment. (Cattell, 1944: 293, cited in

> Lamiell, 1987: 132)

From this perspective, the question of whether personality ratings are objective or subjective is irrelevant. That is, they are both. What the idiothetic approach offers is a view of personality that allows us to make sense of objective ratings and subjective impressions; it is essentially a constructive theory of personality. The advantage of such an approach is that it incorporates a consideration of the processes by which observers assign meaning to behaviour, rather than consigning these to the realm of pure subjectivity. Thus, traits become neither underlying realities, nor simply heuristic devices; rather the trait concept allows the observer to organise and frame an otherwise unwieldy collection of knowledge. As such they are essential to the analysis of variation:

> Personality is not something that one 'adds' to the phenomena but that which *centers* the other phenomena and endows them with psychological import. (Lamiell, 1987: 187, emphasis in original)

What a constructivist account of knowledge offers is a consideration of the means by which individuals understand, structure and organise their knowledge about the world. From this perspective, traditional dichotomies between objective and subjective understanding are artificial. The distinction between 'objective reality' and subjective interpretation of that reality becomes difficult unless one can remove interpretation completely. It has been argued that this is impossible to do within the field of personality assessment, as personality is itself an interpretive concept. Given this point, what are the bases by which judgements of personality should be made, and is it possible to make any suggestions regarding the nature of trait-behaviour relationships?

The study which follows utilises the approach of Kelly (1955). Kelly's theory of personal constructs attempts to make explicit the process by which raters assess the personality of others. It does this by a recognition of the importance of the relationship between rater and ratee. According to Kelly, trait ratings of an individual should not be expected to be consistent across raters, since each rater constructs, to some extent, the personality of the ratee. This is not to say that an individual's personality is purely subjective, dependent upon who is rating him/her at the time. Rather, some consistency in personality is assumed, but personality ratings are structured within the context of subjective interpretation.

By focusing on the role of meaning in personality assessment, constructivist approaches allow the consideration of the role of subjective impressions, and facilitate the investigation of the processes by which observers assess such intangible personal qualities as mood, attitude and behavioural style. In their attempts to understand the processes by which trait ratings are made, such methods arguably provide a more defensible demonstration of the utility of personality assessment in nonhumans.

CHAPTER TWO

The development of a constructivist method of rating the personality of captive chimpanzees *(Pan troglodytes).*

2.1 Introduction and rationale

A constructivist measure of personality was developed to assess the personality of a captive group of chimpanzees. The repertory grid approach was used to generate construct terms (Kelly, 1955). The aim of using this technique was to ensure that the constructs used to rate the animals were ones which were habitually used by the raters, and thus were important and meaningful to them. While this meant that each keeper had certain constructs unique to themselves, it was felt that this was preferable to using a pre-determined set of constructs devised solely by the researcher, or borrowed from studies of human personality.

The repertory grid method is based upon Kelly's personal construct theory (Kelly, 1955). According to this theory, people attempt to understand individuals and events in the world around them by developing a system of related constructs that aid them in anticipating future events and making sense of the world. Kelly defined a construct as:

> ...a reference axis devised by man for establishing a personal orientation toward the various events he encounters. (1955: 146)

According to Kelly's theory of personal constructs, a person's attitudes towards events and objects can be expressed in terms of the constructs that are used to describe them, and by reference to the relationships between constructs. An important facet of constructs is that they are bipolar. Kelly believed that it is only by comparing things in terms of their similarities and differences that constructs are formed. When people are making personality judgements, for instance, the construct terms they use to describe others develop out of a consideration of the ways in which people are similar or different to each other, and, more importantly, out of a process of dialectical reasoning rather than normative reasoning (Lamiell, 1987). That is, a person's position on a personality construct is determined by reference to what that person is, compared to what they might have been, rather than by reference to what everybody else is.

The use of an idiographic approach to the study of nonhuman personality could be advantageous for a number of reasons. Firstly, this relatively new area of research has utilised a wide range of differing rating methods, all of which have produced suggestive findings but most of which have associated problems. Many of these studies have been heavily based upon the theories or rating instruments of human personality research, however, the relevance of these to the study of nonhuman personality has not always been adequately demonstrated. Secondly, much of the work on nonhuman personality has adopted a number of the assumptions underlying the nomothetic approach; namely, the assumption of a generic set of underlying causal traits applicable to all individuals, the expression of these traits in behaviour and the normative distribution of these traits. While these assumptions may be reasonably made with reference to human personality (and there exists substantial criticism of them) we cannot assume their relevance to nonhuman personality. Thirdly, it has been suggested in the last chapter that personality assessment utilises both implicit and explicit personality theories and that the function of the rater-ratee relationship is important in understanding trait ratings. As a constructivist technique, the repertory grid provides a useful way of examining the relationship between implicit and explicit accounts of personality theory. Accordingly, the repertory grid method has been utilised in this initial study of personality in captive chimpanzees.

2.2 Method

2.2.1 Study site and animals

Subjects

The subjects of this study were the chimpanzees housed at the North of England Zoological Society, Chester. At the time of study, the group contained 24 animals: 5 males and 19 females. The sex and age distribution of the animals is presented in Table 2.1.

Table 2.1 Age (in years) and sex class distribution of group members.

	Males	Females	Total
Adults	4	9	13
Adolescents	0	3	3
Juveniles	1	2	3
Infants	0	5	5
Total	5	19	24

Classification into age categories follows that of Goodall (1986). Infants are defined as animals aged from 0 to 5 years (inclusive); juveniles from 6 to 8 years (inclusive); adolescents from 9 to 14 years (inclusive), and adults from 15 years.

History of the Chester group

The chimpanzee colony at Chester is the second-largest group of captive chimpanzees in Europe, and one of the longest-established. The first chimpanzees arrived at Chester in 1948 and were initially housed in three separate groups on adjacent but separate outdoor 'islands'. These were situated on the site of the current outdoor enclosure, and bounded by a moat on three sides, and a large indoor enclosure on the fourth. In 1979-80, the islands were joined into one large outdoor paddock, with all of the animals grouped together for the first time. In 1989, a new enclosure was built on the same site, incorporating new sleeping quarters for the chimpanzees and a new public viewing area. More recently, the outdoor enclosure has been enriched by climbing frames, ropes and large tree trunks to facilitate brachiation and make the enclosure more interesting for the animals.

Most of the chimpanzees in the current group are captive born and parent-reared. The first infant was born in 1956 and the majority of subsequent births occurred at Chester. The exceptions are Halfpenny, Florin and Farthing who were born at Colwyn Bay zoo and subsequently transferred to Chester. Four of the oldest animals were wild caught: Meg, Gloria, Boris and Cleo. The breeding success of the group has been excellent, with the majority of the older females successfully rearing at least one infant.

There has been a wide range of research carried out on the group, examining a range of social behaviour patterns. The large size of the group facilitates the investigation of a large range of possible research questions. In addition, the size and layout of both the indoor and outdoor enclosures means that, when on public view, the majority of the animals are within observation range for most of the time. As well as being a popular choice for undergraduate study, the colony has formed the basis for a number of post-doctoral investigations. Murray (1995) studied the relationship between personality ratings and behaviour, comparing chimpanzee ratings from Chester and a number of other captive chimpanzee groups to ratings of captive gorillas and bonobos (see below for more details). Casperd (1998) examined the nature and the role of reconciliation behaviour within the chimpanzee group. In addition, a number of publications in the primate literature feature research carried out on the colony. An area of research that has received increasing attention has been the effects of the presence of visitors and observers on social behaviour in captive animals (e.g. Cook and Hosey, 1995). Among the great apes, chimpanzees appear especially interested in the behaviour of human visitors, and the investigation of the effects of visitor-animal interactions (although necessarily limited in a zoo setting) may have important consequences for the design of enclosures and the consideration of the welfare of the animals. Other published work involving observations of the Chester group has focused on handling preferences; Manning (1990) for example used the Chester group as part of a study to compare handling preferences across the great apes. More recently, Koyama and Dunbar (1996) focused upon whether chimpanzees appear to anticipate possible conflict situations arising during group feeding sessions.

Housing Conditions

The chimpanzee enclosure at Chester Zoo consists of an outdoor grassed island of approximately 2025 square metres in size, separated from the public by a 3 metre moat. The island contains several dead trees and logs. From the island, the chimpanzees have access to an indoor area of approximately 163 square metres and 12 metres high. The indoor area has a 9 metre high three storey iron frame and ropes and nets are strung from the frame to the walls. The area is lit by large roof windows, and is heated to a constant temperature of 18°C all year. Half of the wall consists of strengthened glass, which allows viewing of the enclosure by the public; a 1 metre wide moat runs underneath the glass. Adjoining this enclosure, but out of sight of the public, is an indoor sleeping area which can be separated into individual cages by the use of sliding doors. Five of the cages measure 15.6 square metres and are 3.3 metres high, one cage measures 13.3 square metres and is 3.35 metres high, and one cage measures 3.2 square metres and is 2 metres high. The sleeping area is heated to a constant temperature of 21°C. Unless the weather is too cold the animals have access during the day to both the indoor enclosure and the outdoor island.

Raters

Seven observers rated the chimpanzees. Six of these were zoo caretakers, all of whom were, or had been, responsible for the care of the chimpanzee colony. One rater, the only female rater, was a postgraduate student. All of the raters were experienced observers of chimpanzee behaviour; their familiarity with the Chester group ranged from two to thirty years.

2.2.2 Procedure

Use of the repertory grid

Each rater was asked to generate pairs of constructs using the repertory grid method (Kelly, 1955). This method entails selecting pairs or triads of people and identifying characteristics, or constructs, that they have in common, or on which they differ. Raters are subsequently asked to identify the opposite of each construct term. Pairs or triads of people are presented for comparison until the rater is unable to generate any new construct pairs. In this study, raters were presented with semi-randomly selected pairs of chimpanzees to compare. That is, two adults were usually chosen together, and two infants. The animals were not presented in any particular order, nor was the order the same for each rater. A potential problem here could arise from the possibility that specific pairings of individuals may elicit particular traits. However, during the course of these initial sessions, raters were presented with a large number of pairings, such that all raters experienced a very large range of pairings. In addition, at the end of these sessions, raters were invited to contribute any additional trait pairs they felt were important. Comparisons involving an adult and an infant were avoided, as the raters found it difficult to compare these different age groups on many characteristics. The rater was asked to compare each pair of chimps in terms of characteristics in which they were both similar, or characteristics on which they differed. When each characteristic, or construct was given, the rater was asked to identify the opposite of that construct. This negative was then placed on the opposite pole to the original term. Continuous pairs of animals were presented for comparison until the rater could not think of any more constructs, or until the constructs that were being expressed were mostly repetitions of earlier ones.

In this way, a separate list of bi-polar constructs was generated by each rater. The initial number of constructs produced by raters ranged from twenty-five to fifty-two. The raters produced their construct lists independently, with no discussion between them. Despite this, there was considerable overlap in the construct terms that were chosen.

Using their own construct list, raters were asked to rate each animal in the colony over the age of five. Younger individuals (i.e. under 5 years of age) were excluded from the assessment as previous discussion with raters indicated that they were under-confident in their ability to rate the personality of infants. There was also a general consensus among the raters that younger animals, particularly infants, did not show a clear pattern of stable personality traits.

A scale of 1—5 was used to rate the animals, with the low extreme of the scale indicating that the animal was most like a particular construct (e.g. dominant) and the high extreme indicating that an animal was most like the opposite of the construct term (e.g. submissive). If two identical pairs of constructs had been given by a particular rater, whatever their polarity, one pair was eliminated. When the rater had produced several words or a sentence to define a construct instead of a single term, the description was reduced, after discussion with the rater, to one or two summary terms.

Each rater was interviewed no more than three weeks after completing the rating tables. The purpose of the interview was to establish the precise contextual meaning of each construct and any behavioural referents upon which it depended. During the interviews, the raters were asked to identify the ten constructs which they believed to be most useful, and most important, in the description of the animals' personality. At the time of the interviews, Rater 2 was no longer working at the zoo; as it was not possible to interview him, the first ten constructs from his list were chosen with the assumption that these would be the most salient for him. The sets of ten constructs were used in further analysis of the ratings, the results of which are presented in Section 2.5 below.

2.2.3 Data analysis

It should be noted primarily that the data in their final form do not meet certain criteria for the use of factor analysis. Specifically, the ratio of elicited constructs to elements (consisting of many more variables than animals) was too high. In addition, the distributions of some of the constructs were not normal, and in several cases were bimodal. However, the method of factor analysis is particularly effective at summarising complex sets of correlation matrices, and at detecting underlying patterns and constructs within such matrices. For this reason, it is the technique most commonly used to explicate the structure of personality, particularly in studies using new methods of personality assessment, and is generally a fairly robust technique (Kline, 1994). One of the most useful aspects of factor analysis is as an exploratory tool to investigate the existence and nature of general factors within a data set, particularly when it is not clear what the most important variables are (Kline, 1994). The initial correlation matrices indicated that many of the items in the present study were highly correlated, and exploratory factor analysis was chosen as the most appropriate method of examining the structure of those relationships. In addition, one of the aims of the present study was to generate a common personality rating scale that could be used by a greater number of raters, on a larger sample of chimpanzees. Factor analysis is the most appropriate way of constructing such an instrument (see Chapter 3). Accordingly, the primary analysis served principally to establish any meaningful patterns within the data set.

Each set of ratings was analysed separately, using the program Statview on an Apple Macintosh computer. The data analysis was performed in three stages:

1. A principal components analysis was performed on each set of data. This is the simplest way of transforming the correlations obtained from the data into a set of principal components that are assumed to be orthogonal (unrelated) to each other. The first component is assumed to account for most of the variance in the data set, the second component for most of the residual variance and so on. The number of factors produced by the principal components analysis was then used in the second stage of the analysis.
2. Using the number of factors obtained by principal components analysis as a guide, an iterated principal axis (a form of common factor analysis) was performed on each data set. The method of factor extraction used was Kaiser's criterion, which retains only factors with eigenvalues greater than one. As this method can produce rather liberal estimates of the number of factors, a scree plot was also used to determine the number of factors. Where neither seemed to offer a clear estimate, the factor loadings produced by retaining differing numbers of factors were compared for clarity and the factor solution which produced the simplest structure retained (Thurstone, 1947; Cattell, 1978).
3. The factor solution was then rotated using a Varimax orthogonal transformation. An orthogonal rotation implies that the elicited factors are uncorrelated with each other. In addition to the orthogonal rotation, Statview automatically performs an oblique rotation on the factor solution if this improves the solution. For each set of data, the orthogonal and oblique solutions were very similar. An oblique rotation implies that the factors are intercorrelated, which might be expected due to the complex nature of the behavioural variables being analysed. For this reason, the oblique solution was the one used in interpretation of the factor loadings.

Significance of factor loadings

One of the problems associated with assessing the significance of factor loadings as correlations in the usual way is that such a consideration fails to take into account the number of variables and the number of factors in each analysis. To avoid this problem, assessment of significance of the factor loadings, and inter-correlations of the factors, in the tables below follows the method suggested by Kline (1994), where only loadings of 0.3 or larger are assumed to be significant (at an alpha level of 0.01). Such loadings, or correlations, are marked by an asterisk in all the tables that follow. The discussion of the loadings centres on the highest loading items on each factor (the majority of which are significant). For a particular factor, italicised items are those items which load highest *on that factor*, rather than on another factor (even though they may load on other factors too).

2.3 Results of initial factor analyses

For four of the raters, the factor analysis produced four factors, for one of the raters the solution consisted of five factors, and two raters produced three factors. The tables that follow show the items which loaded on each of the factors. The interpretation of these factors relies upon the conceptual definitions for each trait term, obtained during the interviews with each rater. Accordingly, each factor has been interpreted by examining the raters' explanations of the highest-loading trait terms on that factor. The names given to each factor are intended to best describe all of the constructs that load highly on it. For example the term 'machiavellianism', with its connotations of political opportunism, was thought to best describe many of the constructs that loaded on this factor, such as *cunning*, *ambitious* and *intelligent*. 'Dominance' was also used as a factor term. This concept is often used in two ways in the literature: to describe the relationship between two or more animals, and also to refer to an intervening variable relating to some trait of the subject, which may then determine social behaviour (Noë, de Waal and van Hooff, 1980). As a trait term the latter definition was used here.

2.3.1 Preliminary analysis of personality constructs: Rater 1

Table 2.2 shows the principal components analysis for Rater 1. Most of the trait terms loaded highly on only one factor, producing a relatively clear five factor structure.

Factor I has been labelled Emotional Stability. The highest loading significant items on this factor are *mood changes quickly*, *laidback*, and *easily irritated*. These items all refer to a tendency to respond in a nervous or impulsive manner, or to be emotionally unstable. The item *vocal* also contributed to this group and referred to the tendency of some individuals to become alarmed and pant-hoot when there seemed to be little cause, although this item did not load significantly. The items *bully*, *bears grudges*, *manipulative*, *spiteful*, and *hard to read* all refer to a tendency to be ambitious and calculating, and an ability to remember and respond to past encounters. Finally, the items *not self-centred*, *loner*, *friendly* and *popular* all refer to social encounters.

An animal scoring highly on Factor I then, would combine the characteristics of emotional instability and unpredictability, a tendency to appear ambitious and calculating and a lack of successful social relationships. When compared to human personality traits, this factor may relate most closely to Neuroticism. High scorers on N experience negative emotional states like fear, anger, anxiety and depression, and are emotionally unstable (Eysenck, 1975).

Factor II has been labelled Social Confidence. The seven highest loading significant terms (except *independent)* refer solely to the adult animals, and seem to describe animals that are older, have been in the group for longer and have more confidence. In addition, the terms *respected* and *has last word* signify animals that are dominant within the group. The latter phrase was used to describe an animal that is assertive, and able to remember past conflicts. *Independent* and *aware* both refer to a dimension of nervousness: an independent animal was described as self-confident, sociable and secure, and *aware* was used to describe a nervous, suspicious response to novel stimuli, e.g. medicine. The items *dominant* and *good with young* are just significant on this factor.

Table 2.2 Factor loadings of original constructs produced by Rater 1

	Factor I	Factor II	Factor III	Factor IV	Factor V
	Emotional Stability	Social Confidence	Machiavellian	Dominance	Anxiety
Mood changes quickly	_.78*_	.18	.33*	-.23	.10
Laidback	_-.76*_	.10	-.44*	.32*	.02
Easily irritated	_.64*_	.07	.04	-.21	-.05
Bully	_.63*_	-.00	.21	.14	.17
Not self-centred	_-.63*_	.02	-.19	-.13	-.21
Bears grudges	_.55*_	.07	-.20	-.10	.09
Irritating	_.49*_	-.20	.01	.11	-.06
Manipulative	_.49*_	-.14	-.17	.09	.01
Loner	_.46*_	.08	-.07	-.08	-.14
Spiteful	_.41*_	-.05	-.21	.14	-.05
Friendly	_-.37*_	-.21	.02	-.05	.17
Hard to read	_.36*_	.12	-.04	.07	-.16
Popular	_-.32*_	-.25	.01	.08	.26
Vocal	_.23_	.07	.13	.19	.02
Experienced	-.18	_.88*_	.05	-.03	-.00
Mature	.01	_.78*_	.02	-.11	-.05
Lazy	-.22	_.69*_	.24	.13	.06
Respected	-.14	_.69*_	.02	.20	.17
Aware	-.31*	_.64*_	-.24	-.04	-.23
Has last word	.21	_.62*_	-.04	.00	.01
Independent	.00	_.61*_	-.25	-.26	.04
Cowardly	.10	.00	_.93*_	.19	-.13
Lacks common sense	-.09	-.15	_.70*_	.12	-.27
Humanised	.19	.16	_.66*_	.10	.07
Potential dominant	.19	-.07	_-.60*_	.00	.06
Streetwise	-.00	.27	_-.59*_	-.00	.10
Wimpy	.06	.01	_.52*_	.30*	.07
Calculating	.15	-.00	_-.52*_	.16	.15
Intelligent	.29	.29	_-.50*_	-.27	.08
Ambitious	.21	-.25	_-.47*_	.14	-.11
Plays with young	.13	-.21	_.38*_	-.10	.18
Good with young	.00	-.31*	_.32*_	-.09	.08
Doesn't like fights	-.27	.09	_.29_	-.18	.13
Gets first choice	-.04	.28	.07	_.62*_	-.00
Good at displaying	.00	-.02	.14	_.58*_	.08
Greedy	.13	-.16	-.07	_.49*_	-.14
Dominant	.02	.38*	-.04	_.47*_	.20
Thieving	.31*	-.29	-.17	_.41*_	-.04
Bossy	.29	.19	.10	_.34*_	.25
Overly protective	-.22	-.02	.20	-.05	_-.75*_
Trusting	-.13	.02	-.20	.09	_.65*_
Suspicious	.14	-.02	-.07	-.16	_-.65*_
Obedient	-.18	.04	.05	-.18	_.48*_
Likes keepers' attention	-.12	-.05	.20	-.13	_.42*_
Happy	-.27	-.18	-.02	-.08	_.37*_
Friendships last	-.23	.16	.14	-.07	_.33*_
Cooperative	-.29	.20	-.00	.06	_.33*_
% Variance	44.4	14.9	8.3	5.4	3.6

The highest loading items on each factor are shown in italics.

The items loading on Factor III may be seen as related to a competitive or machiavellian tendency. The items *cowardly,* and *lacks common sense* refer to a lack of ability to respond appropriately in social situations, e.g. a juvenile behaving aggressively towards a dominant animal. The item *wimpy* indicates a lack of social confidence or self-esteem. *Doesn't like fights,* loading positively (but just below the criterion of significance) on this factor, indicates an animal who avoids conflict; the opposite pole of this construct, *antagonistic,* describes an animal who is confident in conflict, who bears grudges, and is spiteful. This construct also loads moderately on Factor I (Emotional Stability). The descriptions of the items loading negatively on Factor III — *potential dominant, streetwise, calculating, intelligent* and *ambitious* — seem to describe an individual who is confident in social situations and is able to manipulate these situations to their own advantage. The item *laidback* also loads moderately, and significantly, on this factor (-.44). An animal scoring highly on this factor then, would be described as intelligent, competitive, cunning and confident. This type of personality profile bears a resemblance to low Agreeableness (one of the 'Big Five' factors) and the personality factor of machiavellianism in humans.

Factor IV is another factor that seems to incorporate more than one group of items. *Gets first choice, greedy* and *thieving* all relate to obtaining food. *Gets first choice,* however, was described as being related to being dominant (in that a dominant animal may be more successful at obtaining the biggest portion), and indeed the remaining items loading on this factor: *good at displaying, dominant* and *bossy* were all used to refer to characteristics that a dominant animal would display. Factor IV has accordingly been labelled Dominance.

The highest loading items on Factor V, *overly protective, trusting* and *suspicious* are all related to anxious responses. *Obedient* and *likes keepers' attention* refer to chimpanzee-caretaker relations. The items *happy, friendships last* and *cooperative* describe an individual's ability to engage in successful relationships with others. Notably, these items, and the items signifying chimpanzee-caretaker relations, load in the opposite direction to the anxious items; more anxious individuals thus have difficulty in their social relationships.

To summarise, the data from Rater 1 indicate the existence of five obliquely related factors. These factors have been interpreted as Emotional Stability, Social Confidence, Machiavellianism, Dominance and Anxiety.

2.3.2 Preliminary analysis of personality constructs: Rater 2

Since Rater 2 was unable to be interviewed, it was impossible to determine the precise meanings of each of his trait terms. The interpretation of the five factors above then, rely on my own initial understanding of each term as it was generated.

Factor I seems to be composed of characteristics related to dominance; the significant items are: *dominant, low-ranking, tough, cowardly* and *good in conflict;* as well as terms denoting a machiavellian tendency: *takes initiative, ambitious, manipulative*. Three items on this factor relate to social confidence: *confident, less confident, nervous*. An animal scoring highly on this factor might therefore be described as confident, dominant and ambitious.

The significant items loading on Factor II all relate to sociability, both in terms of relationships between the animals, and between animal and caretaker. An interesting significant loading on this factor is that of *neuroticism* (.35); it might be expected that an animal high in sociability is not likely to show neurotic or anxious responses but the loadings suggest that they do. The item *emotionally responsive* also loads moderately, and significantly, on this factor. This item seems intuitively to relate to the other social items loading on this factor, and its loading with *neurotic* seems understandable in the light of Eysenck's definition of the factor of Neuroticism as a dimension of emotional arousability (Eysenck, 1967).

Factor III contains items of a similar nature to the third factor in Rater 1's solution. Both factors seem to indicate what may be called a machiavellian tendency. On both we see a number of traits related to social intelligence, e.g. for Rater 2 *opportunistic,* and *calculating*. In addition, both factors incorporate terms relating to the quality of social relationships; for Rater 2 these are *loner* and *affectionate*. Two other items are just significant for this factor: *responsive to keepers* (-.32) and *intelligent* (.30). The picture overall for this factor suggests an animal who has problems with social interactions with other animals, (and caretakers) and who is mentally tactical.

To summarise, a three factor solution showed the best fit to the data

Table 2.3 Factor loadings of original constructs produced by Rater 2

	Factor I	Factor II	Factor III
	Dominance	Sociability	Machiavellianism
Dominant	_.75*_	-.15	-.19
Less confident	_-.75*_	.05	.16
Low-ranking	_-.74*_	.08	.11
Confident	_.71*_	.02	-.05
Takes initiative	_.70*_	-.18	-.21
Good in conflict	_.64*_	.00	.02
Tough	_.62*_	.04	.03
Nervous	_-.59*_	-.19	.06
Cowardly	_-.56*_	.09	-.05
Ambitious	_.53*_	.00	.18
Manipulative	_.36*_	-.01	.15
Outgoing	-.07	_.74*_	-.10
Caring	.04	_.71*_	.05
Good with young	-.04	_.69*_	-.02
Introvert	.11	_-.59*_	.02
Playful	-.15	_.59*_	-.28
Protective	.15	_.50*_	.15
Responsive to keepers	-.09	_.47*_	-.32*
Greedy	-.16	_.45*_	.21
Emotionally responsive	.01	_.37*_	.19
Intelligent	.19	_.36*_	.30*
Neurotic	.09	_.35*_	.00
Opportunistic	-.14	.16	_.74*_
Calculating	.00	.22	_.71*_
Affectionate	.26	.11	_-.50*_
Loner	.00	-.01	_.49*_
% Variance	37.9	20.2	6.7

The highest loading items on each factor are shown in italics.

for Rater 2. The factors have been tentatively identified as Dominance, Sociability and Machiavellianism. These factors seem similar to the Sociability, Dominance and Machiavellianism factors found for Rater 1, the notable difference is the lack of an Anxiety factor for Rater 2.

2.3.3 Preliminary analysis of personality constructs: Rater 3

Table 2.4 shows a four-factor solution for Rater 3's data. The first factor has been labelled Machiavellianism. The items loading on this factor show a profile of an animal who is confident, calculating, aggressive and sociable. Three of the items *exploratory, habitual* and *intelligent*, refer to a tendency to be flexible and able to adapt to changing circumstances. The last item loading on this factor, *respectful*, describes formal dominance relationships; this item loads negatively on Factor I, indicating an animal who fails to consistently show submissive greetings to more dominant individuals in the group.

The items *dominant* and *high-ranking*, loading highly and significantly on Factor II, seem to denote different types of dominance for this rater. *High-ranking* was defined as an animal's overall position within the dominance hierarchy, whereas *dominant* referred to dominance interactions between individuals. This distinction is essentially the same as de Waal's distinction between formal and real dominance (de Waal, 1982, 1986a). *Stirs up others* was used to describe those animals, usually males, who engage in frequent dominance displays. This factor has accordingly been labelled Dominance. The items *motivated, easily stressed* and *persistent* are just significant on this factor, but the latter two items load negatively, indicating that an animal loading highly on items related to dominance is characterised as lacking in persistence, but not easily stressed.

Factor III is characterised by items that express social relationships. The highest loading significant items on this factor are *protective towards young* and *allo-parents*. The next highest loading item on this factor, *makes alliances easily*, denotes individuals that can successfully persuade others to assist them in agonistic situations. This item also loads significantly on Factor I, Machiavellianism. Three items loading on Factor I also load moderately and significantly on Factor III: *sociable, intelligent* and *respectful*. This factor may therefore be interpreted as Sociability.

The interpretation of Factor IV is not particularly clear-cut. Some of the items loading on this factor relate to social interactions, but the item *sociable* loads negatively (and non-significantly) on this factor. The highest loading item on Factor IV, *more vocal*, refers to species-typical vocalisations

Table 2.4 Factor loadings of original constructs produced by Rater 3

	Factor I	Factor II	Factor III	Factor IV
	Machiavellianism	Dominance	Sociability	Anxiety
Decisive	_.86*_	-.01	.01	.01
Assertive	_.85*_	.20	-.03	-.02
Opportunistic	_.84*_	-.07	-.04	-.09
Cowardly	_-.83*_	-.14	-.21	.15
Cunning	_.74*_	-.13	-.13	.27
Motivated	_.72*_	.31*	-.00	.17
Exploratory	_.72*_	.02	-.10	.16
Easily stressed	_-.71*_	-.32*	-.31*	.10
Persistent	_.68*_	-.33*	-.10	.14
Sociable	_.66*_	-.03	.49*	-.21
Greedy	_.64*_	-.18	.19	.16
Aggressive	_.58*_	.11	.25	.23
Habitual	_-.58*_	-.43*	-.02	.24
Short-tempered	_.49*_	.38*	.06	-.03
Intelligent	_.45*_	.06	.39*	.43*
Respectful	_-.32*_	.08	.31*	.26
Dominant	-.00	_.90*_	.25	.12
High-ranking	-.00	_.76*_	.46*	.19
Stirs up others	.00	_.72*_	-.37*	-.11
Protective to young	.02	.17	_.75*_	-.05
Allo-parents	-.03	-.01	_.73*_	.00
Makes alliances	.40*	.05	_.47*_	.01
More vocal	.15	.12	-.25	_.64*_
Playful	-.02	.20	-.27	_-.56*_
Patient	-.04	-.00	-.03	_-.46*_
Interacts	-.07	-.00	-.05	_.41_
% Variance	37.2	10.7	9.5	6.4

The highest loading items on each factor are shown in italics.

made in a variety of social contexts, e.g. grooming, or aggressive interactions.

Patient similarly refers to an animal's response in several different contexts, e.g. in grooming interactions, when waiting to be fed etc. Most of the animals were described as interacting positively with the public, e.g. by begging for food. The only other items which load significantly on Factor IV are *intelligent* (.43) and *playful* (-.56). However, several of the examples of behaviour given by Rater 3 to describe the former item related to anxious and impatient responses expressed by individuals in social situations. Accordingly, this factor has been tentatively identified as relating to Anxiety.

To summarise, Rater 3's constructs fit a four-factor solution. The factors have been identified as Machiavellianism, Dominance, Sociability and Anxiety. These factors show some similarity with those identified for the previous two raters.

2.3.4 Preliminary analysis of personality constructs: Rater 4

The results for Rater 4 are presented in Table 2.5. The highest loading significant items on Factor I relate to aggressive behaviour. *Thug-like*, for instance, was defined as 'looking for trouble'. Similarly, *arrogant* and *bad-tempered* were also used to denote the tendency to frequently instigate social aggression. *Timid*, loading negatively on this factor, was defined as a tendency to avoid agonistic encounters. The items *awkward*, *brave* and *leader* show lower, but significant, loadings on this factor, which has been labelled Social Aggression.

Factor II has been interpreted as Machiavellianism; some of the items loading on this factor seem to be similar to machiavellian items on previous raters' solutions. For example, *deceitful*, *scheming* and *underhand* describe cunning, deceptive behaviour. Rater 4 explained this behaviour by suggesting that it showed an aggressive response to other individuals. The three highest loading items on this factor, *friendly*, *sociable* and *playful* refer to social responses. This factor therefore seems to combine items that relate to an aggressive, machiavellian response with a lack of positive social responses.

On Factor III, high-loading and significant items such as *dominant*, *top-ranking*, *leader* and *organiser* suggest this factor may be interpreted as related to dominance. Other items, e.g. *trusting*, *suspicious*, *emotionally well-*

developed and *contented* seem to refer more to anxiety. It is notable that the items *nervous* and *cowardly* (defined as nervousness) also load substantially, but negatively, on this factor (-.37 and -.24 respectively). The item *thick* was used to describe an individual who is inflexible, and shows little aptitude for problem-solving. From the loadings on this factor it seems that dominance is characterised by social confidence and intelligence, as well as the ability to influence the rest of the group.

Two of the items loading on Factor IV relate to protective responses: *protective of young* refers to an adult animal retrieving or otherwise protecting an infant in an aggressive social situation. *Protective* was used to describe a general protective response to the group as a whole. Also loading highly on Factor IV is the item *awkward*, which describes an animal who is difficult to manage in care-taking situations, such as giving medicine. *Precocious* and *forward-thinking* both refer to intelligence.

To summarise, the data from Rater 4 suggest four factors. Two of these, Dominance and Machiavellianism, show similarities with factors obtained from the data of the previous raters. The remaining two, Social Aggression and Protectiveness, are more difficult to compare with previous results and seem to be unique to this data set.

Table 2.5 Factor loadings of original constructs produced by Rater 4 (page 58)

(The highest loading items on each factor are shown in italics.)

	Factor I	Factor II	Factor III	Factor IV
	Social Aggression	Machiavellianism	Dominance	Protectiveness
Naughty	.80*	.32*	-.27	-.16
Instigator of fights	.72*	-.12	-.05	.08
Destructive	.70*	.33*	.03	.39*
Noisy	.70*	.07	.02	-.05
Mischeviious	.69*	.39*	-.15	-.21
Calm	-.68*	.00	-.06	.12
Extravert	.66*	-.00	.07	.12
Thug-like	.63*	-.22	.10	.24
Impatient	.59*	.24	-.06	.10
Arrogant	.59*	-.31*	-.03	.16
Bad-tempered	.55*	-.33*	.01	.28
Cowardly	-.54*	.17	-.24	.32*
Nervous	-.49*	.07	-.37*	.34*
Pushy	.48*	-.28	.25	.22
Timid	-.46*	.21	-.27	-.09
Greedy	.42*	-.01	.24	-.08
Friendly	.12	.87*	.16	-.00
Sociable	.07	.87*	-.07	.10
Playful	.47*	.84*	-.26	.05
Poor interactor	.06	-.82*	.00	.00
Lazy	-.38*	-.75*	.00	.06
Nasty	.28	-.67*	.12	.26
Deceitful	.24	-.66*	-.33*	.05
Good with young	-.03	.60*	-.02	.34*
Scheming	.25	-.59*	-.01	-.09
Underhand	.23	-.54*	-.36*	-.06
Slow	-.45*	-.50*	-.01	.33*
Throws faeces	.15	.45*	.31*	.10
Dominant	.11	.04	.78*	-.21
Suspicious	.11	-.15	-.71*	.50*
Sneaky	.00	.02	-.70*	.14
Trusting	-.03	.26	.69*	-.37*
Brave	.34*	.19	.66*	-.09
Top-ranking	.09	-.32*	.65*	.17
Leader	.30*	-.03	.63*	.07
Organiser	-.22	-.46*	.63*	.02
Childish	.03	.37*	-.63*	-.24
Emotionally well-developed	-.14	-.00	.57*	-.07
Interacts with public	.27	.09	.47*	.05
Contented	.23	.33*	.47*	.10
Thick	.01	-.16	-.44*	-.37*
Spits	-.00	.25	.34*	-.04
Protective of young	-.17	.27	.10	.74*
Forward-thinking	.10	-.03	-.19	.73*
Awkward	.39*	-.03	-.55*	.70*
Protective	.03	.39*	-.00	.69*
Precocious	-.09	.24	-.01	-.51*
% Variance	30.3	17.1	13.8	7.4

2.3.5 Preliminary analysis of personality constructs: Rater 5

Table 2.6 presents the factor solution for Rater 5's data. Factor I has been labelled Emotional Stability. Many of the items loading on this factor are similar in nature to those loading on Rater 1's Emotional Stability factor. Both factors contain items that relate to quality of social interactions. For the present factor structure, items *popular, pleasant* and *likes people* (i.e. caretakers) load negatively and significantly on Factor I. The item *obnoxious* loads positively; an obnoxious animal was described as unpopular, and as having difficulty forming lasting social relationships. Several items referred to a tendency to be unpredictable or emotionally unstable. *Calculating* seemed to be used to define an animal as unpredictable or untrustworthy. *Deep* was similar; here the definition referred to an animal who might be characterised as intelligent, but not emotionally expressive. *Unobtrusive* and *troublemaker* both describe a tendency to engage in emotional or aggressive displays. The item *unaggressive* seemed to be related to anxiety; an aggressive animal was defined as being nervous. The item *silly*, as well as describing 'childish' or playful behaviour, was used to indicate excessive nervousness. An animal scoring highly on Factor I, therefore, might be described as unpredictable and nervous, and as experiencing difficult social relationships.

Factor II is characterised by items relating to dominance, e.g. *low-ranking, experienced, intelligent, confident*. The items *nervous* and *wary* load negatively and significantly, and also relate to dominance; a *nervous* animal was described as submissive and as showing little social confidence. Similarly, a *wary* animal was described as showing submissive responses to others. The item *greedy* denoted the ability to obtain food by virtue of being a dominant individual.

Factor III has been labelled Machiavellianism. The item *bossy* described an animal who is deceptive, unsociable and ambitious. *Unfeeling* denotes a similar combination of competitiveness and social isolation. *Subdued* describes an individual who is nervous but ambitious.

To summarise, the data for Rater 5 suggest a three-factor structure of Emotional Stability, Dominance and Machiavellianism. These factors show clear similarities with factors obtained from previous raters.

Table 2.6 Factor loadings of original constructs produced by Rater 5

	Factor I	Factor II	Factor III
	Emotional Stability	Dominance	Machiavellianism
Popular	_-.75*_	.23	.16
Obnoxious	_.71*_	.01	-.01
Pleasant	_-.66*_	.02	-.07
Patient	_-.65*_	.01	-.07
Likes people	_-.63*_	-.15	.21
Schizophrenic	_.61*_	.14	.06
Unaggressive	_-.56*_	-.21	-.15
Silly	_.53*_	-.34*	-.07
Cunning	_.49*_	.33*	.03
Calculating	_.46*_	.20	.22
Unobtrusive	_-.46*_	-.19	-.24
Deep	_.39*_	.01	-.12
Predictable	_-.36*_	-.31*	-.00
Troublemaker	_.34*_	.22	.23
Low-ranking	-.18	_-.91*_	.24
Experienced	.19	_.83*_	-.34*
Wary	.07	_-.81*_	-.10
Nervous	.06	_-.79*_	-.08
Confident	-.00	_.75*_	.19
Intelligent	-.05	_.53*_	.17
Good with young	.02	_.49*_	-.37*
Greedy	.18	_.34*_	.22
Subdued	.23	-.35*	_-.57*_
Ambitious	.27	-.17	_.48*_
Unfeeling	.25	-.13	_.40*_
Bossy	.20	.25	_.39*_
% Variance	48.5	17.9	4.8

The highest loading items on each factor are shown in italics.

2.3.6 Preliminary analysis of personality constructs: Rater 6

Table 2.7 shows the factor solution from Rater 6's data set. Factor I is characterised by items related to a machiavellian tendency. The significant items *ambitious, mentally tactical, cunning, intelligent* and *persistent* refer to the ability to problem-solve, to plan ahead and the tendency to deceive. Also loading positively on this factor are items related to physical agility: *active,* *agile, physically tactical, physically manipulative* and *energetic.* The items *enthusiastic, destructive* and *troublemaker* also load moderately but significantly on Factor I, though they load more highly on other factors. The item *boring,* loading negatively, describes an animal who is inactive, and does not socialise very much. The items *cowardly* and *courageous* both relate to a tendency to become involved in agonistic encounters.

The highest-loading items on Factor II relate to social activities. *Seeks attention* and *affectionate* both relate to interactions between the animals and caretakers. The item *standoffish* was used to describe an individual who did not associate very much with others. *Destructive* similarly relates to social encounters: the rater described some animals as being destructive towards objects in order to gain the caretakers' attention. *Enthusiastic* describes an interest in investigating new objects.

Factor III may best be interpreted as related to dominance. The item *jealous,* which also loads substantially on Factor IV, describes both interactions with other animals and with caretakers. A *jealous* animal was defined as becoming aggressive if it was not receiving attention from others. The item *avoids conflict,* loads negatively on this factor but was described as being related to dominance; the opposite pole of this construct *attacks when necessary,* denotes an animal who will defend themselves, and their own resources (e.g. food) against the attacks of others.

Many of the items loading on Factor IV seem to be related to an anxious tendency. *Troublemaker* described an individual who would behave aggressively towards others in order to gain food or attention. The opposite pole of *quiet* is *loud,* which refers to an individual who vocalises a lot as a result of being nervous, or the victim of aggression. *Gentle* refers to playful interactions and interactions with infants. The item *uninterested* describes an animal who fails to socialise very much with others; this item also loads substantially on Factor II, Sociability. The highest loading item on Factor IV is *arrogant,* this term describes individuals who seem intolerant of other individuals, and aggressive towards others.

To summarise, the data for Rater 6 show a four factor solution. The factors have been identified as Machiavellianism, Sociability, Dominance and Anxiety.

Table 2.7 Factor loadings of original constructs produced by Rater 6

	Factor I	Factor II	Factor III	Factor IV
	Machiavellianism	Sociability	Dominance	Anxiety
Physically manipulative	_.84*_	.03	.00	.11
Ambitious	_.83*_	.06	.01	.18
Agile	_.83*_	.20	-.16	-.30*
Boring	_-.81*_	.01	-.17	.16
Active	_.79*_	.17	-.06	-.04
Mentally tactical	_.73*_	-.28	.24	.00
Physically tactical	_.73*_	.15	-.16	.21
Persistent	_.69*_	-.14	.39*	.17
Cowardly	_-.67*_	.13	-.53*	-.07
Cunning	_.67*_	-.08	.26	.28
Energetic	_.65*_	.14	-.17	-.17
Intelligent	_.61*_	.01	.50*	-.05
Courageous	_.40*_	-.04	.38*	-.00
Playful	.06	_.80*_	-.04	.00
Seeks attention	.21	_.69*_	.10	.39*
Good with infants	.06	_.65*_	-.07	.00
Dislikes company	.43*	_-.63*_	.21	-.04
Standoffish	-.04	_-.63*_	-.01	-.07
Enthusiastic	.36*	_.62*_	-.19	.37*
Destructive	.41*	_.59*_	-.14	.41*
Affectionate	-.19	_.58*_	.31*	-.07
Respected	-.00	.04	_.88*_	-.10
Confident	.24	-.02	_.77*_	.18
Accepted	-.07	.16	_.71*_	-.18
Mature	-.18	-.23	_.69*_	.01
Dominant	.08	.11	_.63*_	.36*
Popular	.11	.38*	_.59*_	-.08
Avoids conflict	-.43*	.29	_-.48*_	-.24
Jealous	.21	.21	_.46*_	.38*
Arrogant	.22	.09	.13	_.69*_
Greedy	-.20	.47*	.00	_.69*_
Troublemaker	.33*	-.11	-.01	_.60*_
Quiet	.00	-.26	.21	_-.59*_
Aggressive	.26	-.00	.11	_.59*_
Easygoing	-.18	.14	-.30*	_-.50*_
Gentle	.23	.13	.08	_-.46*_
Generous	.07	-.04	-.07	_-.45*_
Uninterested	-.06	-.33*	-.03	_.35_
% Variance	32.8	16.2	11.7	7.5

The highest loading items on each factor are shown in italics.

2.3.7 Preliminary analysis of personality constructs: Rater 7

In Table 2.8, Factor I is characterised by items relating to an active, sociable tendency, e.g. *playful, active, likes solitude.* Also loading on this item are terms associated with a more actively aggressive response: *teasing, mischievous, boisterous, impatient* and, loading negatively, *seeks peace.* This last item refers to behaviour which seems to function in order to assuage aggressive encounters between others. Its opposite, *stirs up trouble,* describes a tendency to provoke others, or to aggravate aggressive situations. Factor I has been labelled Sociability.

All of the items loading on Factor II appear to relate to anxiety. *Happy* referred to individuals who were sociable and responded well to others, and this item also loads significantly on Factor I. The term *excitable* was used to describe animals who seem intolerant of stressful situations, or who respond in a nervous or inappropriate way in a range of social situations.

Factor III has been interpreted as Machiavellianism. This factor is characterised by items related to the desire to achieve dominance, e.g. *ambitious, macho.* The latter item was used by this rater to describe a (mainly male) tendency to attempt to increase dominance status. The item *forward-planning* refers to an ability to problem-solve, and to use intelligent methods to obtain a goal. *Inquisitive* refers to the tendency to be interested in unusual objects or events. *Alert* is similar, but refers more to the ability to be vigilant and aware of surrounding social interactions. *Introverted* describes an animal who does not become involved in aggressive situations, and does not appear to engage in aggressive displays for the purpose of asserting dominance over others.

Factor IV has been labelled Protective. The items *maternal* and *protective* refer to interactions with infants. *Noisy* and *naughty* are curious items to load on this factor; *noisy* describes an animal who tends to respond to situations by vocalising loudly and repetitively. *Naughty* seems to refer mainly to the activities of young animals, and seems very similar to *mischievous*.

To summarise, the data for Rater 7 show a four-factor structure. These factors have been identified as Sociability, Anxiety, Machiavellianism and Protectiveness. These factors seem similar to the factors identified in previous raters' data.

Table 2.8 Factor loadings of original constructs produced by Rater 7

	Factor I	Factor II	Factor III	Factor IV
	Sociability	Anxiety	Machiavellianism	Protectiveness
Playful	_.95*_	-.19	-.21	-.18
Active	_.87*_	.08	.13	.03
Teasing	_.74*_	.25	-.00	.25
Likes solitude	_-.65*_	.12	-.46*	.11
Mischievous	_.63*_	.28	-.03	.28
Boisterous	_.57*_	.26	.34*	.24
Impatient	_.52*_	-.41*	.16	-.03
Seeks peace	_-.49*_	-.10	-.47*	-.18
Secure	.02	_.93*_	.02	.01
Fearful	-.03	_-.80*_	-.30*	-.05
Self-assured	-.15	_.78*_	.16	.13
Tense	-.10	_-.71*_	.34*	.17
Happy	.43*	_.63*_	.21	-.11
Easygoing	-.06	_.59*_	-.60*	.09
Excitable	.04	_-.52*_	.35*	.36*
Forward-planning	-.07	-.17	_.89*_	-.09
Ambitious	-.01	.03	_.70*_	.15
Inquisitive	.21	.12	_.62*_	-.02
Alert	.39*	-.00	_.53*_	-.29
Introverted	-.29	-.18	_-.45*_	-.21
Macho	-.01	.24	_.42*_	.10
Maternal	.29	-.31*	.01	_-.67*_
Noisy	.22	-.36*	-.00	_.67*_
Naughty	.43*	-.18	.06	_.54*_
Protective	-.15	-.13	.03	_-.45*_
% Variance	34.2	18.3	11.1	6.7

The highest loading items on each factor are shown in italics.

2.4 Discussion of preliminary factor analyses of original construct loadings

Although the findings of this initial set of ratings must be treated with caution, the results above show that similar factors emerged from each of the seven separate analyses. For each data set, the number of factors accounting for most of the variance ranged from three to five. In total, seven different factors were identified; these were interpreted as: Emotional Stability, Social Confidence, Machiavellianism, Protectiveness, Dominance, Anxiety, and Social Aggression. The factors Social Confidence and Social Aggression were specific to one particular rater only, and the factors of Emotional Stability and Protectiveness identified in only two raters. Dominance, Machiavellianism and Anxiety, however, were reasonably clear to identify in nearly all the raters. It seems, therefore, that it is these three factors that most easily account for most of the variation in chimpanzee personality for these particular raters.

2.5 Additional analysis of construct ratings using primary construct sets

To attempt to eliminate the problems caused by the large number of constructs in each data set, the raters were asked to choose the ten constructs (from their own data set) which they felt were the most important, and most useful, for classifying the animals' personality.

2.5.1 Data analysis

Separate principal components analyses were performed on each rater's reduced set of construct ratings. The methods of factor extraction used were Kaiser's criterion and scree plots. Both orthogonal and oblique rotations were performed. There was little difference between the two solutions and the oblique one was chosen for interpretation.

2.5.2 Results of analyses of primary construct sets

The results of the principal components analyses for each set of ratings are presented in Tables 2.9 to 2.22 below. Following each factor solution, additional tables show the inter-correlations between the elicited factors. These are produced automatically by the program Statview and show values of Pearson's *r*. Significant factor intercorrelations are indicated following the procedure recommended by Kline (1994), i.e. those correlations of 0.3 or above are considered to be significant. The interpretation of these factor correlations is explained in the text as the meanings depend upon the direction of the original loadings. For example, in Table 2.10, the factors Dominance and Machiavellianism correlate substantially, at -.58. Even though this correlation is negative, if the original construct loadings for each factor are examined, it is clear that this correlation actually indicates that more dominant animals are more machiavellian. A negative correlation would be expected here, since most of the items denoting machiavellianism load negatively on this factor; therefore, animals that score highly on Machiavellianism will have *lower* scores on the Machiavellianism factor (because of the direction of the loadings).

2.5.2.1 Analysis of primary construct ratings: Rater 1

The principal components solution for Rater 1 produced three clear factors: Dominance, Sociability and Machiavellianism. This is a considerable reduction in the numbers of factors in the original analysis of this data set. Two of the factors appearing in the original solution do not appear in the present one: Emotional Stability and Social Confidence. Of interest in the present analysis is the construct *laidback*, which was used to refer to degree of social confidence. A *laidback* animal is relaxed in social situations, whereas a *nervous/unstable* animal (the opposite of this construct) may behave in an impulsive manner, possibly due to social anxiety. It is interesting to note that impulsivity is seen as a constituent of extraversion in humans (Eysenck and Eysenck, 1975).

The highest loading item on Factor III is *humanised*. This refers to those animals who have been hand-reared or otherwise experienced substantial human contact. This rater considered humanised animals to be rather 'aloof' in their relationships with other chimpanzees, which fits in well with the nature of the other constructs loading on Machiavellianism. It is conceivable too that humanised animals may actually display higher levels of social intelligence (Fentress, 1992).

Table 2.9 Factor loadings of primary constructs produced by Rater 1

	Factor I	Factor II	Factor III
	Dominance	Sociability	Machiavellianism
Respected	.91*	.44*	.23
Dominant	.75*	.15	.19
Good with young	-.50*	-.10	.16
Laidback	.49*	.87*	-.33*
Loner	-.03	-.65*	.10
Friendly	-.03	.55*	.01
Greedy	.00	-.42*	-.11
Humanised	.26	-.18	.94*
Calculating	.20	-.07	-.42*
Intelligent	.25	-.10	-.33*
% Variance	47.2	18.2	13.6

Table 2.10 Intercorrelations among personality factors Dominance, Sociability and Machiavellianism

	Dominance	Sociability	Machiavellianism
Dominance	1.00	-.75*	-.58*
Sociability	-.75*	1.00	-.54*
Machiavellianism	-.58*	-.54*	1.00

Table 2.10 shows that the three factors correlate quite highly and significantly. The highest correlation is between Dominance and Sociability (-.75), indicating that high scorers on Dominance are less sociable. The correlation of -.58 between Dominance and Machiavellianism indicates that more dominant animals are more machiavellian. Sociability and Machiavellianism also correlate substantially (-.54), showing that more sociable animals are more machiavellian.

2.5.2.2 Analysis of primary construct ratings: Rater 2

The analysis for Rater 2 produced three components, interpreted as Dominance, Sociability and Anxiety.

Table 2.11 Factor loadings of primary constructs produced by Rater 2

	Factor I	Factor II	Factor III
	Dominance	Sociability	Anxiety
Less confident	-.94*	-.08	.05
Cowardly	-.87*	.06	.13
Good in conflict	.81*	-.22	.32*
Dominant	.76*	-.22	.29
Intelligent	.72*	.31*	-.07
Responsive to keepers	-.21	.87*	-.00
Introverted	-.02	-.84*	-.15
Caring	.25	.58*	.47*
Neurotic	-.00	.08	.87*
Good with young	.00	.51*	.60*
% Variance	40.0	28.6	10.1

The factor Machiavellianism, which appeared in the original analysis has here disappeared, and the items *neurotic* and *good with young*, loading originally on Sociability, now load together on the factor of Anxiety (although *good with young* also loads highly on Factor II).

Table 2.12 Intercorrelations among personality factors Dominance, Sociability and Anxiety

	Dominance	Sociability	Anxiety
Dominance	1.00	.02	.12
Sociability	.02	1.00	.13
Anxiety	.12	.13	1.00

Table 2.12 shows the inter-correlations between the three factors. None of the correlations are significant, indicating the relative orthogonality of the factors.

2.5.2.3 Analysis of primary construct ratings: Rater 3

The principal components analysis for Rater 3 produced three factors: Machiavellianism, Sociability and Dominance. These three factors, together with Anxiety, appeared in the original analysis of this rater's data.

Table 2.13 Factor loadings of primary constructs produced by Rater 3

	Factor I	Factor II	Factor III
	Machiavellianism	Sociability	Dominance
Motivated	*.88**	.11	-.01
Habitual	*-.76**	-.20	.19
Aggressive	*.69**	-.01	.28
Short-tempered	*.65**	-.18	.42*
Easily stressed	*-.65**	-.43*	.00
Intelligent	*.50**	.38*	.11
Makes alliances easily	.00	*.81**	.06
Sociable	.16	*.79**	.01
Protective to young	-.18	.22	*.79**
High-ranking	.31*	-.03	*.65**
% Variance	49.8	13.6	11.3

In the original analysis, the item *makes alliances easily* loaded on the Sociability factor, but also loaded substantially on Machiavellianism. The item *sociable* originally loaded on Machiavellianism, but also loaded highly on Sociability. Here, the two items load together and the factor has been interpreted as Sociability.

Table 2.14 Intercorrelations among personality factors Machiavellianism, Sociability and Dominance

	Machiavellianism	Sociability	Dominance
Machiavellianism	1.00	.21	.21
Sociability	.21	1.00	.26
Dominance	.21	.26	1.00

Small correlations were found between the three factors of

Machiavellianism, Sociability and Dominance. The correlation between Machiavellianism and Sociability (.21) suggests that high scorers on Machiavellianism are also more sociable. The positive relationship between Machiavellianism and Dominance (.21) indicates that machiavellian animals are more dominant. In addition, sociable animals are rated as more dominant (.26), although none of the above correlations are significant.

2.5.2.4 Analysis of primary construct ratings: Rater 4

The principal components analysis for Rater 4 produced four factors. Two of the items on Factor I, *timid* and *nervous*, both loaded on Social Aggression in the original analysis. Here, their combination with *dominant* suggests that Factor I be labelled Dominance.

Table 2.15 Factor loadings of primary constructs produced by Rater 4

	Factor I	Factor II	Factor III	Factor IV
	Dominance	Sociability	Food related	Machiavellianism
Timid	_.82*_	.04	.00	.30*
Nervous	_.64*_	.15	-.00	-.12
Dominant	_-.62*_	.03	.04	.37*
Good with young	-.13	_.83*_	-.05	-.19
Sociable	.26	_.81*_	.21	.16
Impatient	.17	.14	_.88*_	-.24
Greedy	-.01	-.21	_.64*_	.00
Interacts with public	-.09	.15	_.64*_	.08
Awkward	-.16	.20	.10	_-.87*_
Trusting	-.32*	.29	-.04	_.64*_
% Variance	38.1	17.2	14.3	11.8

Two items, *sociable* and *good with young*, load highly and significantly on Factor II. The latter item described individuals who spent time playing with infants, and would act to protect younger animals during group aggression. These two items originally loaded on Machiavellianism (in the opposite direction to the 'machiavellian' items on this factor), indicating the lack of social skill that seems indicative of this factor. In the present analysis, Factor IV has been interpreted as Machiavellianism, due to the connotations of *awkward* and *trusting*. The definitions given for these items, however, also indicate their relationship to anxiety, so the nature of this factor is not entirely clear.

Factor III contains an unusual combination of items. *Impatient* relates to an impulsive response in a variety of different situations, e.g. when an animal is waiting to be let out into an enclosure, or waiting to be fed, or in a grooming interaction. *Greedy* and *interacts with public* both refer to food seeking behaviour. Due to the definitions of the latter two items, this factor has been tentatively labelled Food-related, though these items could be interpreted as facets of impatient behaviour.

Table 2.16 Intercorrelations among personality factors Dominance, Sociability, Food-related and Machiavellianism

	Dominance	Sociability	Food-related	Machiavellianism
Dominance	1.00	.23	-.51*	-.32*
Sociability	.23	1.00	-.30*	-.04
Food-related	-.51*	-.30*	1.00	.36*
Machiavellianism	-.32*	-.04	.36*	1.00

Table 2.16 shows a range of high, moderate and low correlations between the four factors identified for Rater 4. The highest significant correlation is between the Dominance and Food-related factors indicating that more dominant animals are more greedy, impatient and interact more with the public. A moderate, but significant, correlation is also found between the Food-related factor and Machiavellianism (.36) suggesting that more 'food-related' behaviour is engaged in by low scorers on Machiavellianism. Dominance and Machiavellianism have a correlation of -.32; more dominant animals are less machiavellian. Sociability and the Food-related factor have a correlation of -.30, indicating that more sociable animals engage in less food-related behaviour. A smaller correlation is found between Dominance and Sociability (.23) showing that more dominant animals are rated as less sociable, but this correlation is not significant.

2.5.2.5 Analysis of primary construct ratings: Rater 5

Table 2.17 Factor loadings of primary constructs produced by Rater 5

	Factor I	Factor II
	Machiavellianism	Dominance
Patient	*.89**	-.04
Ambitious	*-.85**	-.11
Unaggressive	*.85**	-.28
Popular	*.85**	.29
Unobtrusive	*.84**	-.26
Likes people	*.69**	-.07
Cunning	*-.68**	.37*
Low-ranking	-.01	*-.93**
Experienced	.13	*.89**
Confident	-.21	*.80**
% Variance	57.0	23.2

The principal components analysis for Rater 5 produced two factors. The factor Emotional Stability, which appeared in the previous analysis for this rater, was not present here.

Three of the items that loaded highly on the original Dominance factor — *low-ranking, experienced* and *confident* — characterise this same factor in the present analysis.

The item *ambitious,* loading on the original Machiavellianism factor, is one of the highest loading items on this factor in the present analysis. The other items loading on this factor here also loaded on the factor of Emotional Stability in the preliminary analysis. In the Machiavellian factor in the present analysis, we see a combination of more 'positive' machiavellian traits such as *ambitious* and *cunning,* with less favourable traits such as *aggressive* and *low-ranking* that characterise lack of social expertise.

Table 2.18 shows a small but non-significant correlation between the factors of Machiavellianism and Dominance. Animals that were rated as more dominant were also rated as more machiavellian.

Table 2.18 Intercorrelations among personality factors Machiavellianism and Dominance

	Machiavellianism	Dominance
Machiavellianism	1.00	-.20
Dominance	-.20	1.00

2.5.2.6 Analysis of primary construct ratings: Rater 6

Table 2.19 Factor loadings of primary constructs produced by Rater 6

	Factor I	Factor II	Factor III
	Machiavellianism	Dominance	Sociability
Ambitious	*.94**	.03	.15
Persistent	*.85**	.38*	-.04
Cunning	*.83**	.29	-.18
Active	*.70**	-.00	.34*
Respected	-.02	*.95**	.11
Confident	.37*	*.86**	-.04
Dominant	.27	*.85**	-.00
Popular	.00	*.78**	.49*
Playful	-.09	.17	*.93**
Enthusiastic	.50*	.00	*.71**
% Variance	48.2	20.9	16.3

The principal components analysis for Rater 6 produced three of the four factors appearing in the original analysis for this rater: Machiavellianism, Dominance and Sociability, with the loadings in the present analysis closely reflecting the original loadings. The factor loadings produce a relatively simple structure, with most of the items loading highly on only one factor. The exceptions are the items *popular* and *enthusiastic*. The item *popular* loads most highly on Dominance, but also loads substantially on the Sociability factor. *Enthusiastic* loads highly on Sociability, but also loads substantially on Factor I, Machiavellianism.

Table 2.20 Intercorrelations among personality factors Machiavellianism, Dominance and Sociability

	Machiavellianism	Dominance	Sociability
Machiavellianism	1.00	.04	.01
Dominance	.04	1.00	.00
Sociability	.01	.00	1.00

Table 2.20 indicates that the factors of Machiavellianism, Dominance and Sociability for this rater were not correlated to any significant degree.

2.5.2.7 Analysis of primary construct ratings: Rater 7

Table 2.21 Factor loadings of primary constructs produced by Rater 7

	Factor I	Factor II	Factor III
	Sociability	Protectiveness	Anxiety
Playful	.84*	.00	.22
Active	.83*	-.41*	-.03
Seeks Peace	-.49*	.36*	.38*
Impatient	.49*	.24	-.25
Protective	-.40*	.81*	-.00
Maternal	.01	.74*	.03
Self-assured	-.06	-.65*	-.09
Inquisitive	-.00	-.20	-.80*
Easygoing	.24	-.52*	.73*
Introverted	-.28	.48*	.54*
% Variance	35.6	25.4	12.9

The principal components analysis for Rater 7 produced three factors. Factor I, Sociability, shows clear similarity to the Sociability factor produced in the original analysis for this rater.

In the preliminary analysis, *protective* and *maternal* loaded on a

Protectiveness factor, and *self-assured* on the Anxiety factor. Here, all three items load on Factor II.

The items *inquisitive* and *easygoing* loaded on Machiavellianism in the original analysis. The definitions for these items indicate that they both refer to anxiety, though *easygoing* also loads moderately on Factor II. The rater's definition of *introverted* implied an individual who spent time by themselves, and who was reluctant to become involved in agonistic conflicts. The grouping of these items on Factor III suggested that this factor be interpreted as Anxiety.

Table 2.22 Intercorrelations among factors Sociability, Protectiveness and Anxiety

	Sociability	Protectiveness	Anxiety
Sociability	1.00	.37*	-.36*
Protectiveness	.37*	1.00	.00
Anxiety	-.36*	.00	1.00

Table 2.22 shows the factor inter-correlations between the Sociability, Protectiveness and Anxiety factors for Rater 7. Only two of the correlations are significant. Sociability and Protectiveness are positively correlated (.37), indicating that more sociable animals are seen as more protective. Sociability and Anxiety are negatively related (-.36) suggesting that more sociable animals are also rated as more anxious.

2.6 Discussion of factor analysis of primary construct loadings

The factor analyses of the reduced sets of personality items produced six factors overall. Two were specific to only one rater: the Food-related factor appeared in the factor analysis of Rater 4, and the Protectiveness factor appeared only in the analysis of Rater 7. As the repertory grid technique explicitly encourages raters to explore their own interpretations of behaviour, some idiosyncrasy in the constructs produced is to be expected. With reference to the Protectiveness factor, it is interesting to note that Rater 7 was conducting a study involving only the female animals at the time of rating. This might partially explain the predominance of items relating to adult-infant interactions (and the subsequent Protectiveness factor) in her constructs.

Of the remaining factors identified in the primary construct ratings, a Dominance factor appeared in six of the seven analyses. A Sociability factor also appeared in six out of seven analyses. Machiavellianism appeared in four out of seven analyses. Anxiety was a feature of only two analyses, and in both it was the factor that explained the least variance. The factors of Dominance, Sociability, Machiavellianism and Anxiety seem, therefore, to be common in some form to all of the raters, although the final interpretation of these factors is ultimately my own, and therefore not necessarily free of bias.

The factor structures obtained in the second set of factor analyses were very similar to those obtained in the preliminary analyses. The reduction of trait items in the second set of analyses appeared to clarify the positioning of some items. For instance, items loading on the factors of Emotional Stability and Social Aggression, that appeared in the original analysis, loaded on other factors in subsequent analyses, thus simplifying the factor structures.

The factor inter-correlations for most of the raters were small. The exceptions were Rater 1, whose factor correlations ranged from .54 to -.75, and Rater 4, whose correlations ranged from -.04 to -.51.

The patterns of relationship between factors varied from rater to rater. For instance, for two raters the factor intercorrelations indicated that more dominant animals were being classed as less sociable. The relationship between these two factors seemed to be the inverse for another rater; i.e. more dominant animals were seen as more sociable. Similarly, three raters saw more dominant animals as more machiavellian, while one rater saw dominance as indicating less machiavellianism. Of the two raters whose factor structure included both Sociability and Machiavellianism, high scorers on Sociability also seemed to score highly on Machiavellianism. Only two raters produced both Sociability and Anxiety factors; for one rater these were moderately correlated (-.36) such that highly sociable animals were rated as more anxious. For the other rater the two factors were related in the same direction, although the correlation between them was very low (.13).

Table 2.23 shows the mean inter-factor correlations for Dominance, Sociability, Machiavellianism and Anxiety. These four factors only are included, as these were the only factors that appeared in more than one rater's factor structure. None of the correlations are significant.

Table 2.23 Mean intercorrelations for personality factors Dominance, Sociability, Machiavellianism and Anxiety

	Dominance	Sociability	Machiavellianism	Anxiety
Dominance	1.00	.25	.27	.12
Sociability	.25	1.00	.20	.24
Machiavellianism	.27	.20	1.00	#
Anxiety	.12*	.24	#	1.00

*** Only one rater's factor solution included both Dominance and Anxiety, and this figure represents the correlation between these factors for that rater.**

 # These cells are blank as there were no factor solutions which included *both* Machiavellianism and Anxiety.

2.7 General Discussion

The results presented in this chapter show the factor structures obtained from independently generated sets of trait terms. Three factors, identified as Dominance, Machiavellianism and Anxiety seemed to be important features of the initial analyses which utilised the full range of the trait terms generated by each rater. In order to provide a smaller number of trait terms, each rater was asked to identify the ten trait items that he or she felt to be most important. Separate factor analyses of these rating sets again produced the factors of Dominance, Machiavellianism and Anxiety, together with a Sociability factor. In addition, two of the factor structures contained factors that were idiosyncratic to a particular rater. Items relating to food-seeking behaviour loaded on one factor for one of the raters; similar terms did not appear in other sets of trait terms. The factor of Protectiveness appeared in only one factor structure, that of Rater 7.

In order to obtain personality constructs that were salient to the raters involved in this study, and which reflected their impressions of the animals involved, the repertory grid method was used. The factor analyses presented in this chapter indicate the similarity of the elicited personality factors between raters, despite the fact that each rater used an individual set of trait terms to rate the chimpanzees. What this suggests is that raters are conceptualising chimpanzee personality in terms of four or five basic traits. Whether these traits are specific only to this group of chimpanzees, and in what way they correspond to behaviour will be discussed in subsequent chapters.

Even though the raters produced similar factor structures there are sometimes clear differences between them. In the second set of analyses, for example, two factors — Protectiveness and Food-related — were specific to two raters. The nature of the Food-related factor is not entirely clear as at least one item *impatient* also seems to be related to anxiety. The factor of Protectiveness appeared only in the analysis of Rater 7's data. The terms that loaded on this factor were used mainly to describe the behaviour of female animals. This rater had observed the animals for the least amount of time and possessed more experience in observing the female animals of the group, so it seems likely that trait terms that were more relevant to female chimpanzees were more salient for her. It does seem, therefore, that the differences between the factor structures can in some instances be traced to particular characteristics of each rater's perceptions of the animals.

The personality factors generated in this study, interpreted as Dominance, Sociability, Anxiety, Machiavellianism and Protectiveness, appear to be similar to factors found in other studies of great ape personality ratings. Gold and Maple (1994) factored trait ratings for 298 gorillas, producing four factors: extraverted, dominant, fearful and understanding. Five adjectives loaded on the latter factor: understanding, protective, permissible, equable and motherly. This factor seems to bear some resemblance to the Protectiveness factor identified for Rater 7 in the present study.

A recent study by King and Figueredo (1997) identified six factors from ratings of chimpanzee personality. The first factor was interpreted as a dominance factor. In the second set of analyses presented in this chapter, three of the factor structures contained Dominance as the factor accounting for the most variance. In all of the factor structures in the present study this factor was the clearest and easiest to interpret, suggesting that, as King and Figueredo note, dominance appears to be an important component of individual variation in chimpanzees. The remaining five factors identified in the King and Figueredo study bear a distinct resemblance to the Big Five factors identified in humans (Goldberg, 1990). This possible correspondence between human and nonhuman personality factors is an important issue for the field of nonhuman personality research.

Some of the common factors identified across several nonhuman personality studies have their concomitants in human personality work. A sociability or extraversion factor, for example, is one of the key human personality dimensions and has been identified in several nonhuman species: rhesus macaques (Stevenson-Hinde and Zunz, 1978); gorillas (Gold and Maple, 1994); vervets (McGuire *et al.*, 1994); chimpanzees (King and Figueredo, 1997); spotted hyenas (Gosling, 1998). A fearful or anxious factor also features in many nonhuman studies and, together with extraversion, is one of the most important human personality factors. The factor of machiavellianism is interesting as it appears on only some nonhuman personality factor analyses (e.g. McGuire *et al.*, 1994). In humans, machiavellianism appears to be an important component of personality and possibly related to other measures of antisocial tendencies like Eysenck's Psychoticism scale (Kline, 1994). In the present study, some of the items loading on the Machiavellianism factors seemed to describe problems in social interactions.

The analyses presented in this chapter have identified five key personality factors that appear to reflect those found in previous work on human and nonhuman personality. It is particularly significant that the factor solutions for each rater shared key features, since the generation of personality constructs took place independently for each rater. There are, however, important differences between the raters' construct sets, and it is in the identification and examination of these differences that the relationship between implicit and explicit personality theory may best be elucidated.

One of the advantages of using the repertory grid method was that the constructs used to rate the animals had been generated by the raters themselves. This ensured that each rater's items incorporated the universe of personality constructs that they felt was appropriate to describe the animals. While this method allows raters freedom in describing the personality of the animals, this necessarily means that the number of constructs generated can vary substantially across raters. Also, while clear similarities were found between the personality constructs of individual raters, some construct items (especially in the original construct sets) were idiosyncratic and not clearly defined. To clarify the nature of the personality structure, a single rating scale was constructed incorporating items relating to each of the five factors of Dominance, Sociability, Anxiety, Machiavellianism and Protectiveness. This rating scale was then used in a larger personality survey, sampling chimpanzees from a number of different zoos. Chapter Three presents the findings from this study.

CHAPTER THREE

Results of a personality survey of captive chimpanzees, and the relation of sex, age and dominance to personality ratings

3.1 Introduction and rationale

The aim of the study presented here was to construct a single personality scale with which to rate captive chimpanzees, based upon the personality factors obtained in the previous analyses, presented in Chapter Two. The construction of such instruments, in human and nonhuman personality work, has often depended upon the investigator's own implicit beliefs about trait-behaviour relations. Alternately, items from earlier inventories are often used without any clear criteria for selection. In the construction of the present instrument, more objective criteria were used to generate a scale that would be both based upon previous analyses, and appropriate for a particular group of raters.

One of the main problems with attempting to elucidate personality structure is obtaining a sufficient sample size to assess. The presence of general personality traits can best be determined through the factoring of personality ratings from a large sample of individuals. An appropriate sample of captive animals can be difficult to obtain, as housing and care-taking conditions can vary substantially across zoos. For instance, the full range of variation in sociability may not be apparent in animals which are housed singly, or in pairs. The aim of the present study was to obtain ratings of captive chimpanzees that were housed in moderate to large social groups, in order to present a reasonable comparison with the Chester group.

The factor analysis of the Chester ratings had indicated the existence of five traits: labelled Dominance, Sociability, Anxiety, Machiavellianism and Protectiveness. These factors seemed similar to those found in previous studies of nonhuman primate personality. In order to produce a rating scale that could be used by a number of observers, on a larger sample of animals, items loading on the five factors were used to generate one rating scale that was expected to clarify the existence and nature of the five factors. By using a larger sample it was hoped to establish norms for the scale, against which individual animals could be compared, and the influence of sex, age and dominance explored.

3.2 Method

3.2.1 Selection of trait terms and generation of items

To construct the new rating scale, the factor analyses obtained from ratings of the ten most important constructs were used. Each rater's factor solution was examined for items that loaded highly on each of the original five factors. The interview data were scrutinised to clarify the definitions of the original personality terms given by each rater. In order to ensure that the revised rating scale adequately represented each of the five factors, approximately ten of the highest loading personality items were chosen for each factor, producing a total of 46 items on the new scale. It was expected that the items which correlated highly with each factor would discriminate adequately between the factors.

Since the original personality terms had been single adjectives, or short phrases, these had to be extended to full statements in order to make their meaning clear.

Each statement was phrased as clearly and specifically as possible in order to avoid ambiguity. Where possible, statements were based on operational definitions, to make it clear to which general behaviour they referred. The pronouns 'He' and 'She' prefixed each statement; it was felt that attempting to use fuller definitions like this would make it easier for the raters to relate the items to individuals. Statements were rated on a seven-point frequency scale. A scale of this type is relatively easy for observers to use, but has the disadvantage of raters not choosing the extreme points, or conversely, focusing only on the extreme points (Kline, 1993b). For this reason, seven points were used, rather than a smaller number, to provide a wider range of possible responses. Raters were instructed to rate each animal according to the relative frequency (i.e. compared with other animals) of each behaviour. Raters were asked to respond quickly to each statement, without spending too much time deliberating over each response.

The final items selected for the rating scale formed a mixture of trait-like terms, and terms which might be seen as expressing more transient states (Appendix I). Personality theorists often distinguish between traits, for example neuroticism, and states, for example loneliness. In addition, a distinction is commonly drawn between 'temperamental' and 'dynamic' traits. Temperamental traits provide a description of a particular way of behaving, e.g. extraversion; dynamic traits relate more to the underlying motivations or drives that may explain the behaviour, e.g. fear (Kline, 1993a). An example of items on the personality scale discussed here that might be seen as temperamental traits would be *persistent* and *impulsive*. Items such as *fearful* and *aggressive* may be considered to be more dynamic traits. The distinction between traits and states is not necessarily clear-cut. *Playful, fearful* and *impatient* could be fairly transient states, but may also relate to a relatively consistent way of responding. In the construction of the rating scale, it was expected that these different types of items would vary in terms of the ease with which raters could assess their animals. The reliabilities of the ratings, for zoos with multiple raters, and the standard deviations of the scores are discussed in section 3.3.1.

3.2.2 Sample selection and characteristics

Thirty-eight zoos and research institutions around the world were contacted and asked to participate in the study. The criteria for this initial selection was that the size of the chimpanzee population be at least five and that the animals were kept in a social group, rather than housed separately. Eighteen institutions responded and thirteen agreed to take part in the study. Rating scales were eventually returned from seven institutions, providing ratings for 76 animals. Some zoos had more than one chimpanzee caretaker and each one was asked to rate the animals, as well as to provide information about their gender and the length of time they had worked with the chimpanzees. The zoos that provided ratings for their chimpanzees were: Aalborg Zoo, Denmark; Krefelder Zoo, Germany; Tygerberg Zoopark, South Africa; Twycross Zoo, England; Sedgewick County Zoo, USA; Belfast Zoo, Northern Ireland; Chester Zoo, England.

Biographical details for each chimpanzee in the sample can be found in Appendix II. Table 3.1 below shows the age and sex distribution of all the chimpanzees rated in this study.

Table 3.1 Age/sex class distribution of sample.

	Males	Females	Total
Adults	12	29	41
Adolescents	7	13	20
Juveniles	6	3	9
Infants	1	5	6
Total	26	50	76

3.3 Results

3.3.1 Reliability of personality ratings

At three of the zoos, Tygerberg, Twycross and Krefelder, only one rater had rated the animals. At Aalborg and Belfast, two raters had rated the chimps; from Sedgewick, ratings had been received from five raters. This section presents the inter-judge reliability of the different ratings, this was examined separately for each zoo. Two sets of reliability results are presented for Chester as the animals were rated in 1996 and also in 1999. The figures for 1996 are based on ratings by the head keeper on the chimp section and a postgraduate student who was observing the animals at the time. The 1999 reliabilities are based upon ratings made by the same keeper, and ratings made by myself. It was thought appropriate to utilise my own ratings for the following reasons. Firstly, an important aspect of the study was to obtain ratings from *experienced* observers who had known the animals over a period of time, in order to obtain reliable personality ratings. Previous work indicates that familiarity with the subjects being rated is a crucial aspect of personality ratings (Norman and Goldberg, 1966; Funder and Colvin, 1988). One of the basic assumptions of this thesis is the importance of the rater-ratee relationship; the preliminary data presented in Chapter 2 (involving the repertory grid technique accompanied by interviews) were collected using a constructivist method, which assumes that raters know their subjects well (Kelly, 1955). It was felt to be important to continue to use familiar raters in the study presented in this chapter. At the time this study was carried out, myself and the head caretaker were the only people who knew the animals well enough to rate them. Secondly, my own ratings and those of the head caretaker were carried out independently, with no discussion between us. In addition, this was in many ways an exploratory study. The aim was not necessarily to generate a final version of a personality rating scale for chimpanzees, but rather to generate a preliminary rating scale that could then be used to explore possible behavioural correlates of some personality differences. Ideally, a larger sample of raters would have completed questionnaires so that reliability could be fully examined; such an exercise, however, requires raters who are both experienced and willing to spend considerable time completing large scales. The number of raters used in the present investigation is similar to the number used in comparable studies in the literature (e.g. Gold and Maple, 1994; Murray, 1995; King and Figueredo, 1997); i.e. all of the experienced raters at the time were utilised. However, this study built upon previous work by comparing inter-rater reliability within zoos, as well as over time (with the Chester ratings). Obtaining ratings from observers who were not very familiar with the animals would have invalidated such comparisons; therefore, ratings from a smaller number of familiar raters were judged to be more valuable at this stage than a larger number of ratings from inexperienced observers who did not know the animals well.

Kendall's coefficient of concordance was calculated for the ratings on each trait item. This test was chosen as it measures the degree of correlation between a number of ranked variables, and is particularly appropriate for inter-judge reliability (Siegel and Castellan, 1988; Lehner, 1998). This coefficient is based upon the index of the divergence of ratings from the maximum possible (i.e. perfect) agreement. Table 3.2 shows the rating concordance (average r_s) for each item on the rating scale, presented zoo by zoo (the second row shows number of raters per zoo). To test for significance, W was converted to the average Spearman correlation between all possible pairs of rankings, as recommended by Hays (1981) and Howell (1982). The 0.05 alpha level of significance was adjusted to 0.001 using the

Bonferroni correction, to allow for multiple tests on each item (i.e. 46 tests in total).

Table 3.2 Reliability of trait items (average r_s)

	Aalborg	Belfast	Sedgewick	Chester 1996	Chester 1999
Number of raters	N = 2	N = 2	N = 5	N = 2	N = 2
Number of chimpanzees	N = 6	N = 8	N = 10	N = 23	N = 23
Persistent	.44	.84	.06	.32	.70
Adaptable	-.38	.88	.08	.16	.52
Unreasonably aggressive	.40	.48	.48	.54	.80*
Associates with others	.10	.58	.48	.52	.82*
Moody	00	.70	.48	.18	.66*
Unpredictable	.00	.78	.38	.56	.78*
Unexplained fear	-.46	.98*	.18	.22	.44
Popular	.00	.76	.47	.40	.84*
Reconciles	.82	.94	.41	.52	.84*
Anxious	.42	.54	.32	.42	.86*
Can enlist support	.60	.64	.46	.64*	.86*
Intervenes	.86	.90	.61	.40	.76*
Inquisitive	.00	.90	.28	.40	.78*
Reassures	.42	.76	.78	.54	.84*
Bold	.70	.88	.65	.40	.84*
Avoids aggression	.64	.90	.38	.36	.76*
Dominant	.88	.98*	.82	.70*	.76*
Investigative	.24	.88	.21	.32	.90*
Submissively greets	.50	.74	.23	.66*	.84*
Impatient	.70	.88	.45	.02	.88*
Interacts with other	.00	.84	.57	.06	.74*
Socially aware	.00	-.16	.20	.24	.62*
Impulsive	.84	.92	.40	.62#	.62*
Resourceful	.52	.64	.07	-.02	.68*
Displays	.10	.66	.73	.56	.60
Dominance motivated	.82	.96*	.55	.52	.78*
Easily frightened	-.88	.86	.26	.38	.64*
Interacts infants & juveniles	.42	1.00*	.73	.30	.70*
Associates with dominants	.12	.76	-.11	.06	.70*
Influential	.94	.92	.63	.44	.86*
Causes conflicts	.72	.98*	.42	.76*	.72*
Deceptive	-.84	.56	.06	.00	.82*
Aggressive	.10	.86	.48	.56	.42
Submissive	.50	.82	.42	.44	.80*

(Table 3.2 continued)

	Aalborg	Belfast	Sedgewick	Chester 1996	Chester 1999
Active	.12	.86	.52	.60	.88*
Nervous	.30	.68	.07	.18	.42
Intelligent	-.66	.32	.47	.40	.66*
Difficulty forming friendships	.00	.90	.41	.64*	.68*
Confident	.00	.70	.41	.44	.34
Playful	.98	.84	.80	.54	.60*
Protective	.00	.82	.41	.04	.60*
Stereotypic	.00	.60	.68	.12	.40
Supported by allies	.66	.84	.41	.48	.76*
Withdrawn	.00	.86	.53	.02	.56
Inflexible	.76	.70	.03	.24	.56
Trusting	.00	.14	.57	.32	.58
Median	.27	.84	.42	.40	.73
Range	.66	.22	.29	.32	.22

* Items significant at $p < 0.001$

There was a missing value for one of the animals on this item, so the reliability was computed using only 22 cases, instead of 23.

The magnitude of the reliabilities varied quite widely between items, and between zoos. For Aalborg, none of the reliabilities were significant to the required level of alpha, though some items showed moderate to high correlations; notably items related to dominance or conflict situations (e.g. *reconciles others* (.82), *dominant* (.88), *intervenes in conflict* (.86), *dominance motivated* (.82), *causes conflicts* (.72) and *influential* (.94)). Poor reliabilities were found for items *moody* (.00), *unpredictable* (.00), *adaptable* (-.38), *inquisitive* (.00), *socially aware* (.00), *intelligent* (-.66), *stereotypic* (.00) and *deceptive* (-.84), among others. It is possible that some of the latter items were more difficult to rate and involved more complex inferences on the part of the raters.

Only five items were significantly reliable for the Belfast raters: *unexplained fear* (.98), *dominant* (.98), *dominance motivated* (.96), *interacts with infants and juveniles* (1.00) and *causes conflicts* (.98). However, several other items approached significance, including *reconciles others* (.94), *impulsive* (.92), *influential* (.92), *intervenes in conflicts* (.90) and *difficulty forming friendships* (.90). Many other items showed moderate to high loadings. Particularly low reliabilities were found for *socially aware* (-.16), *intelligent* (.32) and *trusting* (.14).

For the five Sedgewick raters, none of the items were significantly reliable at the corrected level of significance. Items approaching reliability were *reassures* (.78), *dominant* (.82), *displays* (.73), *interacts with infants and juveniles* (.73) and *playful* (.80). Very low reliabilites were found for *persistent* (.06), *adaptable* (.08), *associates with dominants* (-.11) and *inflexible* (.03).

For the earlier (1996) Chester ratings the following items were significant: *can enlist support* (.64), *dominant* (.70), *submissively greets* (.66), *causes conflicts* (.76) and *difficulty forming friendships* (.64). Items with the highest reliabilities here seem to refer to dominance related characteristics. Items approaching significance included *impulsive* (.62), *aggressive* (.56), *displays* (.56) and *unpredictable* (.56). Poor reliabilities were found for *adaptable* (.16), *moody* (.18), *impatient* (.02), *interacts with others* (.06), *resourceful* (-.02), *associates with dominants* (.06), *deceptive* (.00), *protective* (.04) and *withdrawn* (.02).

The later Chester ratings (1999) include the largest number of significantly reliable items. One possible reason for this may rest with the familiarity of the raters with the animals. One rater, the head caretaker of the chimpanzee section, rated the animals in both years. However, the second rater in 1996 had spent considerably less time studying the group than the second rater in 1999. Increased experience of the raters with their subjects has been found to increase inter-rater reliability in studies on human personality (Norman and Goldberg, 1966, cited in King and Figueredo, 1997). The highest reliabilities in 1999 were found for *investigative* (.90), *active* (.88), *impatient* (.88), *can enlist support* (.86), *anxious* (.86) and *influential* (.86). The lowest reliabilities were found for *adaptable* (.52), *fearful* (.44), *aggressive* (.42), *nervous* (.42) and *confident* (.34).

To examine the reliability of each item in more detail, Table 3.3 shows the median of the reliabilities across zoos, for each item.

The items with the highest median reliabilities are *influential* (.86), *reconciles* (.82), *dominant* (.82), *playful* (.80), *dominance motivated* (.78), *intervenes* (.76), *reassures* (.76), *submissively greets* (.74) and *causes conflicts* (.72). All of these items, with the exception of *playful*, relate to dominant behaviour, or

Table 3.3 Median reliabilities for each item

Persistent	.44	Resourceful	.52
Adaptable	.16	Displays	.60
Unreasonably aggressive	.48	Dominance motivated	.78
Associates with others	.52	Easily frightened	.38
Moody	.48	Interacts with infants & juveniles	.70
Unpredictable	.56	Associates with dominants	.12
Unexplained fear	.22	Influential	.86
Popular	.47	Causes conflicts	.72
Reconciles	.82	Deceptive	.06
Anxious	.42	Aggressive	.48
Can enlist support	.64	Submissive	.50
Intervenes	.76	Active	.52
Inquisitive	.40	Nervous	.30
Reassures	.76	Intelligent	.40
Bold	.70	Difficulty forming friendships	.64
Avoids aggression	.64	Confident	.41
Dominant	.82	Playful	.80
Investigative	.32	Protective	.41
Submissively greets	.74	Stereotypic	.40
Impatient	.45	Supported by allies	.66
Interacts with others	.57	Socially withdrawn	.53
Socially aware	.20	Inflexible	.56
Impulsive	.62	Trusting	.32

behaviour that might be expressed by a dominant individual. This suggests, as the findings in the previous chapter do, that the concept of dominance is highly salient to the raters, and is the aspect of behaviour upon which they agree the most.

The items with the lowest median reliabilities are *deceptive* (.06), *associates with dominants* (.12), *adaptable* (.16), *socially aware* (.20), *fearful* (.22), *trusting* (.32) and *investigative* (.32).

An aspect which characterises some of the latter items is the extent to which raters must assess the animal with regard to more complex thinking or social awareness, which appears to be problematic for some raters. For example, the item *deceptive* is one which many raters seemed to have difficulty with. The Aalborg, Sedgewick and Chester (1996) raters in particular had very low reliabilities on this item. This is perhaps to be expected, as the extent to which chimpanzees can deceive is a complex issue, and instances of possibly deceptive behaviour rare. Two of the Sedgewick raters commented that they were not sure they had ever actually observed deceptive behaviour in the group, with one observing that the only behaviour he could apply the item to was bluff displays, which in itself suggests that this rater might be applying an idiosyncratic interpretation of the term *deceptive.*

The relative salience, or observability, of trait terms is an important factor in the reliability of human personality ratings (John and Robins, 1993) and also seems to be an important factor influencing reliability in ratings of animals (Gosling, 2001). In studies of human personality, reliabilities for trait terms loading on the Extraversion and Neuroticism factors of the Five Factor model (FFM) are generally higher than for terms loading on Agreeableness. In a comparison of four studies of animal personality, Gosling (2001) found a similar pattern of reliability, with terms relating to Extraversion (e.g. sociable, dominant, active) and Neuroticism (e.g. tense, confident, anxious) showing more reliability than those relating to Agreeableness (e.g. aggressive, nurturant, protective). Those items showing the highest reliability in the present study are all related to either sociable or dominant behaviours (categorised by Gosling (2001) as relating to the human Extraversion factor). In humans, the high reliabilities generally reported for such traits may be explained by their high observability (John and Robins, 1993; Gosling, 2001). Some of the items with the lowest reliabilities in the present study refer to complex, less observable aspects of thought or behaviour. Similar items in Gosling (2001) were classified as belonging to the human Intellect or Conscientious factors, and were characterised by low reliabilities in that study (and indeed have low reliabilities in human ratings).

3.3.2 Effects of sex and experience of raters

If personality ratings are in some measure an expression of the rater-ratee relationship, then characteristics of the raters may have an important effect on trait ratings. For instance, characteristics such as the sex of the rater, or in particular their level of experience, may affect reliability between raters. Few studies of animal personality have examined the effects of such rater characteristics on trait ratings, but Martau *et al.* (1985) found that cross-temporal reliability was lower for less experienced raters (i.e. with a maximum of only five hours observation prior to completing ratings) when compared to raters who were more familiar with the animals.

It was difficult to fully examine the effects of sex and experience in this study for several reasons. Firstly, by necessity the raters were a self-selected sample, and all were familiar with the animals by virtue of being caretakers, or experienced doctorate students engaged in long-term study of the animals (minimum familiarity among all the raters was 6 months). Secondly, raters did not rate the whole sample of animals, so reliability is best considered within, rather than between, zoos (and for some zoos only one, or two, raters were able to provide ratings thus making it difficult to compare possible effects of sex or level of experience of the raters on the same animals).

However, in order to examine possible effects of sex and experience of raters, comparisons on item scores were made between male and female raters, and between more and less experienced raters across the whole sample. Such comparisons would be expected to at least highlight any broad differences in general patterns of responding between groups (i.e. across but not within zoos).

Comparison of item scores for males and females

In order to compare patterns of ratings between male and female raters, two median scores were calculated for each item on the personality rating scale (N=46); one median score for male raters (N = 9) and one for female raters (N = 5). Mann-Whitney tests were performed on median scores for each item, and values of *U* and associated p values for all items are presented in Appendix III. To test for significance, a criterion alpha level of 0.05 was corrected for the number of comparisons performed in this section (i.e. comparisons for 46 items for sex differences, plus 46 items for differences in rater experience (see below)) to give a corrected alpha level of 0.0005.

No significant differences between male and female raters were found for any of the 46 items on the questionnaire. Two items approached significance (i.e. would have been significant at the uncorrected 0.05 level): *socially anxious* (U = 5.00, p = .01) and *causes conflicts* (U = 2.00, p = .006), but these were not significant at the corrected level. For both of these items, female raters gave higher raters than male raters.

Comparison of item scores and rater experience

To examine possible effects of rater experience, raters were categorised into two levels of experience: over 5 years familiarity with the animals (N = 8) and less than five years familiarity (N = 6). Mann-Whitney tests were performed on median scores for each item; values of U and associated p values for all items are presented in Appendix IV.

No significant differences were found between the two groups of raters. Six items were significant at the uncorrected level of $p \leq 0.05$ (but were not significant at the corrected level of significance). These were three items loading on the Sociability factor: *reconciles others* (U = 5.00, p = .01), *can enlist support* (U = 9.00, p = .05), and *associates with dominants* (U = 9.00, p = .05) and three items loading on the Curiosity factor: *inquisitive* (U = 6.50, p = .02), *obtains goals* (U = 8.00, p = .03 and *physically active* (U = 7.50, p = .03). More experienced raters were found to rate animals slightly higher than less experienced raters on all of these items. In general, however, there are no clear systematic (or significant) differences between raters of varying levels of experience.

No previous work on animal personality has quantitatively examined item ratings in terms of sex or age differences, so it is difficult to draw general conclusions on the basis of the limited analysis presented here. Clearly, this is an area that needs further examination.

3.3.3 Effects of housing conditions upon ratings

There has been little attempt in the literature to examine possible effects of housing and keeping conditions upon personality ratings of zoo animals. While the physical constraints of captivity may in some cases function to limit the range and quality of an animal's behaviour (e.g. Woodgush and Vestergaard, 1991; Wemelsfelder, 1997a), it is unclear whether more subtle aspects of housing and caretaking conditions would affect ratings. King and Figueredo (1997), for instance, found that substantial differences in physical conditions and social grouping had no effect on personality ratings in their large inter-zoo sample of 100 chimpanzees. This might suggest that personality ratings are inherent characteristics of individuals (e.g. King, Rumbaugh and Savage-Rumbaugh, 2000). A constructivist position on personality, however, assumes that personality ratings are also functions of the content and quality of social relationships (Hinde, 1976, 1979b, 1995). Thus personality ratings express (often dynamic) aspects of the individual in *social relation*. The quality of an individual's relationships, and hence the range of behaviour expressed, may therefore be an important influence on personality ratings. Thus the aspect of keeping conditions that is most likely to affect ratings would be the size of the group an individual was housed with. To some extent, absolute group size may not be so important as the quality of social interaction the group permits. In intensely social species like chimpanzees, large groups may provide inexperienced raters with more of an opportunity to observe the total possible range of behaviour than small groups. However, even if animals are kept in smaller groups (or even pairs), a good range of social behaviour should be apparent to experienced raters.

To examine possible effects of social grouping on personality ratings, all zoos were asked to provide information about the size of the social group in which each animal was usually housed (i.e. were the individuals who were rated housed together, or kept in smaller subgroups). For all zoos except Twycross, all animals were housed together at all times, and there were no differences in housing or feeding conditions for each member of a group. The Twycross animals were, however, housed in two subgroups. The larger group consisted of Samantha, Rosie, Holly, Jolly, Elly and Benji; the smaller constituted William and Melody. These two subgroups were too small to permit inferential statistics to compare possible differences in ratings. However, personality profiles of these animals (Fig. 3.1) were examined for any differences.

Fig. 3.1 Personality profiles for the Twycross chimpanzees

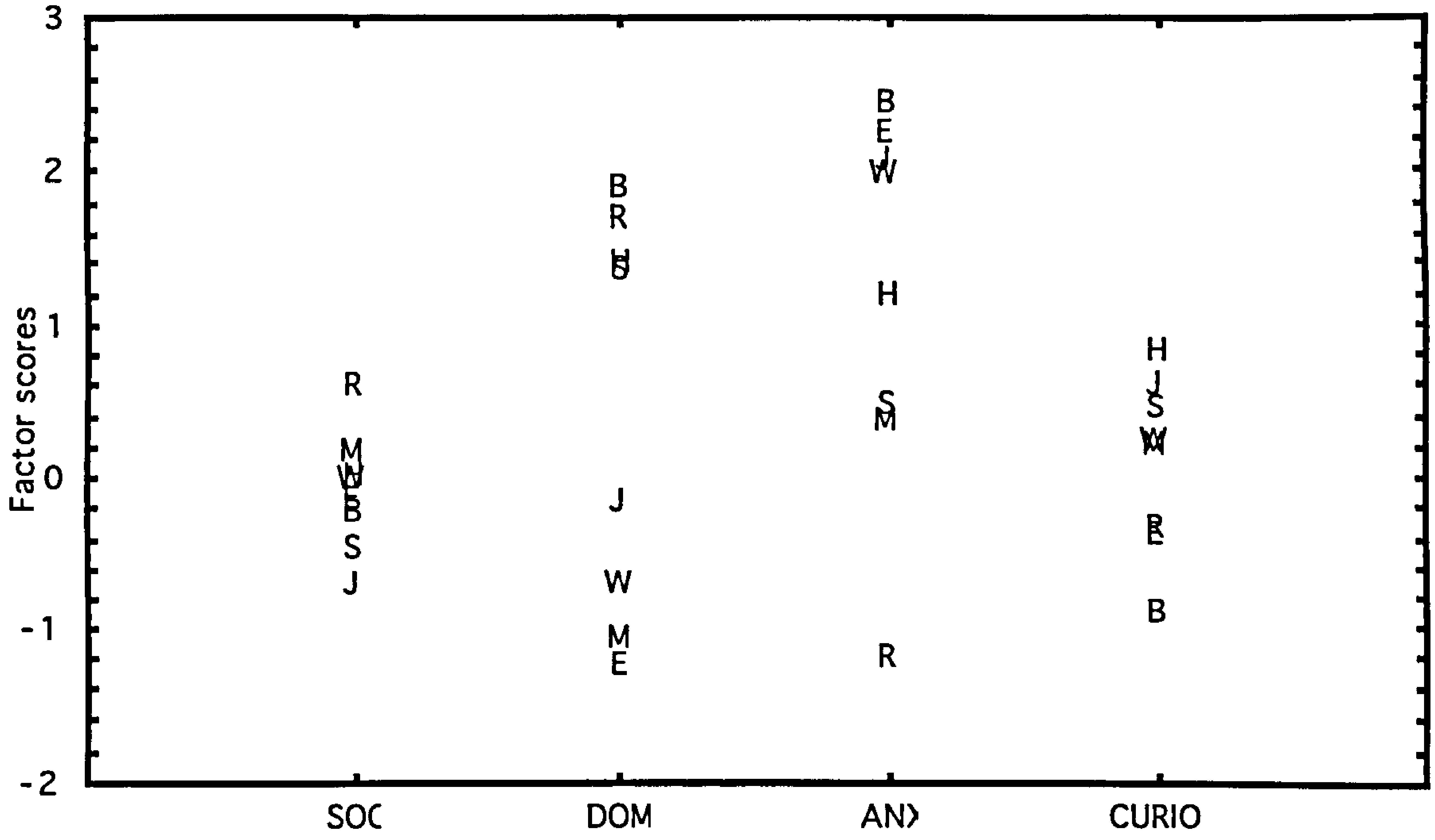

Figure 3.1 shows factor scores on Sociability, Dominance, Anxiety and Curiosity for the eight chimpanzees (see 3.3.4 for definition of factor scores). There are no clear differences between the subgroups on any of the factors. In fact, thirteen year old William's profile most closely resembles that of adolescent female Jolly. On Sociability and Curiosity, William and Melody share similar scores, but differ widely on Anxiety, with the younger William rated as more anxious than the adult female Melody (aged 39).

The Twycross animals were rated by one caretaker, who was familiar with all the group. This caretaker experienced no difficulty in applying any of the personality items to the animals. It is unlikely, therefore, that the use of subgroups in this zoo had any influence on ratings. However, variation in group size may well be an important influence upon the process of *generating* relevant trait terms. Familiarity with a small rather than a large number of animals might act to constrain the possible range of personality items produced, although the general experience of the rater here is obviously an important factor. Even in small groups, as long as the animals are not housed alone, a large range of social behaviour would presumably be observed over a long period of time. In the present study, the initial trait terms which formed the basis for the rating scale were generated by raters familiar with a large number of animals (i.e. the Chester group) housed in a semi-natural setting. This suggests that this scale sampled a substantial range of the variation in chimpanzee personality.

3.3.4 Factor analysis of ratings

The mean item rating was calculated for each animal, and converted to standard scores. An exploratory principal components analysis was performed; both Kaiser's criterion of eigenvalues greater than one, and Cattell's Scree test (Cattell, 1966) were used to determine the number of factors to retain. In addition three, four, five and six factor solutions were all examined for interpretability. Both orthogonal (Varimax) and oblique (Orthotran) rotations were performed. Both solutions were examined, and were very similar in structure. Since the correlations between the factors were fairly low (with a mean correlation of .23) the orthogonal solution was chosen.

Correlation of factor scores with social and life-history variables

Factor scores were calculated for each animal and were used in the subsequent analyses examining age, sex and dominance differences. Factor scores are summary scores for each individual on each factor, weighted by the magnitude of variable loadings on each factor (Kline, 1994). They can thus be conceptualised as the actual values for each individual on each of the generated factors and thus allow comparison of these with additional external variables.

Table 3.4 shows the item loadings for the four factors retained. The four factors account for 53% of the variance, with the first two factors accounting for nearly the same amount of variance.

Significant factor loadings (i.e. loadings over 0.3) have been indicated by an asterisk, following the rationale detailed in Chapter 2 (section 2.2.3).

The items loading significantly on Factor I appear to encompass several different aspects of social behaviour. Some items (e.g. *associates with others, interacts with infants and juveniles*) relate simply to the amount of time the animal spends with others.

Table 3.4 Results of principal components analysis (N=76)

	Factor I	Factor II	Factor III	Factor IV
	Sociability	Dominance	Anxiety	Curiosity
Associates with others	.86*	.01	.07	.22
Interacts with others	.84*	-.01	.02	.16
Popular	.82*	.00	-.33*	.02
Difficulty forming	-.75*	.31*	.27	-.06
Associates with dominants	.75*	.12	-.05	.28
Can enlist support	.75*	.15	-.24	-.14
Trusting	.71*	-.00	-.31*	.11
Interacts with inf. & juv.	.65*	-.33*	.34*	.18
Protective towards inf.	.62*	-.05	.41*	-.08
Socially aware	.61*	.24	-.12	.13
Confident	.61*	.18	-.55*	.18
Reconciles others	.59*	.28	-.08	-.34*
Supported by allies	.57*	.12	-.35*	-.04
Withdrawn	-.54*	.10	.17	-.36*
Motivated to dominate	.20	.83*	-.10	.07
Displays	.11	.82*	.07	.15
Aggressive	-.12	.81*	-.03	.07
Unexplained aggression	-.07	.79*	-.06	.24
Influential	.36*	.72*	-.29	-.09
Dominant	.29	.70*	-.40*	-.24
Avoids aggression	-.15	-.67*	.32*	-.09
Causes aggression	-.08	.67*	.11	.13
Bold	.31*	.66*	-.47*	.01
Submissive	-.16	-.66*	.47*	.15
Moody	-.34*	.66*	.25	.00
Submissively greets	-.09	-.65*	.39*	.21
Reassures	.41*	.55*	-.39*	-.30*
Unpredictable	.04	.54*	.33*	.15
Intervenes	.46*	.51*	-.23	-.33*
Impatient	-.19	.49*	.21	.11
Deceitful	-.33*	.45*	-.12	.25
Inflexible	-.09	.23	-.00	-.16
Easily frightened	-.05	-.09	.86*	-.06
Nervous	-.06	-.05	.84*	-.06
Unexplained fear	-.02	-.03	.81*	-.05
Anxious	-.25	-.19	.79*	-.04
Impulsive	-.05	.42*	.56*	.09
Intelligent	.21	.15	-.40*	.36*

continued on page 97

	Factor I	Factor II	Factor III	Factor IV
	Sociability	Dominance	Anxiety	Curiosity
Adaptable	.34*	-.18	-.36*	.28
Stereotyped	-.23	.00	.35*	-.30*
Active	.18	.03	.17	.66*
Investigative	-.10	.03	-.14	.64*
Resourceful	-.01	.13	-.25	.59*
Inquisitive	.21	.20	.01	.59*
Playful	.50*	-.23	.34*	.59*
Persistent	.22	.32*	-.36*	.43*
Variance	.195	.194	.135	.075

Other items capture more of the quality of those social interactions (e.g. *trusting, confident, popular, playful*). Six items apply mostly to behaviour in conflict interactions: *can enlist support, reconciles others, associates with dominants, supported by allies, intervenes in conflicts* and *reassures others.* These items load relatively insubstantially on Factor II (Dominance), so appear to relate more to social skills or popularity. The items *withdrawn* and *difficulty forming relationships* load negatively on this factor, i.e. in the opposite direction to the more 'sociable' items.

Factor II is characterised by items which relate to dominant and aggressive behaviour, e.g. the items *dominant, causes aggression, motivated to dominate* all load highly on this factor. Other high loading items seem good descriptors for dominant individuals: *influential, bold, reassures, displays.* The two items referring to submissive behaviour — *submissive* and *submissively greets* — load negatively. Six items which load moderately on this factor — *moody, unpredictable, impatient, deceitful, inflexible, impulsive* — are more complex trait terms that refer to a somewhat negative social style. In the analyses of the preliminary data, presented in Chapter Two, these items often loaded on the factors labelled as 'Machiavellian'.

The highest loading significant items on Factor III all relate to fearful, anxious responses. The item *stereotyped* (describing individuals who engage in stereotypic behaviour patterns) also loads on this factor. *Impulsive* also loads positively, and *intelligent* and *adaptable* load negatively. Items which load significantly on this factor (though more highly on other factors) include *confident, dominant, bold* (all loading negatively) and *submissive* (loading positively). The item *protective towards infants* also loads significantly here.

Factor IV is characterised by items relating to active, exploratory and inquisitive behaviour. The item *resourceful* described the tendency to use physical objects to obtain a particular goal, or resource. The final item loading on this factor is *persistent*, which perhaps is an important part of goal-directed behaviour. *Intelligent* also loads significantly here, though loading higher on Factor III.

3.3.5 Comparison of the factor structure to the human Five Factor Model

There have been many models proposed to capture the structure of human personality, but in more recent years the consensus has fallen upon the Five Factor model of personality. Originally developed from the factor analysis of lay personality terms (John, 1990), the five personality dimensions (the 'Big Five') have been identified in many subsequent analyses, and are assumed by many researchers to be the main personality dimensions underlying many other classification schemes (Costa and McCrae, 1992; Goldberg, 1992).

The nominal labels for the five personality factors, or dimensions, are: Neuroticism, Agreeableness, Extraversion, Openness to Experience and Conscientiousness. Each of these broad factors encompasses more specific facets; for example, the factor of Neuroticism consists of six facets, including anxiety, angry hostility and depression. These facets in turn are summaries of specific traits or behaviours; e.g. angry hostility subsumes the behaviours anxious, irritable, impatient, excitable, moody.

As the five-factor model has proved so useful in conceptualising human personality, it is interesting to consider whether ratings of nonhumans, particularly other primates, might elicit a similar structure. The only study of chimpanzees to deliberately use adjectives derived from the five-factor model (FFM) to explore the factor structure of ratings was that of King and Figueredo (1997). This study utilised 43 adjectives, 41 of which were from Goldberg's (1990) taxonomy of FFM adjectives. One hundred chimpanzees were rated using these terms, and the ratings subjected to factor analysis, producing six orthogonal factors. The factor accounting for most of the variance (20.8%) was labelled as dominance, and the authors interpret the remaining five factors as the Big Five personality dimensions. In a later study, Gosling and Bonnenburg (1998) obtained ratings of six species of pets (dogs, cats, horses, ferrets, rabbits and hedgehogs) from a large sample of owners (N=1640). The rating scale consisted of 50 personality trait terms, comprising a subset of both Goldberg's (1992) and Saucier's (1994) FFM adjectives. This study is interesting as an attempt to apply a standard rating scale to several different taxa, and the authors discuss the advantages and limitations of this.

In a review study Gosling and John (1999) attempted to examine the incidence of the FFM in a large number of nonhuman personality studies. They compared the factor structures in 19 studies (conducted on a range of species) for their similarities to the FFM. Data on a range of primate species was examined (chimpanzees, gorillas, rhesus monkeys, vervet monkeys) as well as other taxa (hyenas, dogs, cats, donkeys, pigs, rats, guppies, octopuses). The factors of Neuroticism, Agreeableness and Extraversion appeared in most of the studies, with Openness appearing in only eight. Conscientiousness was apparent only in the chimpanzee studies. Despite the difficulty of interpreting factors ad hoc, this study does suggest that personality ratings of a range of nonhuman species may well yield a structure similar to the FFM.

Although the trait terms used in the present study were generated solely by the chimpanzee caretakers, there exists some overlap between these terms and some of the FFM adjectives. The items loading positively on Factor I (Sociability) are similar to the adjective terms denoting high Extraversion on the FFM. For example, items such as *associates with others, confident* and *socially aware* reflect important aspects of the human Extraversion dimension. *Playful,* which loads highest on Factor IV (Curiosity) actually loads substantially on Sociability also (.50), and again this trait is indicative of the E dimension in the FFM. *Withdrawn* is an item that signifies low E, and this item loads negatively on the Sociability factor in the present analysis. Four items loading on Sociability apply more to the Agreeableness factor of the FFM. *Trusting, popular, protective* and *reconciles others* are all characteristics indicative of high levels of Agreeableness.

Factor III in the present study has been labelled Anxiety. Most of the items loading on this factor are mirrored on the Neuroticism dimension of the FFM. Positively loading items refer to anxious, nervous responses, and to a tendency to exhibit stereotypic behaviour patterns. The item *adaptable* loads negatively, which fits in well with the overall sense of this factor. Intelligent is also a negative loader, and this item actually loads substantially on Factor IV (Curiosity); in humans, measures of intelligence have been associated with the Openness factor (Costa and McCrae, 1992), although intelligence is also a characteristic of high Conscientiousness in the FFM. The item *confident*, although loading highest on Sociability, also loads substantially on the Anxiety factor (-.55). The same pattern is found in the FFM, where the adjective confident is indicative of high E and low N.

Factor IV, Curiosity, loads only six items, so any interpretation of the nature of this factor must be treated with caution. This factor seems most related to the Openness factor of the FFM. The factors of Openness and Conscientiousness are the most difficult to apply to nonhumans. Openness denotes a tendency to be receptive to one or more areas of experience: ideas, actions, feelings, values, fantasy and aesthetics. Thus an individual who is 'open to actions' might be someone who is willing to try new foods, visit new places, adopt new hobbies (Costa and McCrae, 1992). Gosling and John (1999), in their review of 19 nonhuman personality studies, found that nine studies identified factors which were characterised by items relating to curiosity/exploration, playfulness and trainability in experimental tasks, all of which they suggest are similar to the human Openness dimension. In the present study, Factor IV appears to be most like this dimension, with items such as *investigative*, *resourceful*, *inquisitive* and *playful* having concomitants in the human definitions for O. Two items, however, *persistent* and *resourceful*, are items which are found on the Conscientiousness factor.

Factor II in the present analysis has been labelled Dominance. Gosling and John (1999), in their cross-species review of personality factors, added the separate dimensions of Dominance and Activity to the FFM. While a separate Activity dimension was apparent in only 2 out of the 19 studies they examined, a dominance factor was identified in 7 of the 19 studies, and most of these studies were on apes and monkeys. In King and Figueredo's (1997) study, dominance was the factor accounting for the largest amount of variance. As discussed in Chapter 2, it seems likely that the central role of dominance interactions to social primates might be reflected in personality ratings, yet the exact nature of the dominance factor is complex. Only four of the studies discussed by Gosling and John explicitly reported a factor that had been labelled dominance/submission. Two of these were chimpanzee studies (van Hooff, 1973; King and Figueredo, 1997). One study investigated gorilla personality (Gold and Maple, 1994), and one focused on dogs (Coren, 1998). In the other three studies that found a dominance factor, this factor was variously labelled as confidence (Stevenson-Hinde and Zunz, 1978; Stevenson-Hinde *et al.*, 1980a, 1980b on rhesus monkeys), social competence (McGuire *et a*l., 1994 on vervets) and assertiveness (Gosling, 1998 on hyenas), though Gosling and John suggest that these factors correlated substantially with dominance rank. As they note, however, if there is a dominance factor in nonhumans it appears to relate to more than one of the FFM dimensions. In humans, dominance is related mostly to the Extraversion dimension; in nonhuman personality studies it appears to relate to physical aggression (indicative of low Agreeableness scores), boldness or assertiveness (indicative of high Extraversion scores) and low fearfulness (low Neuroticism) (Gosling and John, 1999). This pattern appears to be reflected in the Dominance factor identified in the present study. Several of the high loading items on this factor are found in descriptions of the FFM factors. Thus the group of items *bold, dominant, motivated to dominate* and *aggressive* are indicative of high levels of Extraversion. *Submissive, intervenes* and *reassures* all denote high Agreeableness scores, and low E scores. *Deceitful, inflexible* and *aggressive* signify low Agreeableness. *Submissive, moody, unpredictable* and *impatient* are all indicative of high Neuroticism scores, and although these items load highest on the Dominance factor, they also load moderately on Anxiety. (This pattern differs from that identified by Gosling and John (1999), where low N seemed to be characteristic of dominance).

It would therefore seem that personality ratings of chimpanzees elicit a dominance factor that relates to more facets of personality and behaviour than the corresponding factor in humans. While dominance in humans appears to relate mainly to Extraversion scores, both this study and seven of the studies reviewed by Gosling and John (1999) seem to show a dominance dimension that consists of several facets. In the present study, the items loading on the Dominance factor relate to the FFM in four main ways: items signifying dominant, aggressive, assertive behaviour (high E); items signifying submissive, protective, affiliative behaviour (high A); items representing aggressive, deceitful behaviour (low A) and those items describing anxious or emotionally labile responses (high N).

To summarise, the factor analysis of the chimpanzee rating scale suggests four personality factors, and these have been interpreted as Sociability, Dominance, Anxiety and Curiosity. The first three of these factors were identified in the analyses presented in Chapter 2. The factors of Machiavellianism and Protectiveness, identified in those earlier analyses, did not appear in the present factor structure, and thus seem to be more specific to the raters in the last study. The Sociability, Dominance, Anxiety and Curiosity factors appear to be similar to the personality dimensions identified in previous factor-analytic studies of primate personality. Comparing the items loading on the four factors to those composing the FFM, the Sociability factor appears to be similar to the Extraversion factor in the FFM, with some items also relating to Agreeableness. The Anxiety factor bears clear resemblance to the Neuroticism scale of the FFM. The Curiosity factor is similar to Openness in humans, though two items on Curiosity appear in the definition of Conscientiousness. In addition to these personality factors, the present analysis identified a factor of Dominance, that accounted for almost as much variance as Sociability. Whilst a separate dominance factor has been identified in other studies of primate personality, the exact nature of this factor, and its relation to the other personality factors is unclear. In order to explore the nature of the Dominance factor, the next section examines the relationship of each of the four factors to a simple measure of dominance rank.

3.3.6 Comparison of dominance and personality factor scores

Both the present study and Gosling and John's (1999) review suggest that a dominance factor is a common feature of the factor analysis of nonhuman personality ratings (particularly of primates). Moreover, the interpretation of this factor is difficult as it appears to subsume a variety of different personality facets. This range of facets for dominance is perhaps not surprising, given both the importance and the complexity of dominance relationships in apes and monkeys. However, the epistemological relationship between personality and the concept of dominance remains problematic.

While some studies focus on the physiological basis for basic temperamental differences like reactivity (e.g. Suomi, 1991) and aggression (e.g. Karli, 1989) there are problems in assuming that dominance can be characterised as such a simple measure. For instance, researchers have for a long time recognised that dominance rank in primates, and particularly in great apes, does not always, or often, correlate with simple measures of physical aggression (Mason, 1993 provides a useful critique). Thus dominance rank itself is probably only one expression of a set of complex behaviour patterns and relationships. Moreover, any attempt to explain individual differences in dominance encounters the difficulties inherent in defining the concept. At one extreme the term may be used to describe relatively simple measures of rank order, at the other it may be used as a conceptual 'catch-all' to effectively summarise a variety of behaviour patterns. What is clear is that the epistemological nature of the term is not always expressed clearly, and this has particular implications for the study of individual differences. As Mason (1993) notes, discussion of status conflicts often assumes some kind of drive or motivation behind the behaviour (i.e. a 'striving' for dominance status (de Waal, 1992)). While this may be an acceptable assumption in discussions of primate dominance relationships, at present it is not clear to what extent dominance relationships express consistent ways of responding that differentiate between individuals. What seems clear is that the personality factor of 'dominance' is not a unitary factor, but expresses relationships between other personality factors. The extent to which this is the case may vary according to the complexity of the social structure of a particular species. In apes, for instance, social relationships (and hence dominance relationships) are extremely complex. Thus in apes, dominance may be better expressed as an aspect of a relationship(s); i.e. it is closely tied to other aspects of social responding. In nonprimates, such as dogs, however, dominance may be more readily associated with simpler forms of territoriality, and may well form a separate dimension (e.g. Coren (1998) identified a separate 'dominance-territoriality' dimension in dogs).

Since dominance is such an important aspect of group life for some species, it may be that it forms the basis of observer ratings of all other personality aspects (Gosling, 1998). In order to examine the relationship between a traditional estimate of dominance, and ratings on the four personality factors, each animal's score on Item 17 (*He/she is successful at dominating other group members*) was taken. This basic measure of rank was then correlated with factor scores for the four personality dimensions.

Frequency distributions for factor scores on the four factors and dominance rank are found in Appendix V. In order to compare these distributions to the normal distribution, two tests were used: the Chi-Square test and the Kolmogorov-Smirnov single-sample test. Both of these tests evaluate the fit of the observed data to the normal distribution. The factor scores for Sociability and Curiosity closely approximate the normal distribution (see Figs. 1 and 4 respectively in Appendix V), and the values of the test statistics indicate that these distributions do not differ significantly from the normal distribution. The distribution of the factor scores for Dominance, however, does differ significantly from the normal distribution (Fig. 2 in Appendix V), with the value of chi-square significant at an alpha of 0.05 (although the Kolmogorov-Smirnov test is not significant). The distribution of Dominance scores appears to be bi-modal; this may reflect the possibility of different distributions for males and females on this factor. The distribution of Anxiety factor scores is not perfectly normal, although it does not differ significantly from normal (the Kolmogorov-Smirnov test was not significant, and chi-square was not significant at an alpha of 0.05, although it approached significance at $p = .08$).

The distribution of the basic measure of dominance rank (Fig. 5 in Appendix V) differs significantly from normal. In chimpanzees, a normal distribution for basic rank would not necessarily be expected; instead one might predict the existence of distinct rank distributions within a group, based upon sex and age groupings. In fact, this distribution has several peaks suggesting raters may base their estimates of rank for a given individual upon a consideration of how that individual compares to others in the same age/sex class.

Table 3.5 shows Spearman correlations between factor scores on each personality factor and dominance rank[1]. In this chapter, and those which follow, Spearman's rho has been used to explore trait-behaviour relationships, due to the small samples sizes used, and the lack of normality in the distributions of the factor scores. The alpha level for this test was set at 0.0002 following a Bonferroni correction to allow for the total number of tests performed on the personality and behavioural measures (196).

Table 3.5 Correlations between personality factor scores and estimated dominance rank (N=76)

	Sociability	Dominance	Anxiety	Curiosity
Sociability				
Dominance	.05			
Anxiety	.00	.00		
Curiosity	.00	.01	.01	
Dominance rank	.30	.71*	-.36	-.21

*r_s significant at $p < 0.0002$ (two-tailed)

Table 3.5 shows that the correlations between the personality factors are all very small, suggesting that the factor structure is indeed orthogonal. The correlations between the estimated measure of dominance rank and the personality factors are moderate to large. As might be expected, the strongest relationship was found between rank and scores on the Dominance factor (.71), and this relationship was highly significant at the required level. A (nonsignificant) positive relationship was also found between rank and Sociability (.30), suggesting that high-ranking animals are rated as more sociable ($p = .004$). There was a negative relationship between rank and

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[1] In this chapter, and in those which follow, Spearman's *rho* was used to investigate trait-behaviour relationships, due to the small sample size, and the lack of normality in the distribution of the factor scores.

Anxiety (-.36), suggesting that high-ranking animals are less anxious (this was not significant at the required level but approached significance at p = .001). A negative relationship was also found between rank and Curiosity (-.21); high-ranking individuals would seem to be rated as less curious. This relationship was not significant at the required level.

The association of high Sociability (E) and low Anxiety (N) with dominance, is one which has already been identified in previous work and discussed above. A similar pattern was also found by Gosling (1998), in his study on hyena personality. In this study, a significant relationship was found between a simple measure of dominance rank (scores on two of the personality items and position in the dominance hierarchy) and Gosling's assertiveness factor, which seems very similar to the Dominance factor identified in other studies.

It seems, therefore, that personality ratings are not entirely independent from measures of basic dominance rank (although the rank estimation used here was relatively crude). In fact it may be a difficult task to statistically (and conceptually) separate 'dominance' from 'personality' (Nash and Chamove, 1981). What is interesting is that personality ratings may provide a useful picture of the type of animal that is, or is likely to become, dominant. The relationship between the personality factors and dominance is explored in more detail in Chapter 7, focusing on the personality profiles of the Chester group.

3.3.7 Comparison of sex differences and personality factor scores

Among the social primates, there are often substantial differences between the sexes in many aspects of social behaviour. In chimpanzees, individual variation in behaviour has to be considered within the framework of sex-specific reproductive strategies (de Waal, 1993b). Basic patterns of sociality, for instance, vary between the sexes. Male chimpanzees (particularly adolescents) tend to spend more time in each other's company, whereas females spend more time with other females, and specifically with offspring and siblings. Dominance relationships among male chimpanzees are more hierarchical, feature more direct forms of agonistic expression (e.g. displaying) and may involve complex social strategies like coalitions; female relationships are based more on affiliation and support for kin and close associates (de Waal, 1984, 1986b, 1993a, 1993b).

In a species with such pronounced sex differences in observable behaviour, there is a possibility that such differences may unduly bias personality ratings (e.g. form part of an implicit personality theory). For example, an observer's prior knowledge of expected differences between the sexes may lead him/her to rate a particular animal according to the expected 'norms' for its sex (e.g. automatically rating male chimps as 'aggressive' and females as 'submissive', regardless of inter-individual variation). However, there is little to suggest that this might be the case in ratings of chimpanzees. Informal accounts of chimpanzees suggest great variation in behaviour within the sexes, and there is no reason to believe that this variation would not be reflected in ratings, if the raters know the animals reasonably well.

To examine the possible influence of sex on personality scores, point-biserial correlations were performed between sex and factor scores on Sociability, Dominance, Anxiety and Curiosity (Table 3.6).

Table 3.6 Point-biserial correlations between sex and the four personality factors (N=76)

	Sociability	Dominance	Anxiety	Curiosity
Sociability				
Dominance	.05			
Anxiety	.00	.00		
Curiosity	.00	.01	.01	
Sex	-.03	-.52*	-.17	-.10

* r_s significant at $p < 0.0002$ (two-tailed)

The only significant correlation was found between sex and Dominance, with males scoring higher than females.

Appendix VI shows distributions of male and female factor scores, with values of Chi-Square and the Kolmogorov-Smirnov test. Most of the distributions are close to the normal distribution. The exception are factor scores for females on Dominance; this distribution is significantly different from normal, and the scores are skewed towards the lower end of the distribution.

The results in Table 3.6 suggest that it is unlikely that observers are overtly influenced by sex differences in their ratings. The significant difference for the Dominance factor is not surprising, given the salient differences in dominance relationships for male and female chimpanzees. As discussed above, the structure of the Dominance factor is more complex than the other three factors, and it seems likely that it is conceptually distinct from other personality factors.

Several studies of nonhumans have identified sex differences in dominance related factors. Buirski *et al.* (1978) found that male baboons were rated as more 'gregarious' and 'distrustful' than females, who were rated as more 'timid' and 'trustful' than males. Stevenson-Hinde *et al.* (1980) found that rhesus males scored higher than females on a 'confident factor', and females higher than males on 'excitability'. Lardeux-Gillaux (1995) investigated personality in orang-utans and found that females were rated as more 'cautious' and 'submissive' than males, who were rated as more 'aggressive'. In all of these species, males are the dominant sex, and the rating of females as more submissive, timid and anxious reflects this (this difference in dominance is also characteristic of humans). In Gosling's (1998) factor analysis of hyena personality ratings, the only sex difference was found on the 'assertiveness' factor, with females scoring much higher than males on this factor (in hyenas, females are the more dominant sex, with dominance transmitted down the matrilineal line (Gosling, 1998)).

3.3.8 Comparison of age differences and personality factor scores

In neotonous species like primates, many important aspects of social behaviour may depend upon learning or maturational processes. In humans, some aspects of personality appear to change over the life span, while others seem remarkably consistent. This pattern may well be the same for chimpanzees, with early individual variation developing into differences in social strategies within an increasingly complex social arena.

Several studies of nonhuman personality have discovered significant changes in personality scores across different age groups. McGuire *et al.*

(1994) found that juvenile and subadult vervets scored higher on a 'playful/curious' factor and an 'opportunistic' factor than adults. Scores on these factors changed over time, suggesting that individual development is reflected in observer ratings. Lardeux-Gilloux (1995) also found age differences in ratings of playfulness, with juvenile orangs being rated as more playful than adults.

Stevenson-Hinde and her colleagues have studied age-related changes in personality scores, and the relationship between mother and offspring scores in rhesus monkeys. Stevenson-Hinde and Zunz (1978) found that 1-5 year old rhesus, and adult females, scored lower on a 'confident — fearful' dimension than adult males. On a 'sociable — solitary' dimension, the adult females and youngsters were rated higher than adult males. Stevenson-Hinde *et al.* (1980a) examined the stability of ratings of rhesus over a four year period. Scores on a 'confident' factor were stable over this period, for animals of all ages, while scores on 'excitable' and 'sociable' were not stable until adulthood. Comparing rhesus mothers and one-year-old infants showed that confident and sociable mothers had confident and sociable offspring, while mothers scoring highly on excitable had infants who were not confident (Stevenson-Hinde *et al.*, 1980a).

The range of personality rating instruments used, and personality dimensions identified, in these studies, make it difficult to determine the exact nature of the effects of age on personality ratings. However, the increased levels of activity and playfulness associated with juvenile primates seem to be reflected in observer ratings. It is more difficult to determine the effects of age on other factors because of the small number of factor analytic studies that have explored age-related effects.

Frequency distributions for factor scores by age category are found in Appendix VII. The age groups 'infants' and 'juveniles' have been collapsed into one group for this purpose, giving just 13 individuals in this group. The distributions with the closest proximity to normal are those of the adults, particularly for Sociability and Curiosity. For adolescents, and the infant and juvenile group, distributions of the factors are less clearly normal, though the Kolmogorov-Smirnov values suggest that these distributions are not significantly different from normal.

Factor scores on the four dimensions identified in this study were correlated with age of each animal in years (Table 3.7).

Table 3.7 Personality factor scores correlated with age (N=76)

	Sociability	Dominance	Anxiety	Curiosity
Sociability				
Dominance	.05			
Anxiety	.00	.00		
Curiosity	.00	.01	.01	
Age	.12	.23#	-.02	-.55*

* r_s significant at $p < 0.0002$ (two-tailed)

\# r_s significant at $p < 0.04$ (two-tailed)

The strongest relationship was found between age and Curiosity scores. Younger animals are rated significantly higher on this dimension than older animals. This relationship of age to Curiosity would seem to indicate the increased levels of playfulness and activity normally associated with younger animals, and identified in previous nonhuman personality studies (e.g. Buirski *et al.*, 1973).

A moderate correlation was found between age and Dominance, with older animals rated higher on this factor; though this relationship was not significant. This could indicate that dominance-related qualities are only applicable to older animals and that this factor simply estimates rank, rather than stable differences between animals in motivational factors relating to dominance. Alternatively, it may be that such personality differences are expressed through different behaviours over the life span. The issue of which behaviours might correlate to specific personality factors is a complex one, and is discussed in more detail in the next chapter.

3.3.9 Temporal changes in personality ratings: Chester group

Like humans, chimpanzees may display temporal consistency in some aspects of personality and discontinuity in other aspects. In fact, temporal and cross-situational consistency in personality scores may often be low, since the expression of basic motivations or cognitions may depend upon a range of different behaviours. For instance, a child who is rated as emotionally unstable may express this through aggression at school, but may become nervous and clinging at home (Stevenson-Hinde and Hinde, 1986). The comparison of personality scores across a period of time is subject to the same difficulty. Even a basic trait like anxiety will be expressed through different behaviours as the animal develops. The study of exactly how personality is expressed at different stages of life can therefore provide an important area within which to examine animal-environment relationships.

In order to compare personality ratings of the chimpanzees over a period of time, ratings were obtained of the Chester group of chimpanzees in 1996 and 1999. At both these times, the group was rated by the head chimpanzee caretaker, who was the most experienced of the Chester raters. Ideally, cross-temporal reliability would have been computed for a larger number of raters, but the only other rater who rated the animals in 1996 was not available to provide further ratings in 1999. Each animal was rated on all of the items on the questionnaire, and Spearman correlations calculated for each item (Table 3.8). Significance levels were corrected for multiple correlations using the Bonferroni correction (number of comparisons = 46).

One-tailed tests were used as positive correlations between the items were expected. Correlations were high for most of the items, with some items showing moderate correlations. The lowest correlations were found for the following items: *adaptable* (.50), *persistent* (.60), *avoids aggression* (.63), *moody* (.64), *socially withdrawn* (.65), and *fearful* (.66), with the former two items showing non-significant correlations.

For each of these items, ratings for both years were examined to determine which animals' scores had changed. Over these six items, the largest changes (of 2 or more points) occurred for female chimps. The adult female Kate, for instance, showed changes in her scores on *fearful*, *adaptable*, *moody* and *socially withdrawn*; over the time period, she had become more fearful, more moody, more socially withdrawn and less adaptable. Kate had originally been part of the Chester group, but had been moved to the Colwyn Bay colony; she had been moved back to Chester in 1993. She had originally been one of the most dominant females, but her absence from the group has meant that she is now much less dominant, and has experienced difficulty integrating into the group. Kate spends much of her time with her daughter Kankan, and grand-daughter Patti. During times of group tension or anticipation, e.g. just before feeding time, Kate will panthoot and sometimes scream, and she is the only female chimpanzee who regularly engages in aggressive displays towards male and female group members.

Table 3.8 Comparison of 1996 and 1999 ratings on each item for the Chester group

Persistent	.60	Obtains goals	.88*
Adaptable	.50	Displays	.77*
Unreasonably aggressive	.83*	Dominance motivated	.82*
Associates with others	.74*	Easily frightened	.71*
Moody	.64*	Interacts with infants & juveniles	.81*
Unpredictable	.70*	Associates with dominants	.79*
Fearful	.66*	Influential	.72*
Popular	.79*	Causes conflicts	.90*
Reconciles	.79*	Deceptive	.90*
Socially anxious	.78*	Aggressive	.84*
Attracts support	.76*	Submissive	.68*
Intervenes	.87*	Physically active	.86*
Inquisitive	.75*	Nervous	.74*
Reassures	.90*	Intelligent	.88*
Bold	.73*	Difficulty forming friendships	.73*
Avoids aggression	.63*	Socially confident	.82*
Dominant	.85*	Playful	.86*
Investigative	.92*	Protective	.75*
Submissively greets	.78*	Stereotypic	.90*
Impatient	.72*	Supported by others	.75*
Socially interacts	.79*	Socially withdrawn	.65*
Socially aware	.69*	Inflexible	.72*
Impulsive	.69*	Trusting	.79*

* r_s significant at $p < 0.001$ for a one-tailed test (N=23)

Several of the animals showed differences in scores on the *avoids aggression* item. Meg, the oldest chimpanzee in the group (52 years), was rated lower on this item in 1999, while Cleo and Heidi's scores increased, indicating that they increasingly avoided aggression. These latter females are among the most dominant females in the group; one possible explanation for the difference in ratings is that they are responding to the increased tension in the group, resulting from a challenge to the alpha male by the adolescent male Dylan. Interestingly, the other two females showing a change on this item, Kankan and Sarah, are rated as showing less avoidance of aggression. These females both had infants either while, or just after, the 1996 ratings were completed. Sarah's score on *persistent* actually increased over the three years. That the birth of an infant has an effect on the mother's behaviour is not surprising, what is interesting is whether this effect is similar for different females. Stevenson-Hinde *et al*. (1980a) report changes in confident and sociable scores for seven primiparous rhesus mothers rated before and after the birth of their infants (though they do not report in which direction the changes occurred). The changes reported here for Sarah and Kankan would seem to suggest that the birth of an offspring, and the resultant changes in social activity that this may engender, acts to increase social confidence in young females. There are unusual circumstances, however, in which this pattern may be reversed.

One of the greatest changes in scoring occurred on the item *socially withdrawn*, for the female Halfpenny, whose score on this item increased from 2 to 6 over the three year period. In 1996, Halfpenny gave birth to an infant diagnosed with a form of cerebral palsy. Kiki, the infant, survived and has made some progress in development. However, Kiki's condition makes it difficult for her to move around on her own, and Halfpenny consequently spends the majority of her time grooming, playing with, or carrying the infant. Although the other members of the group show a great interest in Kiki, probably because of her infant Halfpenny's social interactions now seem to be less numerous. The difficulty she experiences in moving around quickly, due to the weight of Kiki, has meant that she is less involved in some group interactions, e.g. polyadic conflicts. Prior to the birth she was one of the highest ranking females in the group. Halfpenny's score has also changed on other personality items; she now scores lower on *associates with others, associates with dominant animals*, and *impulsive*. Her scores on *submissive* and *stereotyped* have increased.

Some of the younger animals also show interesting changes on some of the items. The juvenile Kaylie has shown a decrease in her *fearful* score, and an increase in *moodiness*. Alice, a year younger than Kaylie, was rated as more *persistent*, more *adaptable* and less *fearful* in 1999. These changes may highlight a pattern of increasing confidence as juveniles mature, and a corresponding lack of fearful responses. A similar pattern was found in 2-3 year old rhesus macaques by Stevenson-Hinde *et al.* (1980a). They found that scores on a confident factor significantly increased over four years for these animals, but not for adult males or females.

To summarise, chimpanzees, like humans, appear to show changes in some personality characteristics over time, and there appear to be the same complex interactions between environmental factors and maturational factors that are typical for humans. What seems to be clear from the Chester ratings is that the animals can be reliably rated over a three year time span, and that these ratings seem to reflect specific personality changes that may be tied to internal or external changes.

3.3.10 Comparison of personality factor scores for mothers and offspring

Across five of the zoos, twenty mother and offspring pairs were identified (for Sedgewick and Tygerberg, information was not provided about lineage). Each mother-offspring pair was compared, using each animal's factor scores for Sociability, Dominance, Anxiety and Curiosity. Table 3.9 shows age and relationship for all of the animals involved in this comparison.

To compare mothers' scores on each of the four factors with their offsprings' scores, Spearman correlations were performed on the factor scores. Where females had more than one offspring, their scores were correlated with those of the youngest offspring only (it was assumed that younger offspring would be more similar to their mothers in terms of personality). Scatterplots showing these relationships are presented in Figures 3.2 to 3.5 below. Significance of the correlations were assessed using an alpha level of 0.001, following Bonferroni correction for the number of tests performed (46). (Note that the shape of dots in these plots is a by-product of the graphics used, and has no numerical significance).

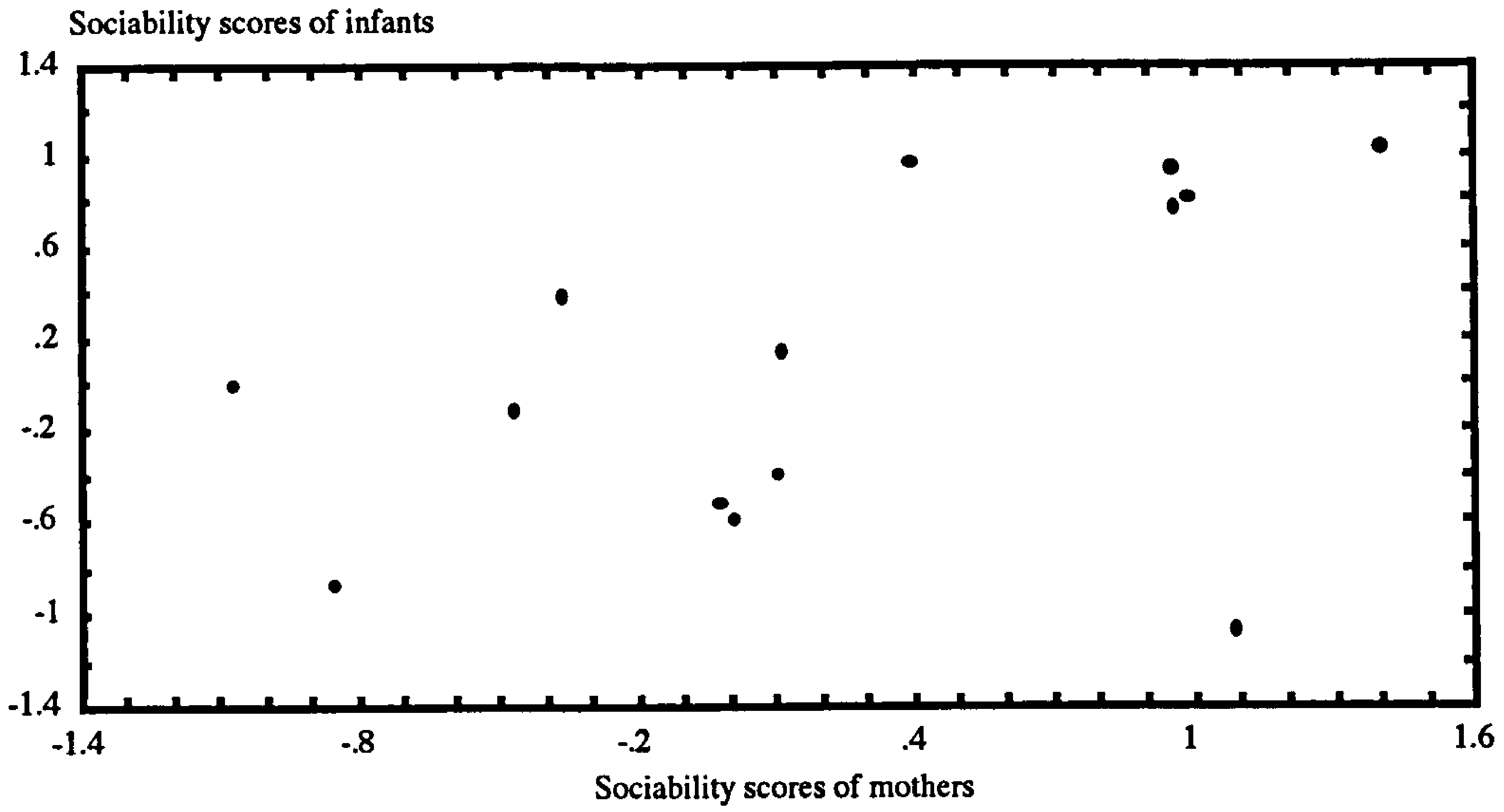
Table 3.9 Characteristics of mothers and their offspring compared for similarity of personality profiles

Mother		Offspring			Zoo
Name	Age (in yrs)*	Name	Sex	Age	
Florin	19	Alice	F	8	Chester
Kate	29	KanKan	F	16	Chester
KanKan	16	Whitney	F	6	Chester
Mandy	22	ZeeZee	F	5	Chester
Farthing	24	Layla	F	9	Chester
Farthing	24	Dylan	M	12	Chester
Halfpenny	24	Kaylie	F	9	Chester
Rosie	26	Sally	F	11	Chester
Heidi	27	Wanda	F	12	Chester
Jutta	22	Marco	M	5	Aalborg
Jutta	22	Martin	M	7	Aalborg
Flo	23	Lara	F	14	Krefeld
Flo	23	Fulani	F	9	Krefeld
Gombe	23	Menolly	F	12	Krefeld
Gombe	23	Hubert	M	6	Krefeld
Elizabeth	24	Kim	F	12	Belfast
Helga	24	Angela	F	14	Belfast
Helga	24	Austin	M	5	Belfast
Kim	12	Katie	F	4	Belfast
Samantha	16	Elly	F	6	Twycross

* For the Chester animals, 1999 ages are given, as the comparisons were based on the 1999

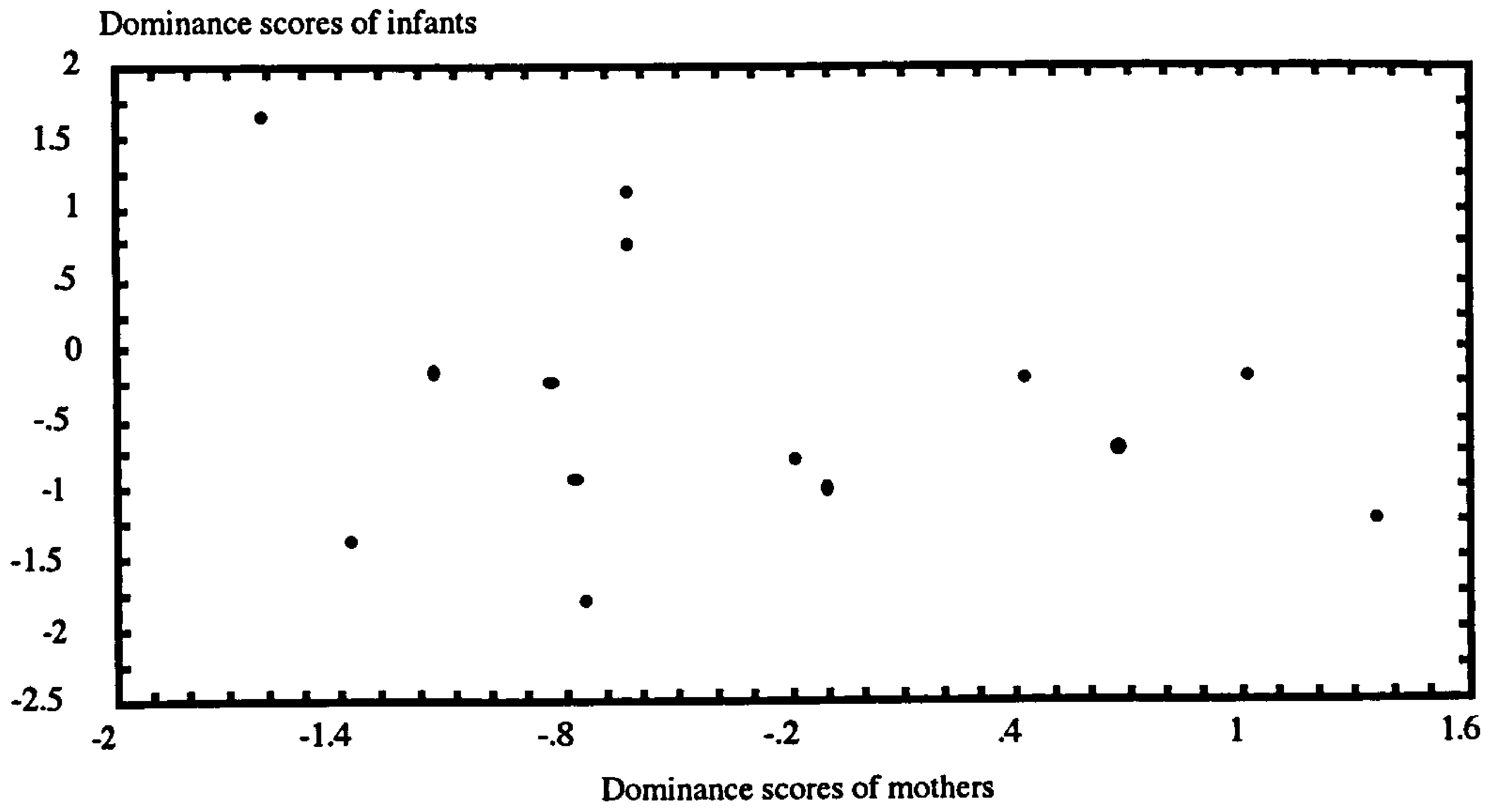
ratings

Fig. 3.2 Correlation between mothers' Sociability scores and infants' Sociability scores



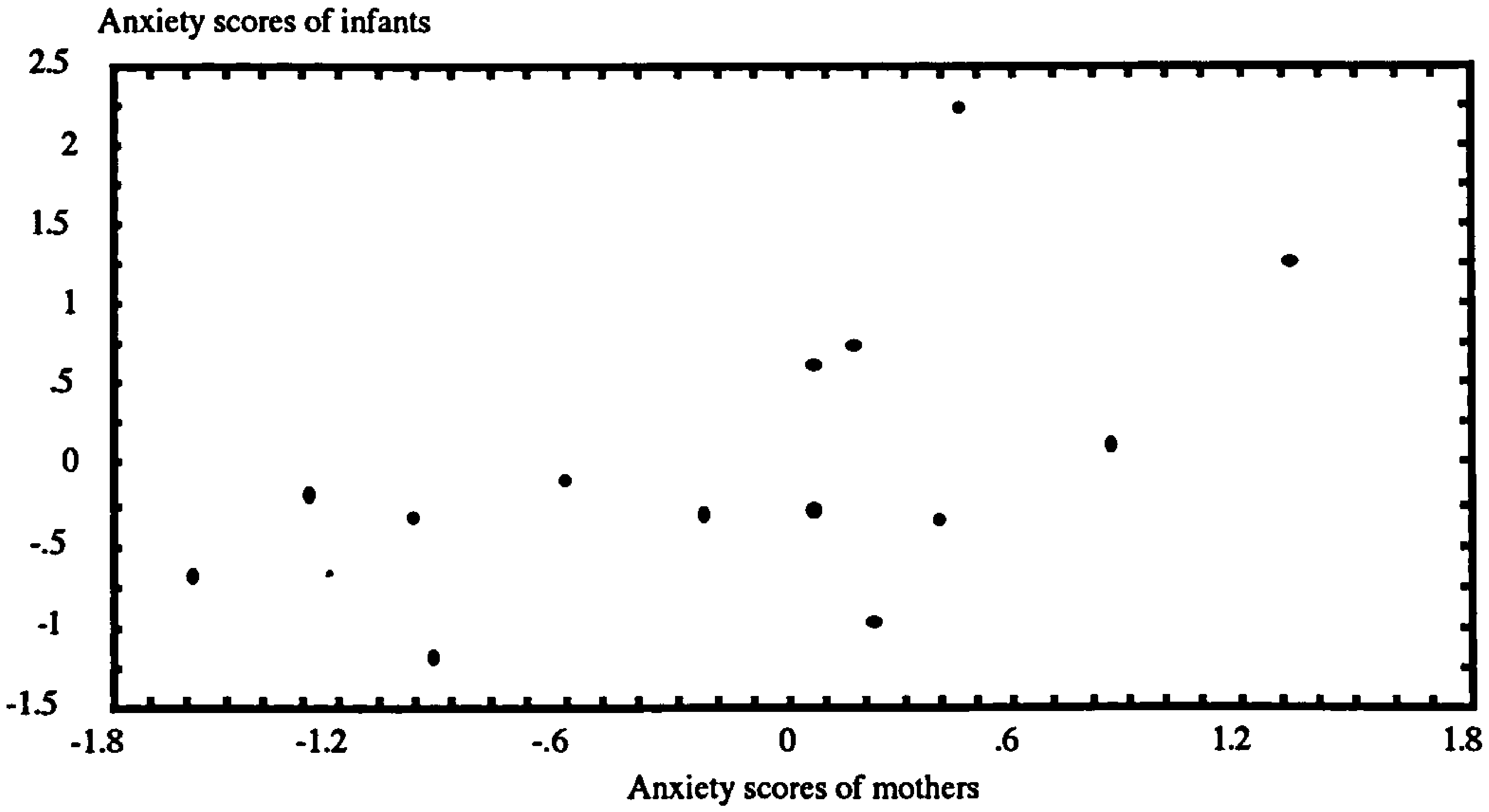
The value of $r_s = .47$, and is significant at p = .05 but is not significant at the corrected level of significance.

Fig. 3.3 Correlation between mothers' Dominance scores and infants' Dominance scores



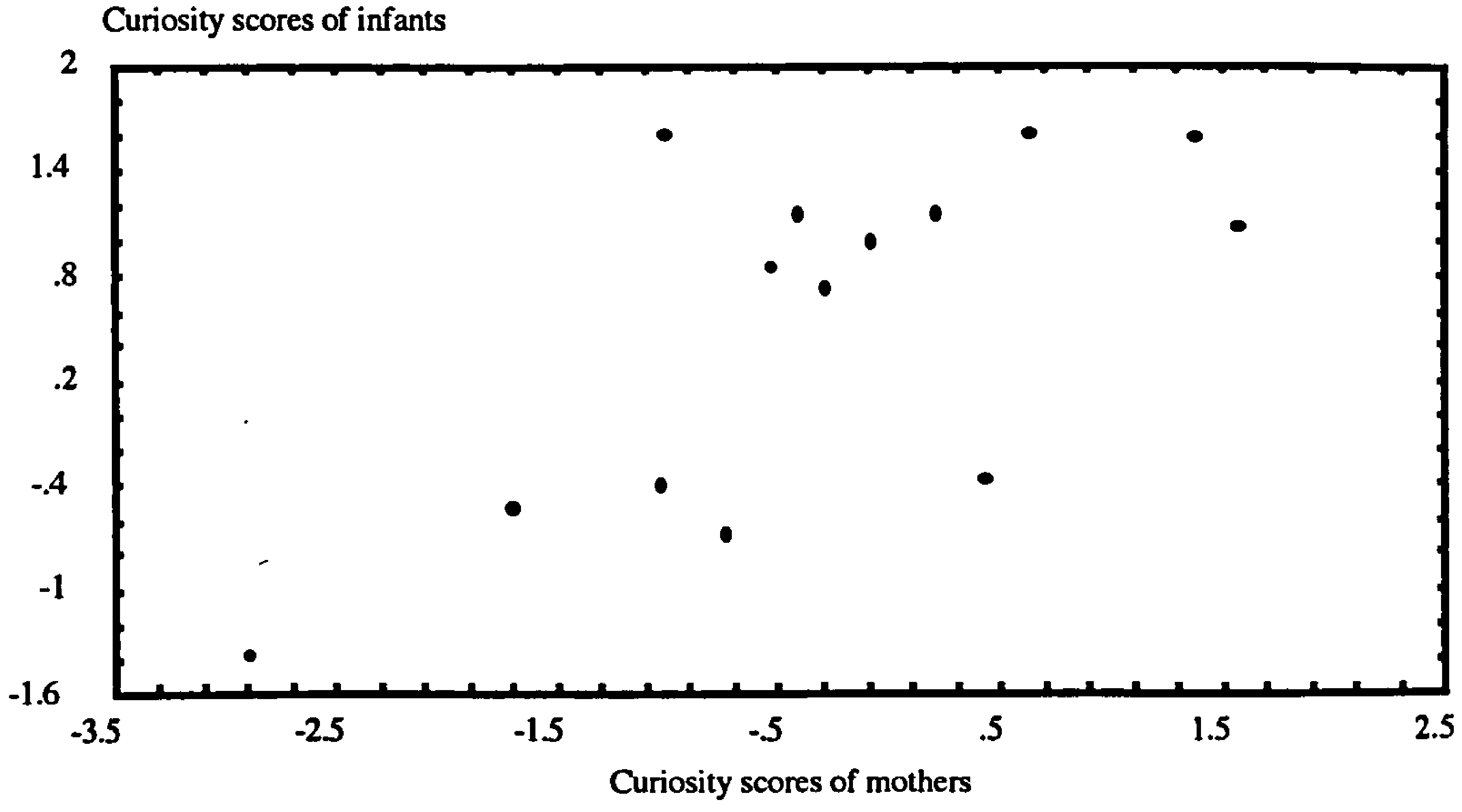
The value of $r_s = -.29$ and is not significant ($p = .25$).

Fig. 3.4 Correlation between mothers' Anxiety scores and infants' Anxiety scores



The value of $r_s = .56$, which is significant at $p = .02$ but not significant after the Bonferroni correction.

Fig 3.5 Correlation between mothers' Curiosity scores and infants' Curiosity scores



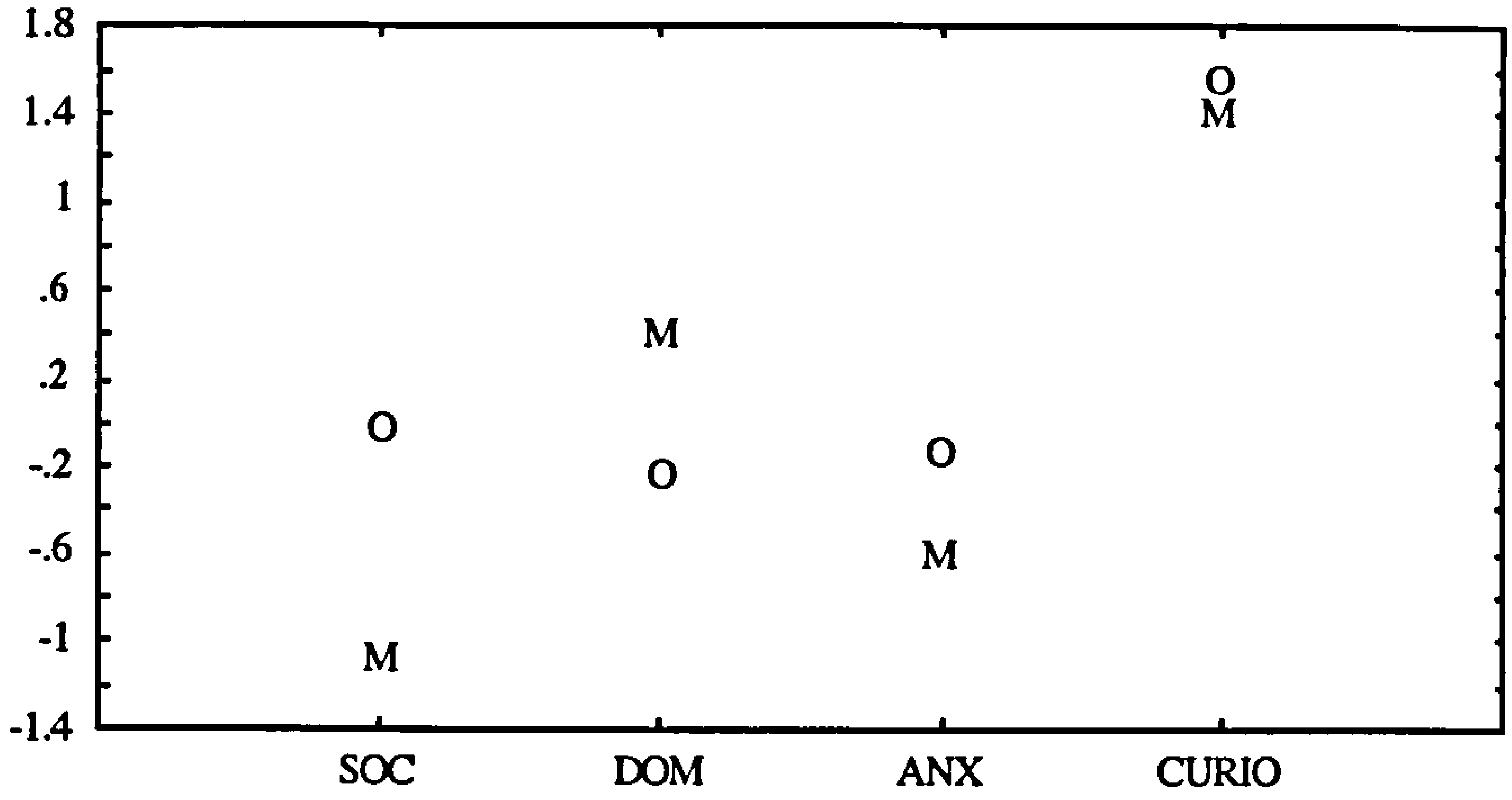
The value of $r_s = .67$ which is significant at p = .005 but not significant after the Bonferroni correction.

The correlations between mothers' and infants' factor scores are suggestive. Dominance scores were correlated negatively, and this correlation was small and not significant at an acceptable level. Correlations for Sociability, Anxiety and Curiosity were all positive and though not significant to the required level, were moderate to high. The strongest correlation was found for Curiosity scores (.67) and this approached significance at an alpha level of .005. The sample size used for this comparison was small, and it is likely that more significant relationships would have been found with a larger sample.

Such group correlations are useful to examine overall similarities between individuals, but may not highlight important differences in mother-infant relationships. Previous work (e.g. Stevenson-Hinde *et al.*, 1980a) suggests that personality of offspring may best be understood as a function of the mother-infant relationship, and that sex and age of the infant are important influences on the nature of this relationship. To draw general conclusions regarding the nature and development of personality within the mother-offspring unit, large samples of animals would need to be rated over a number of years, and the influence of sex and age factored out. With this relatively small sample, individual mother-offspring relationships have been examined in some detail below by comparing personality profiles of each mother-infant pair. Many psychometric personality tests utilise visual profiles to aid in interpretation of an individual's scoring on the test, and to help comparison with the scores of others. These profiles provide a simple way to obtain a more holistic sense of the pattern of scoring for each individual and help to clarify any possible effects of sex and age of offspring.

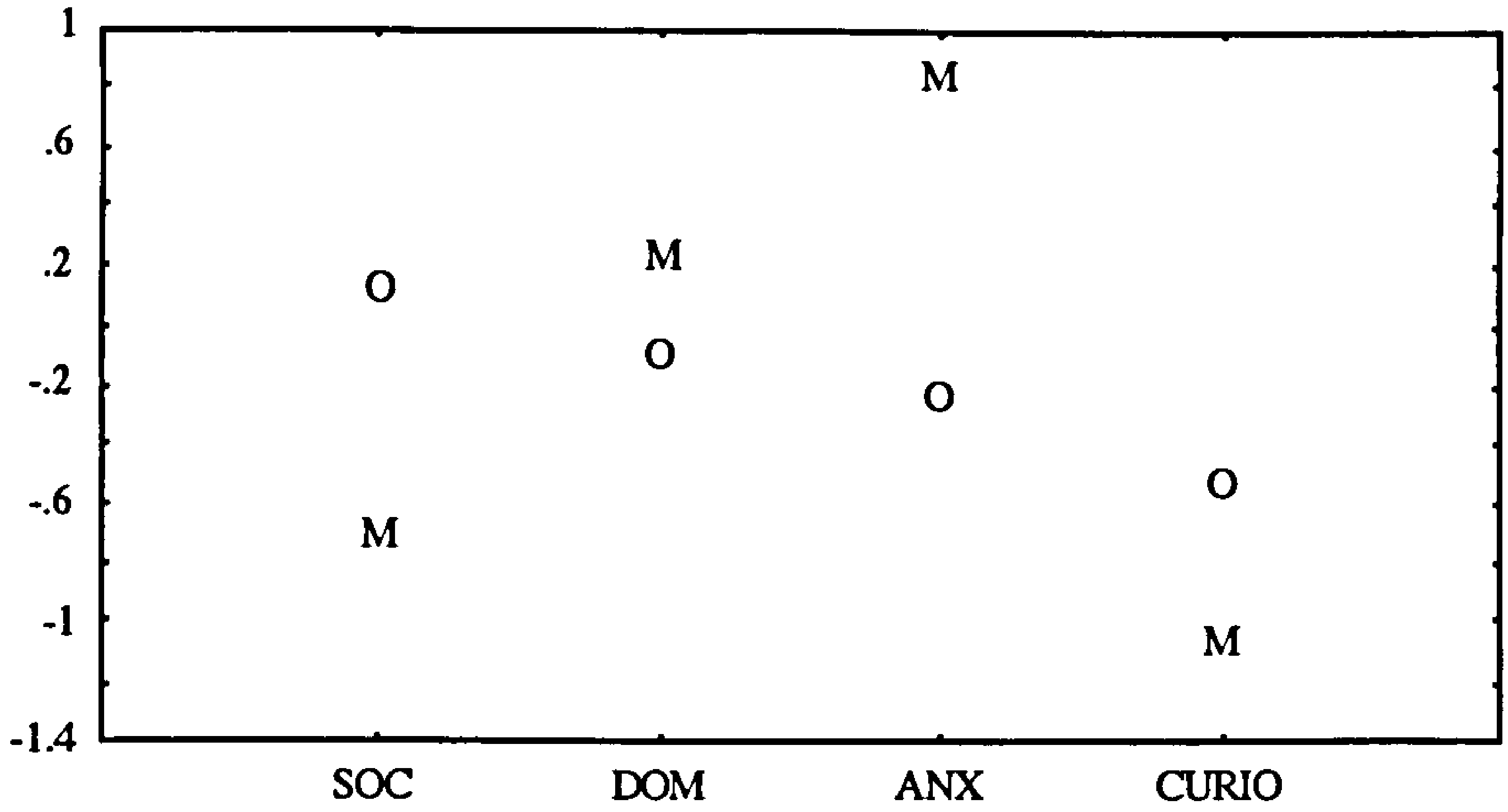
Figures 3.6 to 3.25 below represent factors scores on Sociability, Dominance, Anxiety and Curiosity for each mother-infant pair. For all plots, M signifies the mother, and O signifies the offspring.

Fig 3.6 Personality factor scores for Florin and Alice



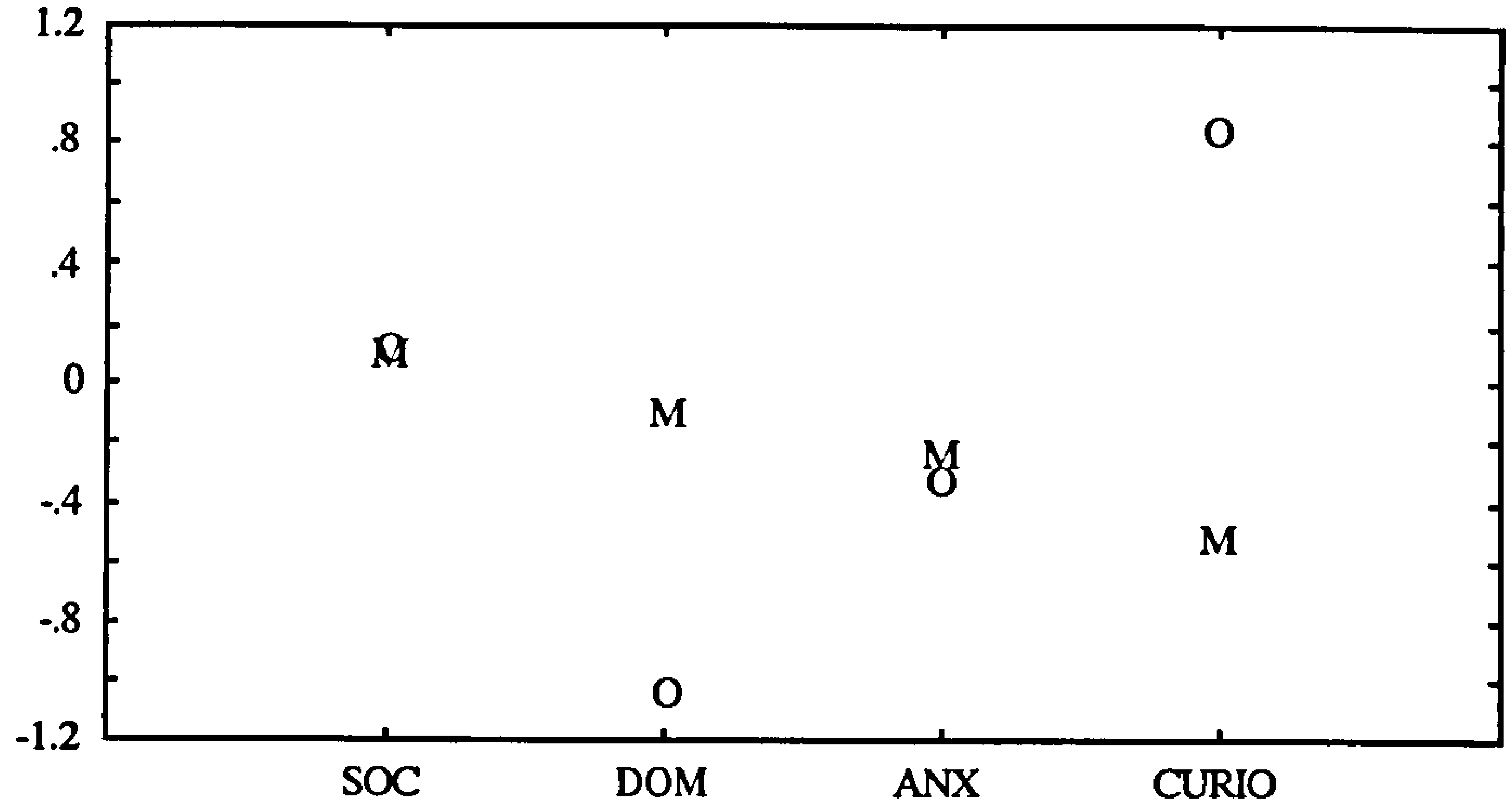
Alice is Florin's first child (Chrissie, Florin's second infant, was too young to be rated). The profile shows divergence on the Sociability and Dominance factors, with Florin being rated higher on Dominance and lower on Sociability. The Anxiety and Curiosity scores are similar, with Alice rated higher on both of these.

Fig 3.7 Personality factor scores for Kate and Kankan



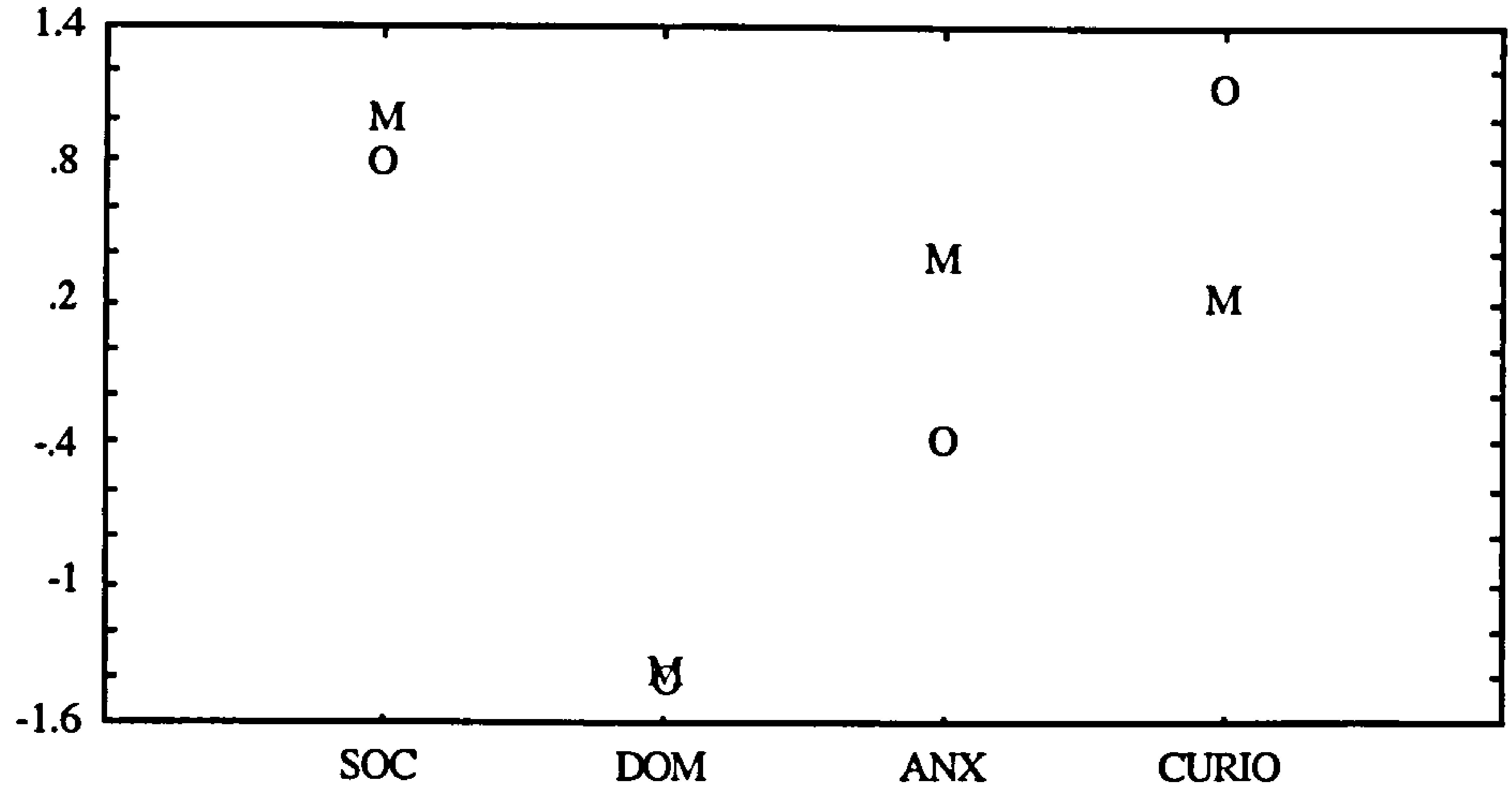
Kate is one of the most anxious females in the group, and this is apparent on the profile, with her adult daughter Kankan rated as less anxious. They also differ on Sociability; Kate is rather less sociable than Kankan, and less curious.

Fig 3.8 Personality factor scores for Kankan and Whitney



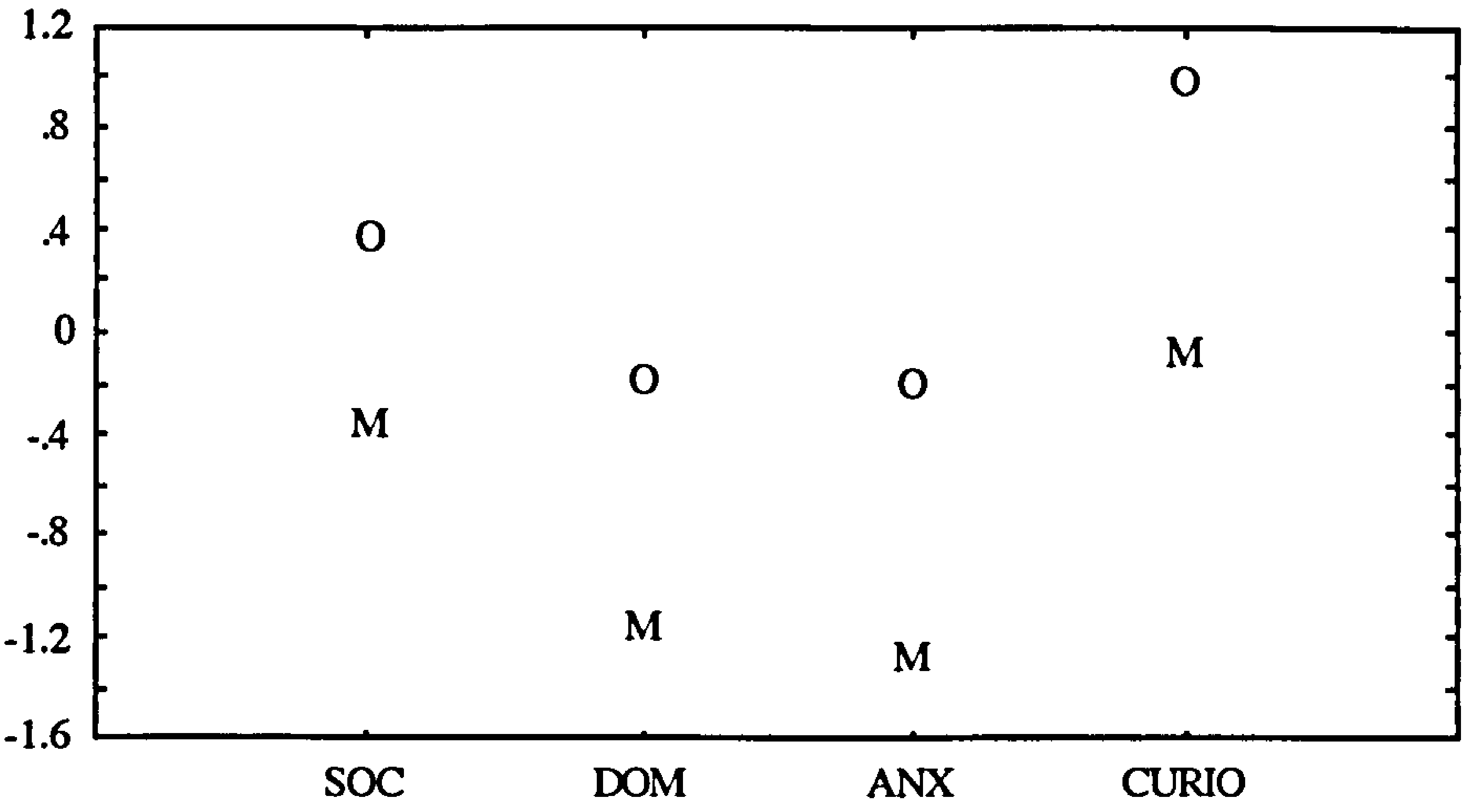
Whitney is Kankan's first daughter, she gave birth to a second daughter in 1997. The scores are very similar for Sociability and Anxiety, with large differences for the other two factors: Kankan is more dominant than her infant, and Whitney is more curious.

Fig 3.9 Personality factor scores for Mandy and Zeezee



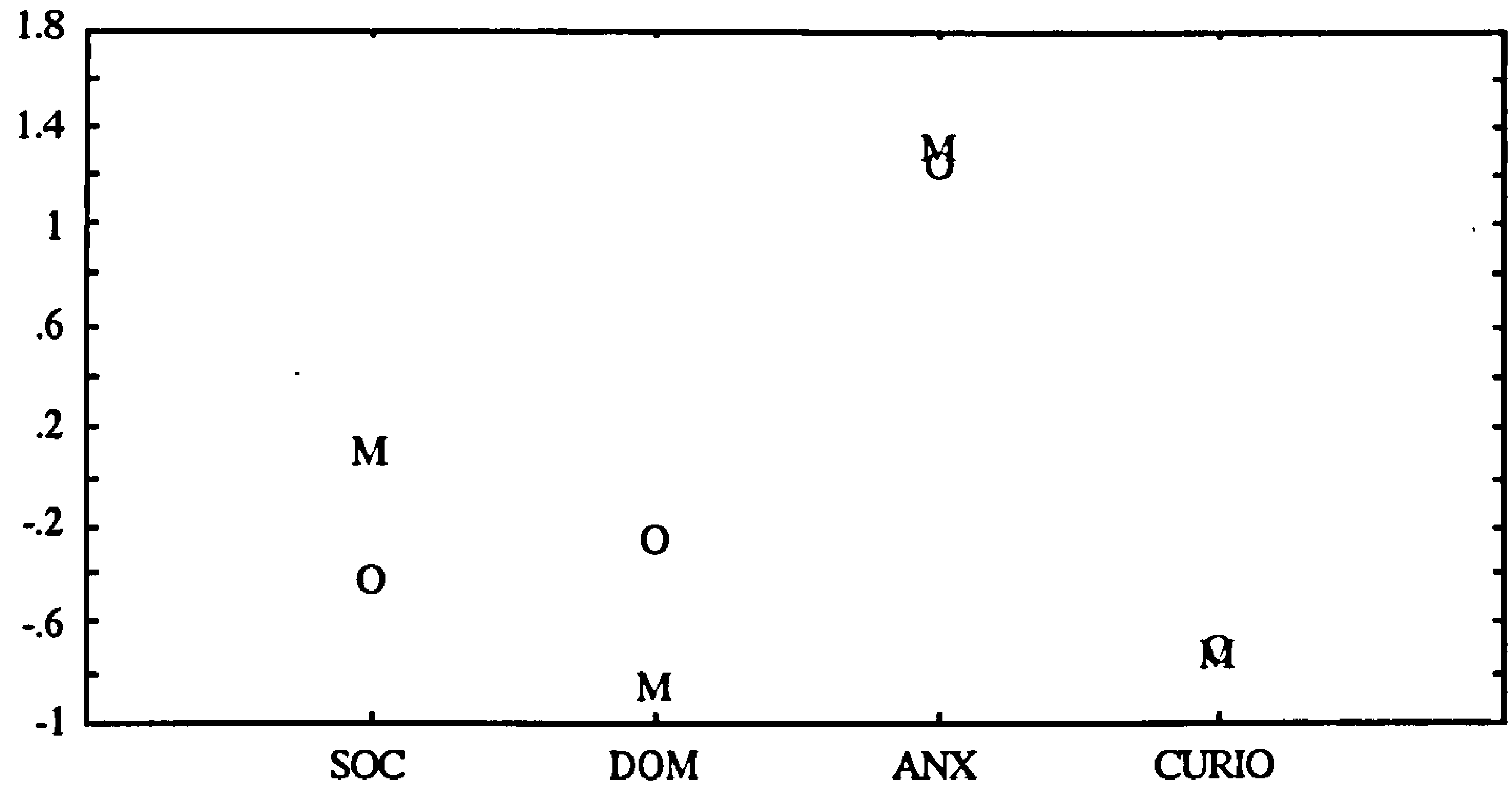
The profiles for Mandy and her five-year old daughter Zeezee are very similar, but Mandy scores higher on Anxiety than Zeezee and Zeezee is rated as more curious. Both score low on Dominance, and both are actually quite nervous individuals

Fig 3.10 Personality factor scores for Halfpenny and Kaylie



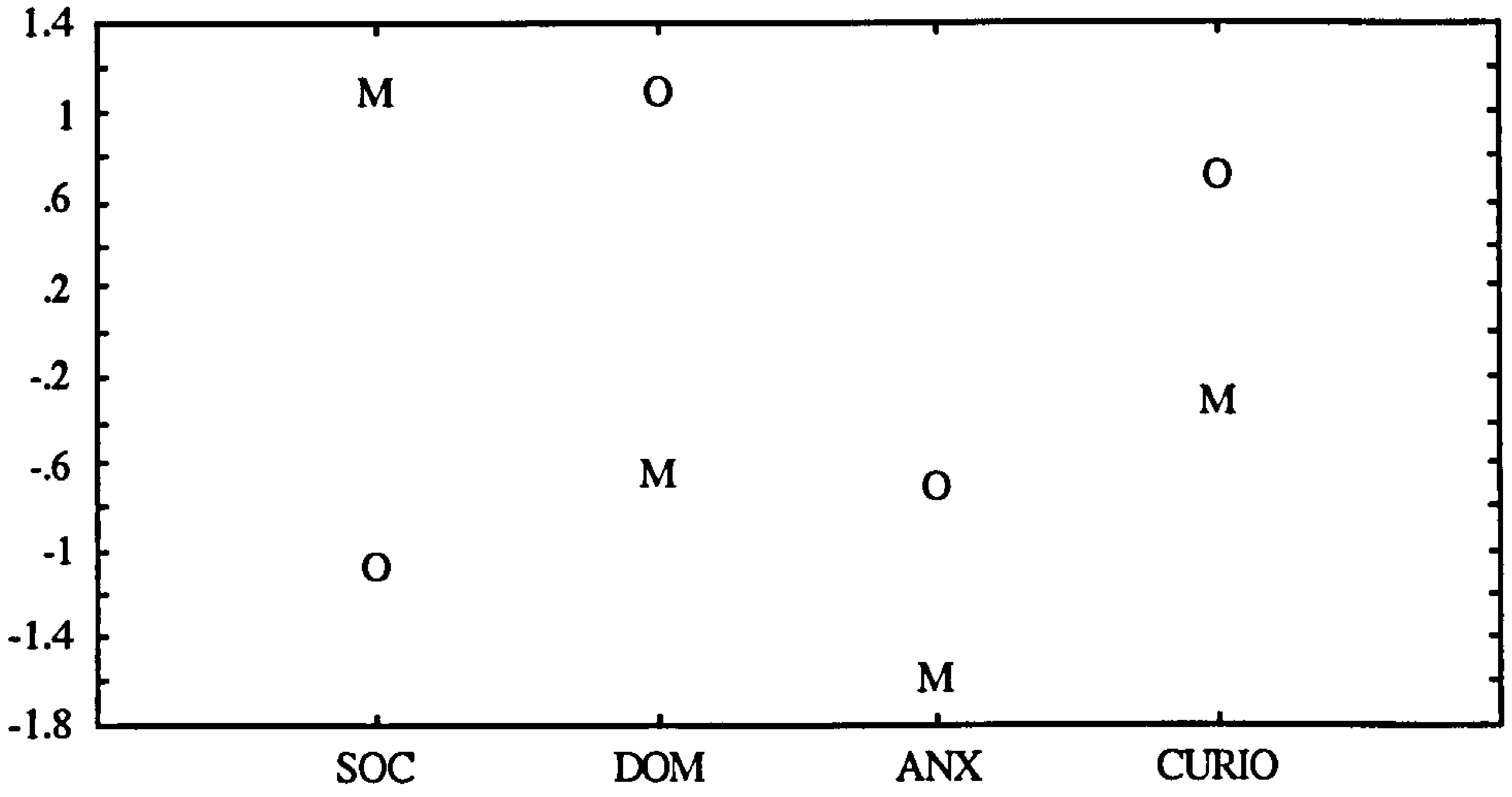
Halfpenny's scores on all of the factors are lower than her daughter Kaylie's, but the profile across the four factors is very similar. As discussed above, Halfpenny's sociability and dominance scores seem to have decreased following the birth of her second infant Kiki.

Fig 3.11 Personality factor scores for Rosie and Sally



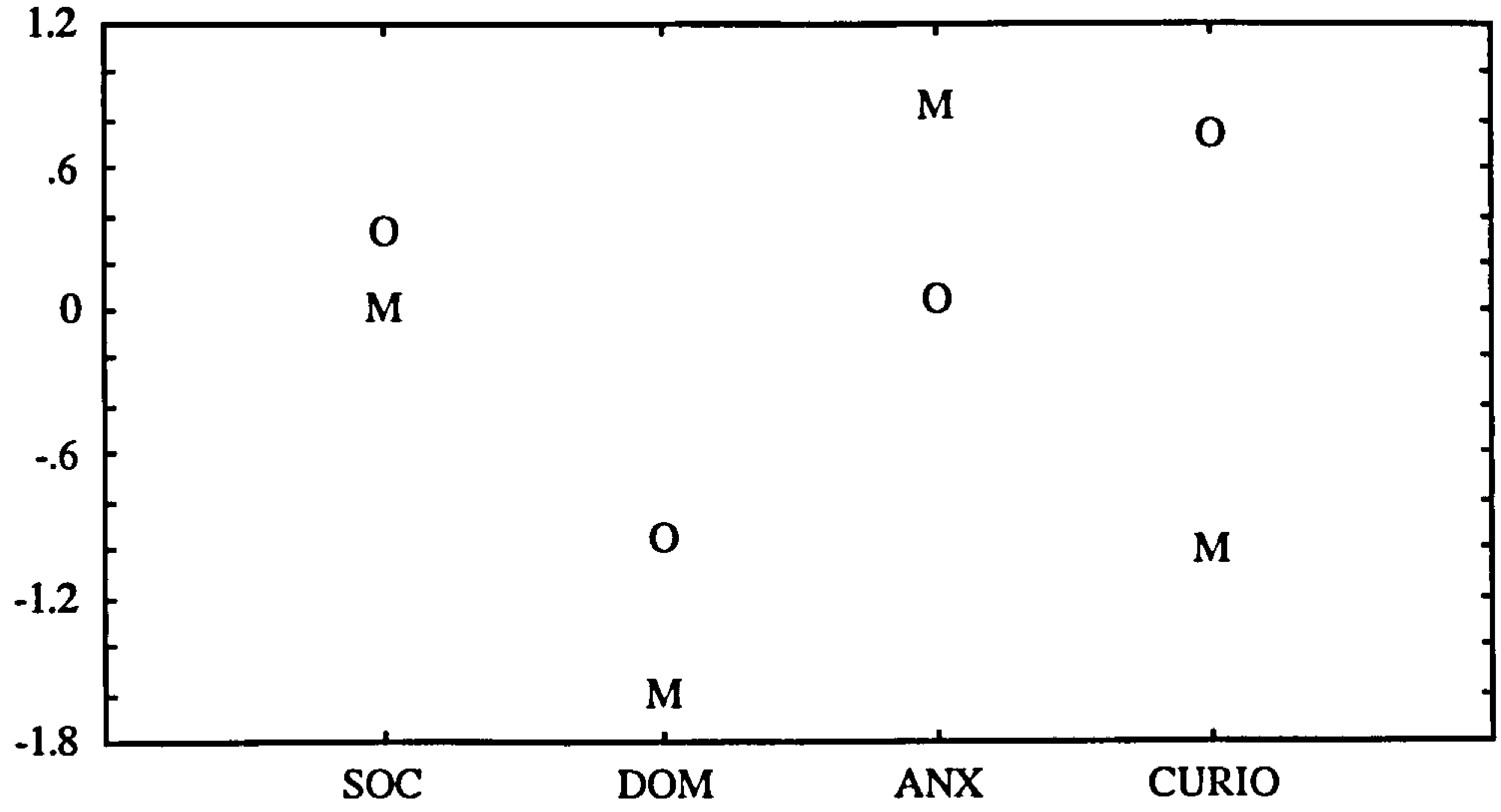
The profiles for Rosie and her daughter Sally are very similar across all four factors, and their scores for Anxiety and Curiosity are practically the same. Even though Sally is eleven, her behaviour is often typical of a younger animal, and she shares with Rosie a nervous disposition (Sally has for the last few years engaged in excessive hair-plucking, an activity usually associated with anxiety). Particularly interesting are the Curiosity scores for mother and daughter; younger animals tend to score higher on Curiosity, but Sally has a very low score that matches that of her mother.

Fig 3.12 Personality factor scores for Heidi and Wanda



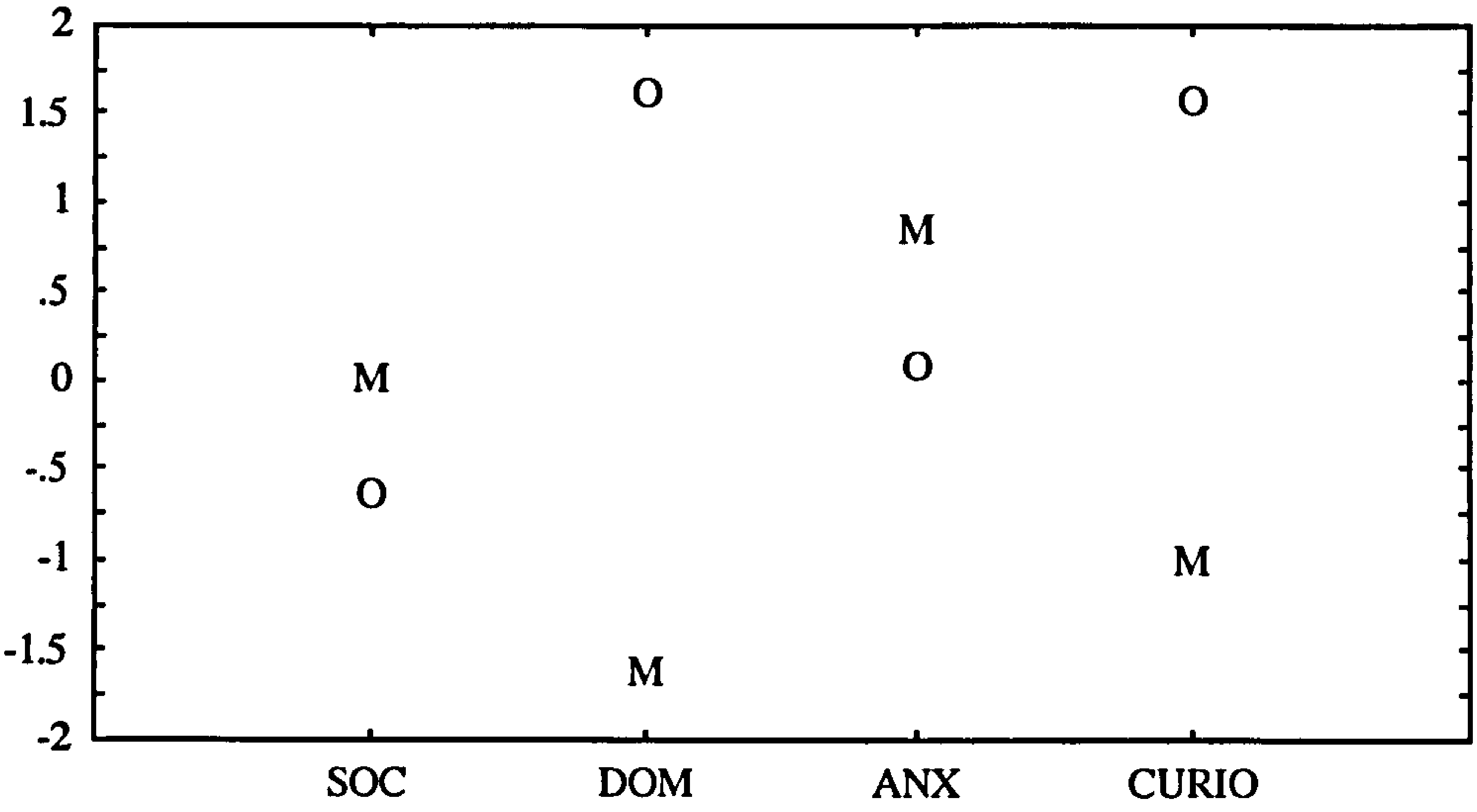
For the Anxiety and Curiosity factors, the profiles for Heidi and her 12 year old daughter Wanda are similar, but their scores are very different on Sociability and Dominance. Heidi is actually one of the most dominant of the adult females, and she is a very sociable animal. Wanda spends a great deal of time on her own, but is often involved in conflicts; she is considered to be an 'ambitious' animal by the raters.

Fig 3.13 Personality factor scores for Farthing and Layla



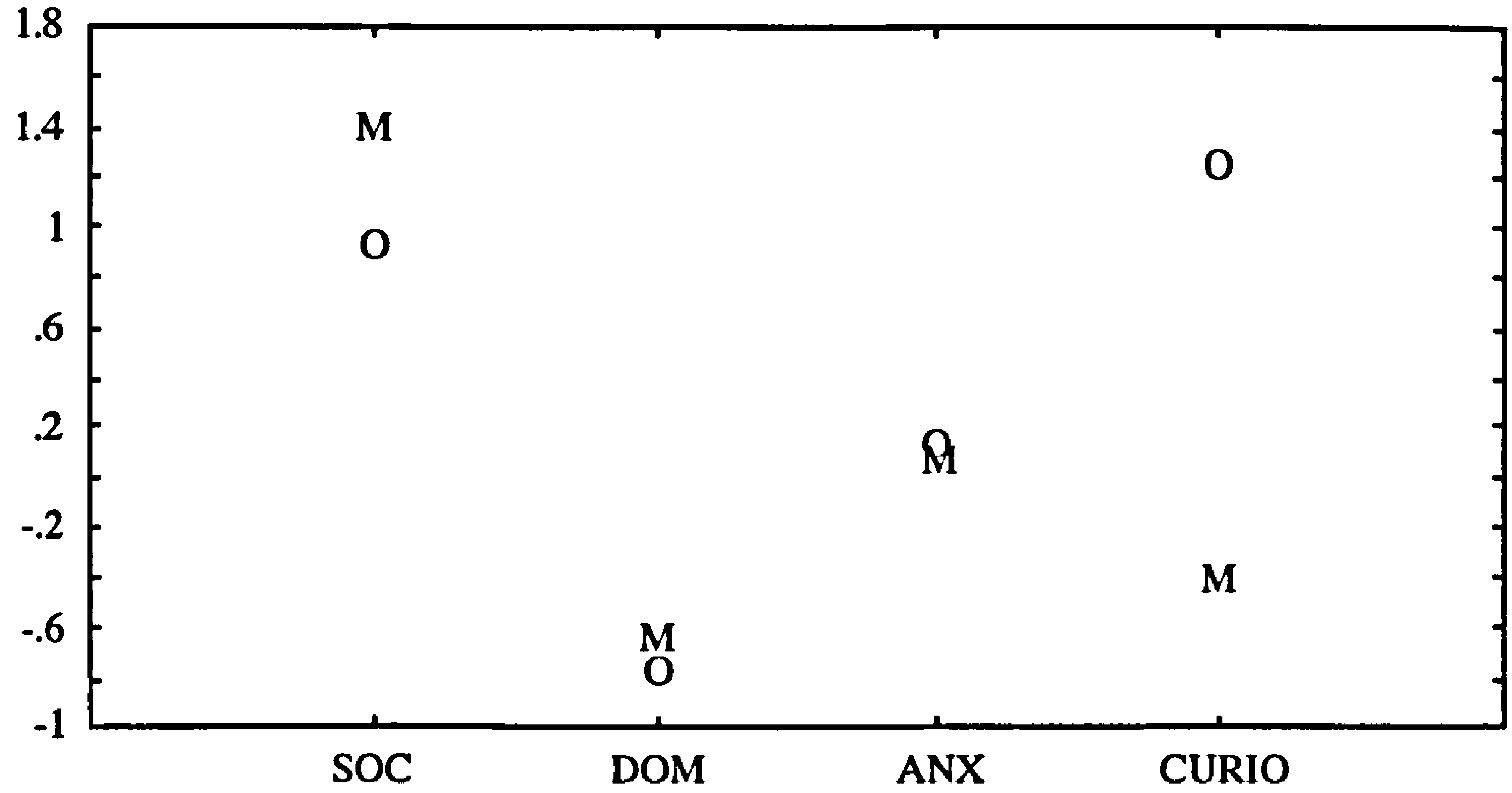
Layla's profile mirrors that of her mother's, particularly regarding sociability and dominance. Farthing is rated as more anxious, and Layla as more curious.

Fig 3.14 Personality factor scores for Farthing and Dylan



There is a much greater difference in the profiles for Farthing and her 12 year old son Dylan. Dylan's scores for Anxiety and Curiosity are actually similar to his sibling's, but he is rated as much more dominant than Farthing and Layla, and slightly less sociable.

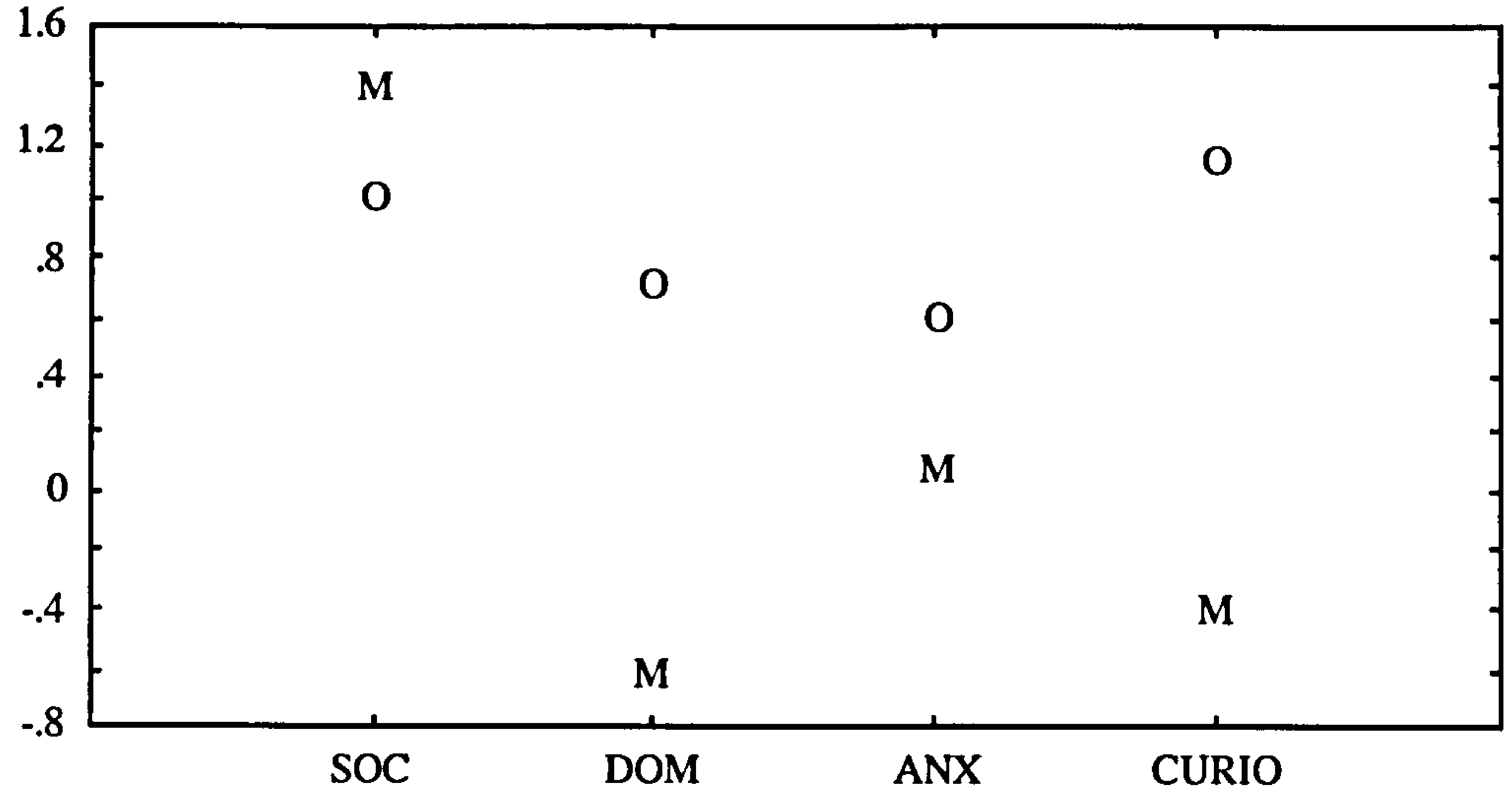
Fig 3.15 Personality factor scores for Jutta and Marco



The profiles for Jutta and her 5 year old infant Marco are remarkably similar.

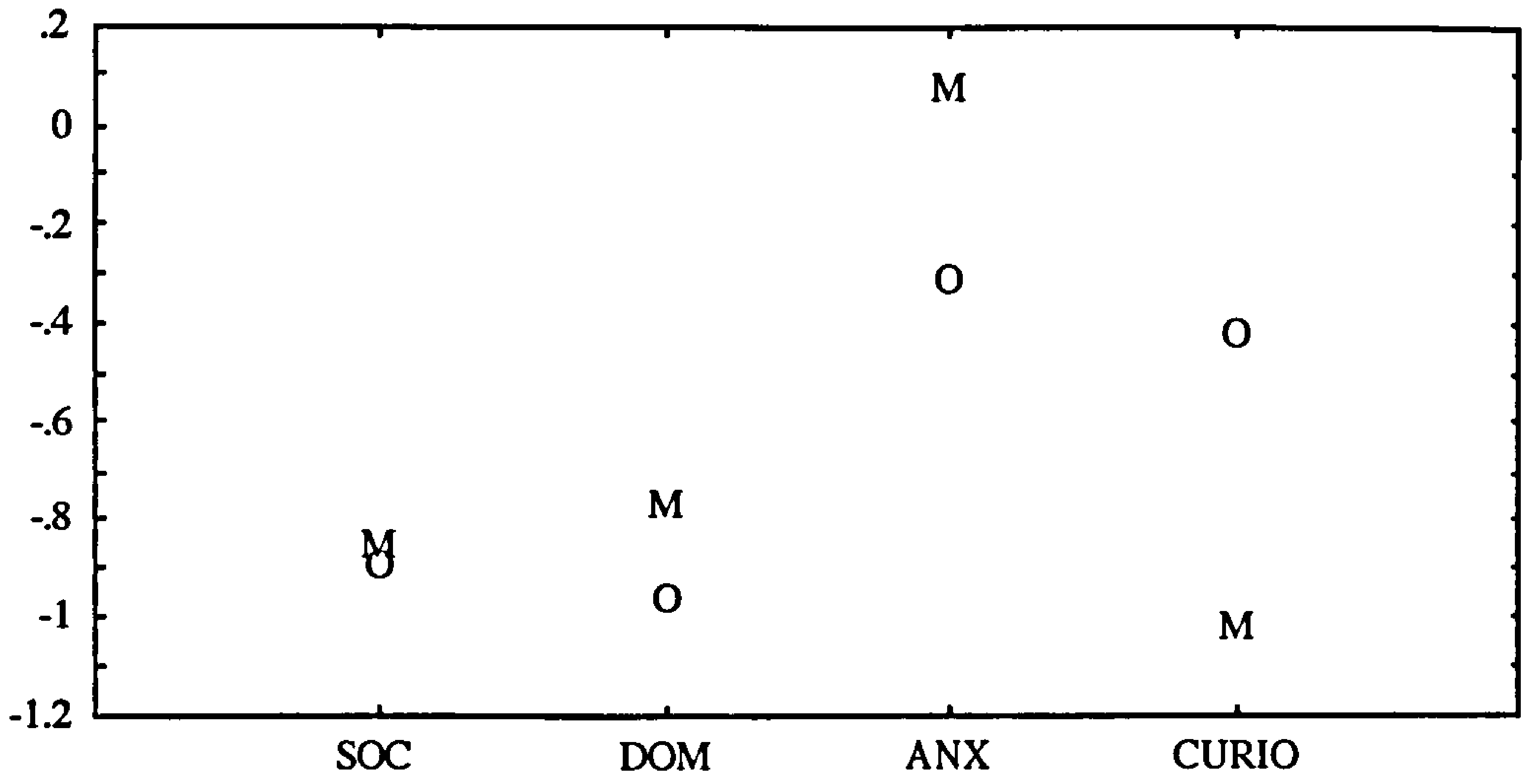
The main difference lies in the Curiosity scores, with Marco rated as much more curious than his mother.

Fig 3.16 Personality factor scores for Jutta and Martin



When Jutta's profile is compared to that of her older offspring Martin (7 years), there is a greater disparity between the two. Jutta is rated as slightly more sociable than her son, but Martin's scores on Dominance, Anxiety and Curiosity are much higher.

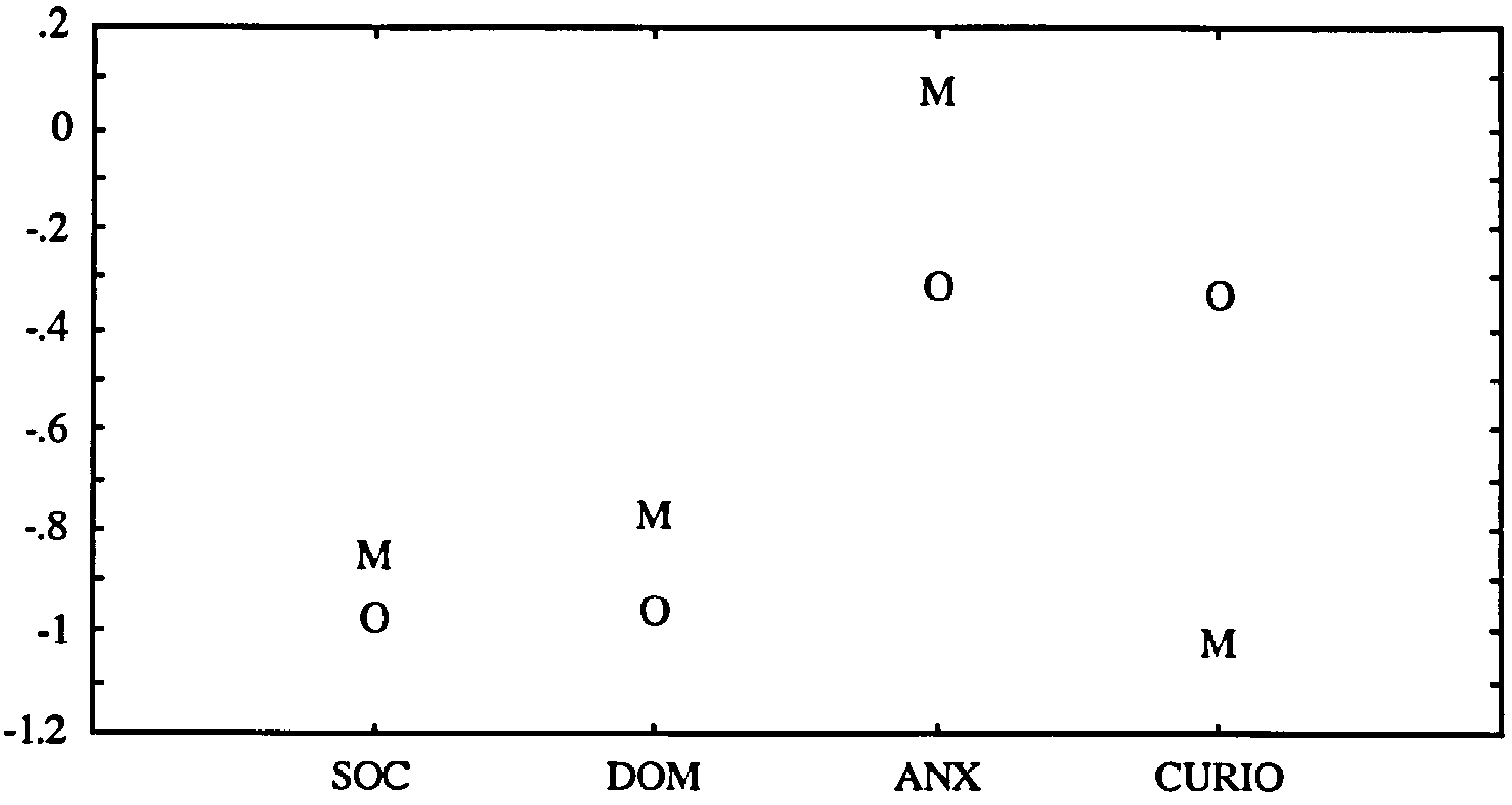
Fig 3.17 Personality factor scores for Flo and Lara



Flo and her 14 year old daughter Lara share very similar profiles across three of the factors, with Flo's scores slightly higher for Sociability, Dominance and

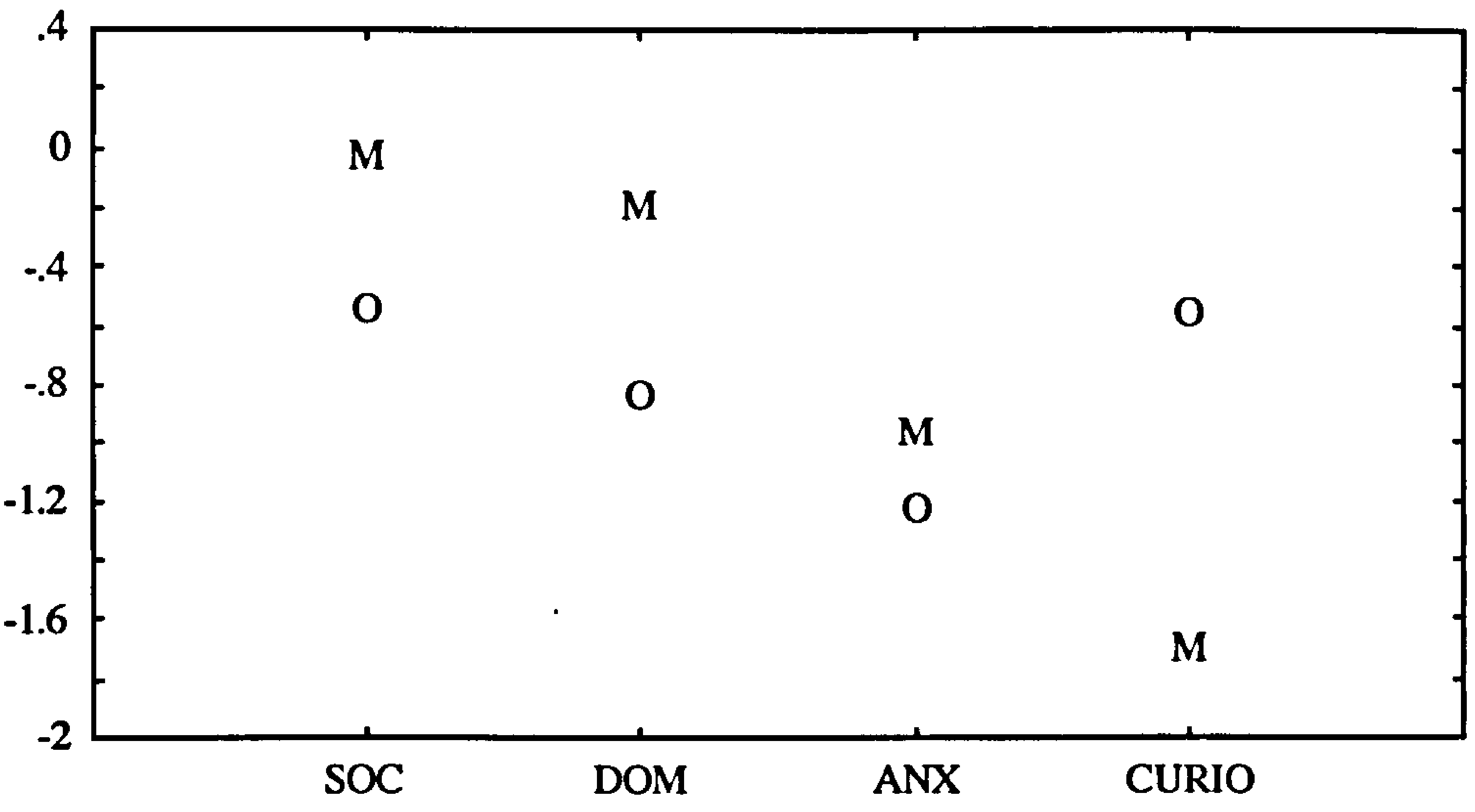
Anxiety. There is a greater difference between them on Curiosity, with Lara rated as much more curious than her mother.

Fig 3.18 Personality factor scores for Flo and Fulani



The profile of 9 year old Fulani is very similar to that of her sibling Lara, and again Flo scores slightly higher than her daughter on Sociability, Dominance and Anxiety. Fulani's score on Curiosity is higher than Flo's and slightly higher than her sister Lara's. Fulani is rated slightly lower on Sociability than Lara.

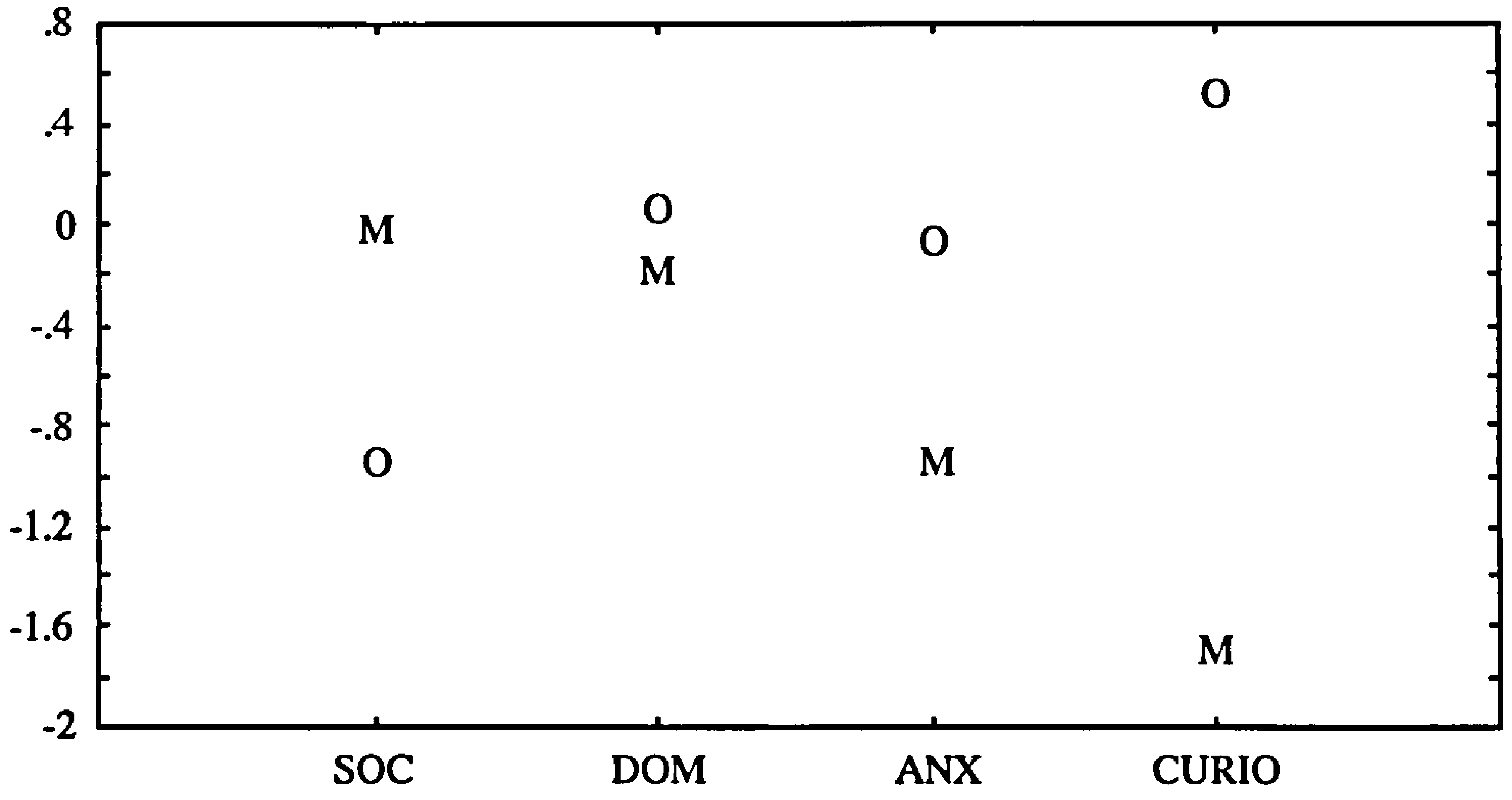
Fig 3.19 Personality factor scores for Gombe and Menolly



Gombe is rated as more sociable, more dominant and more anxious than her

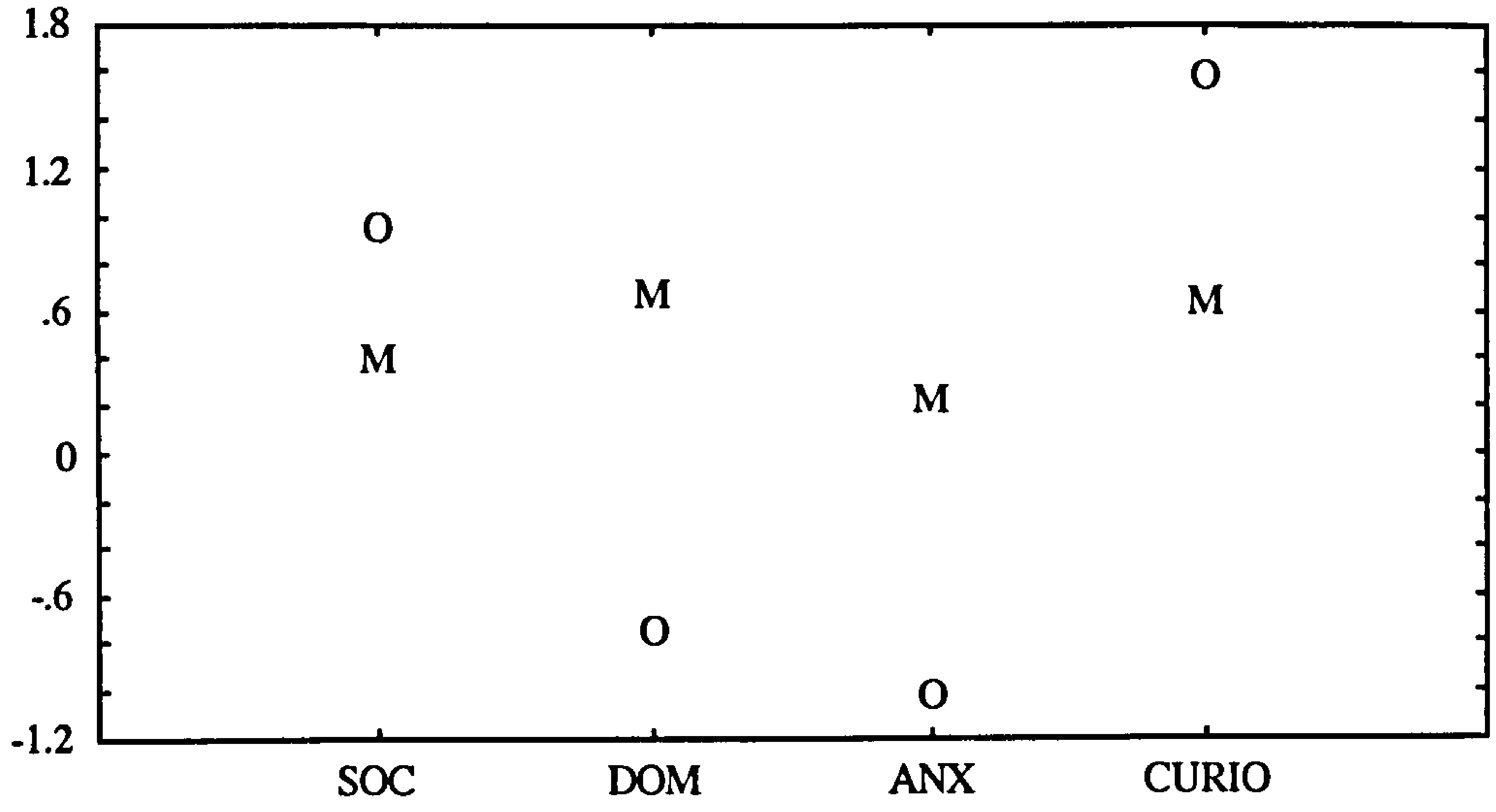
12 year old daughter Menolly, but the profiles over these three factors are similar. On Curiosity, however, Menolly is rated much higher than her mother.

Fig 3.20 Personality factor scores for Gombe and Hubert



There is less similarity between the profiles of Gombe and her 6 year old son Hubert. Hubert is rated as more dominant, less sociable, more anxious and more curious than his mother. The difference between them is similar to that between Farthing and her son Dylan, presented above.

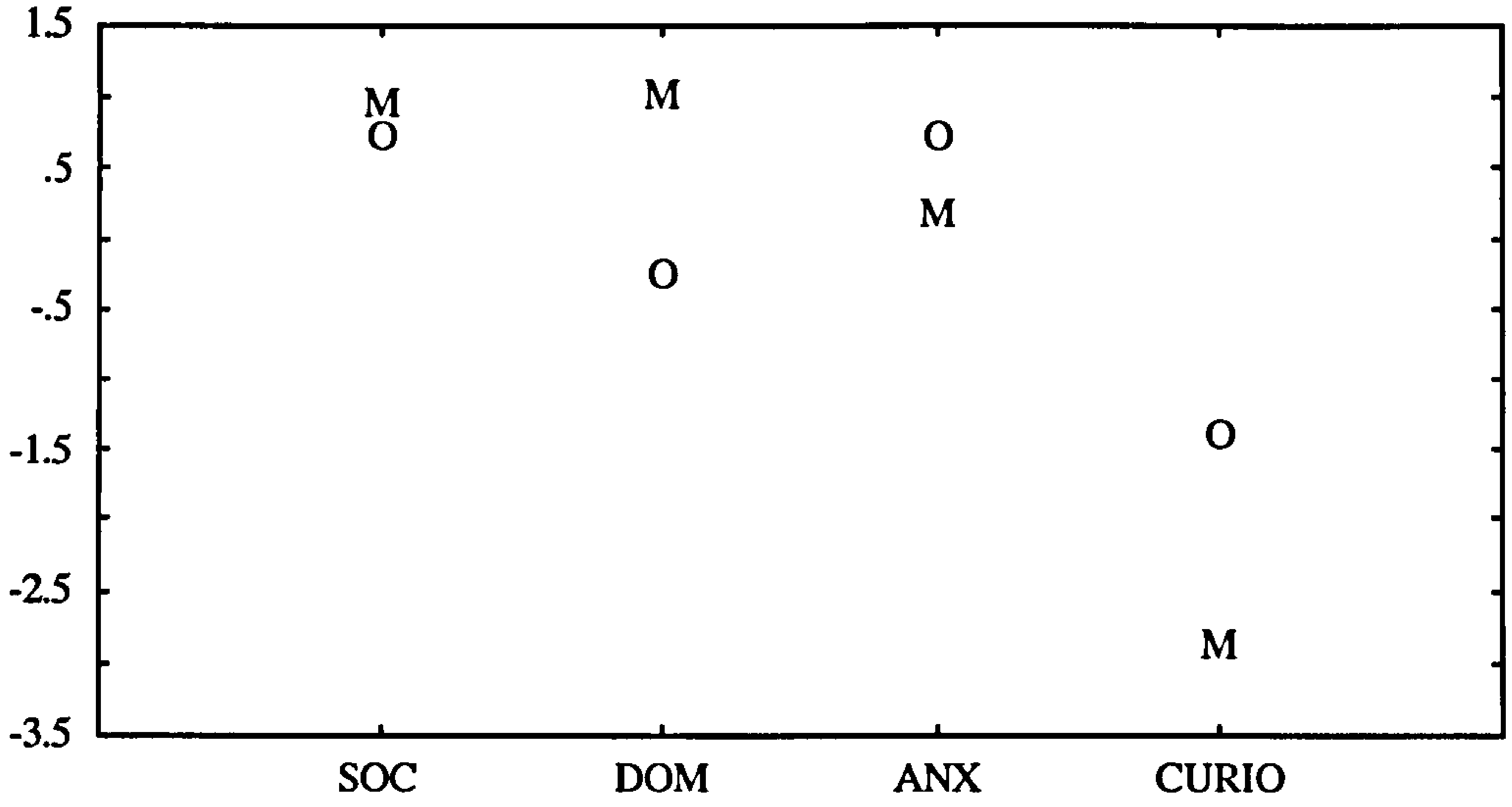
Fig 3.21 Personality factor scores for Elizabeth and Kim



Elizabeth scores higher than her 12 year old daughter Kim on both

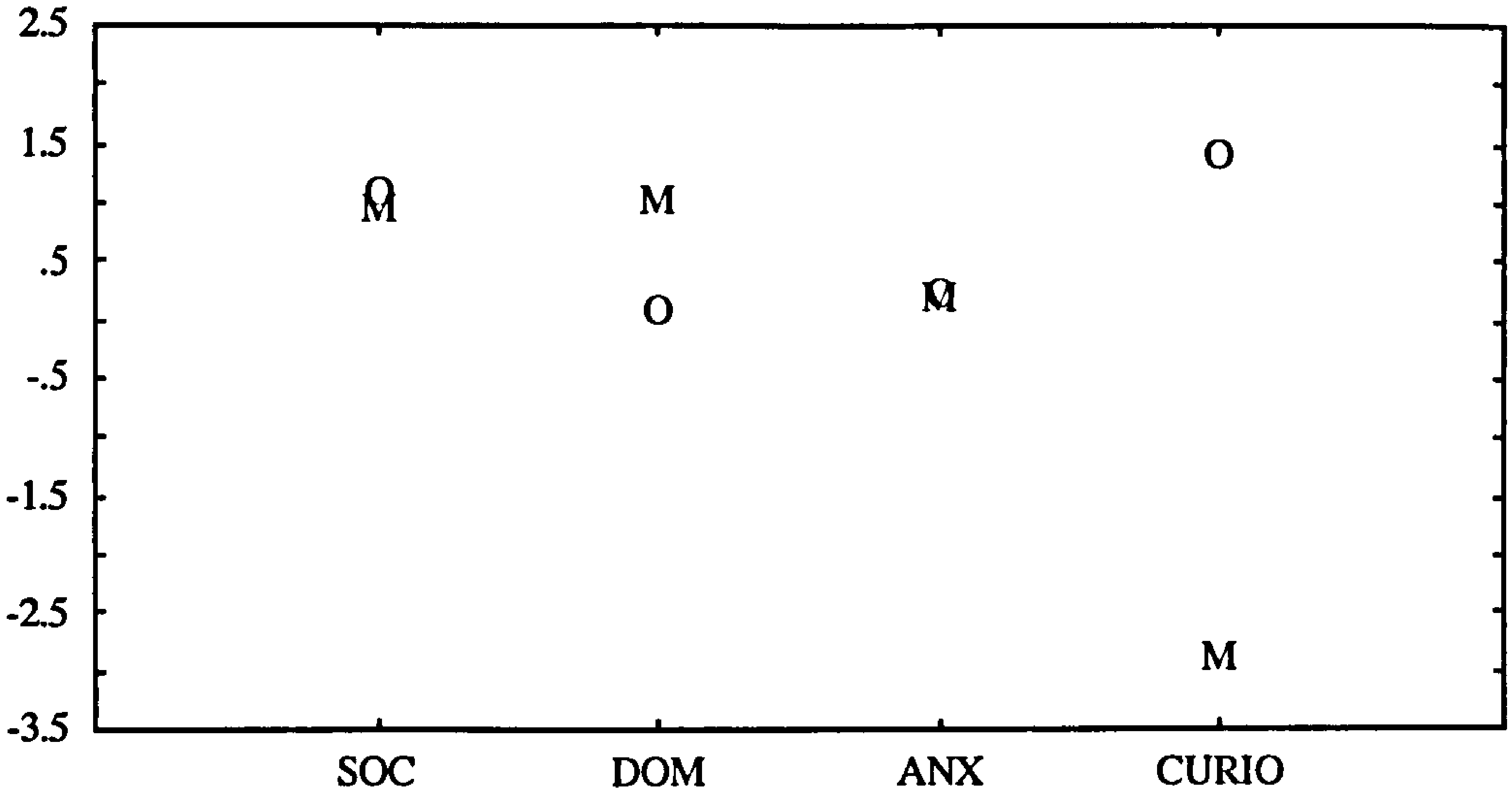
Dominance and Anxiety. Kim is rated as slightly more sociable and much more curious that her mother.

Fig 3.22 Personality factor scores for Helga and Angela



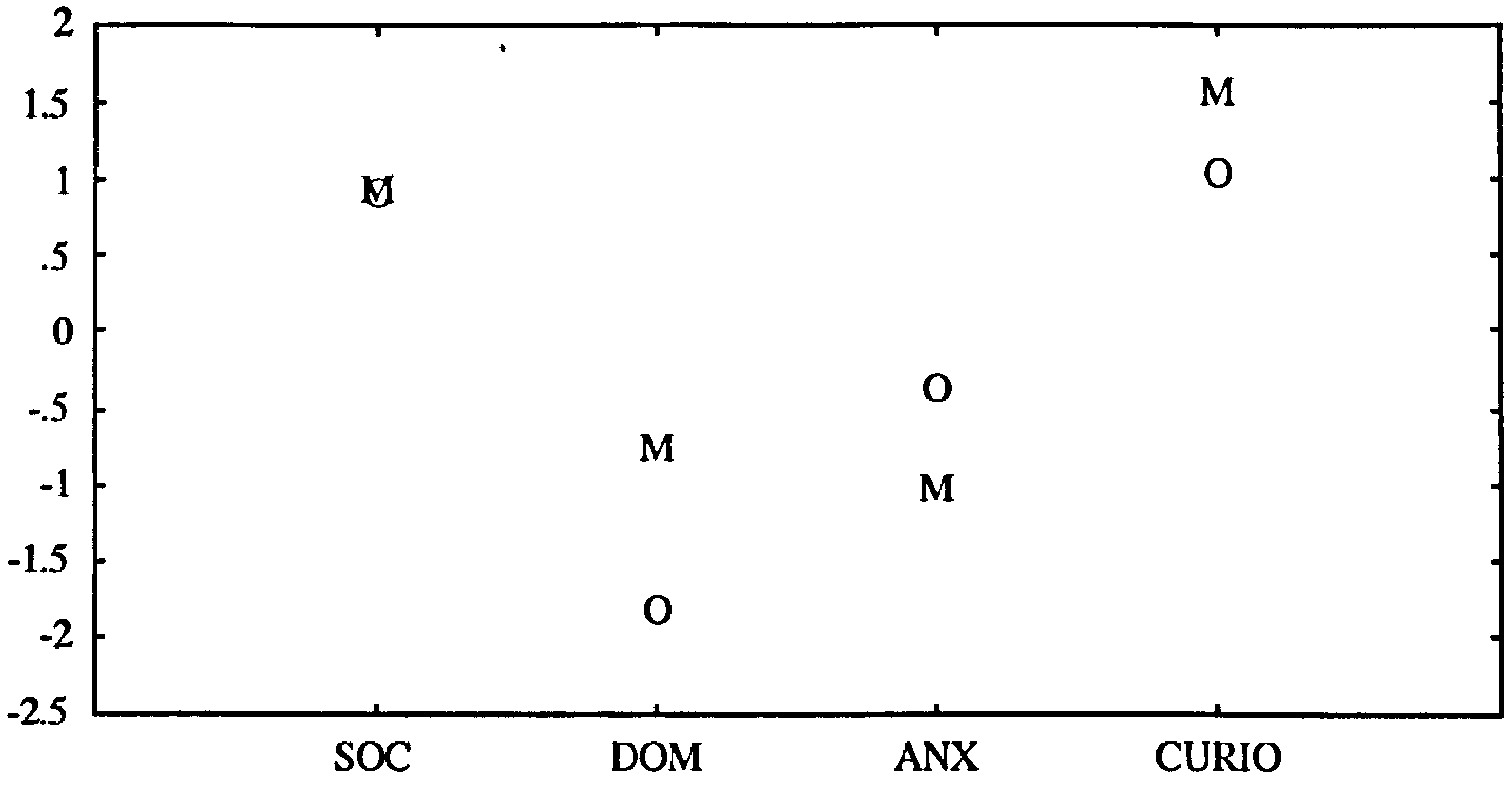
Helga shows particularly high scores on Dominance, Sociability and Anxiety, with low Curiosity. Her 14 year old daughter Angela is rated as less dominant than her mother, and as more anxious and more curious.

Fig 3.23 Personality factor scores for Helga and Austin



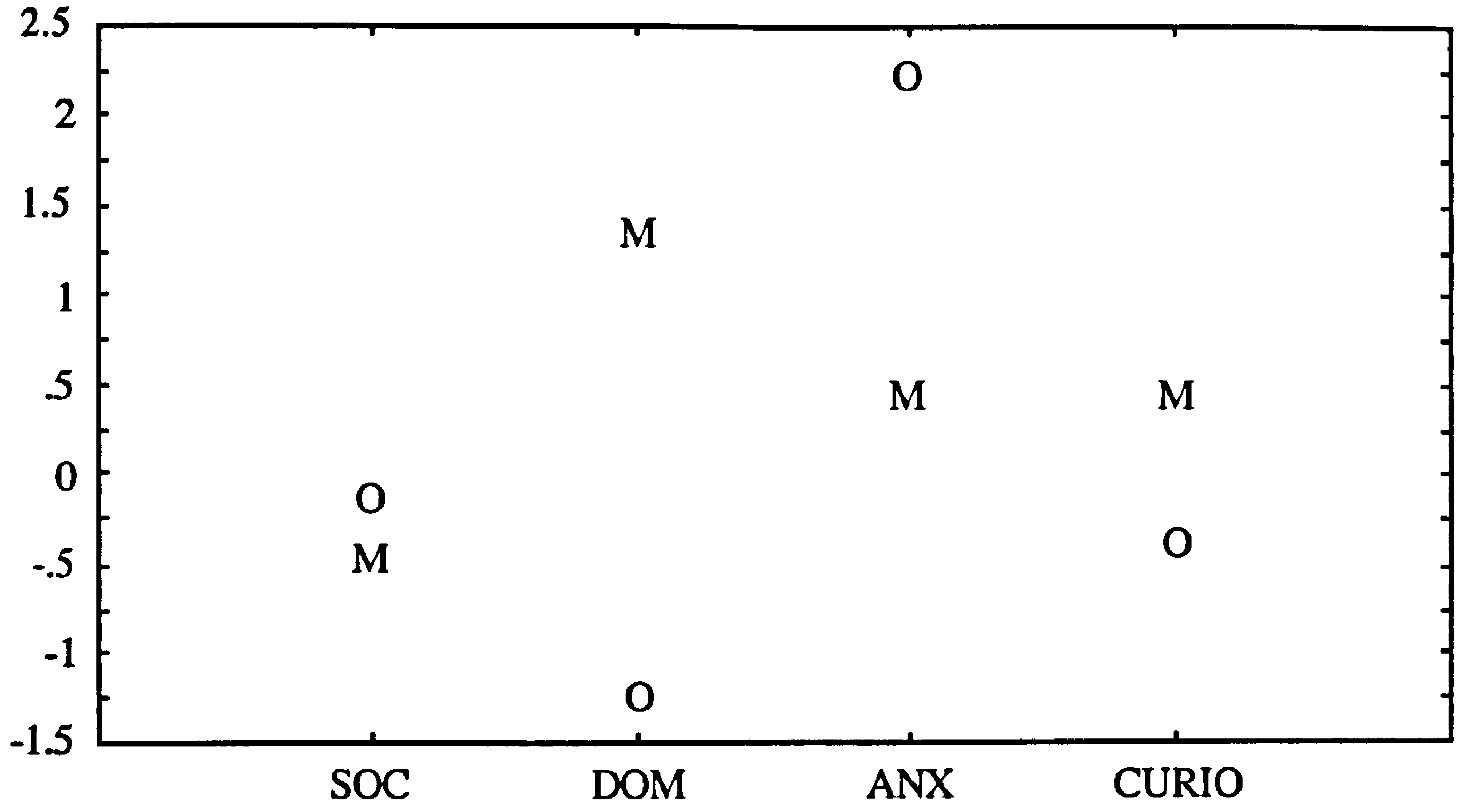
Five year old Austin's profile is similar to his sister's, but Austin is rated as more dominant and less anxious than his sister Angela, but more curious than both his mother and sister.

Fig 3.24 Personality factor scores for Kim and Katie



Four year old Katie is Kim's first infant, and her factor scores mirror Kim's quite closely. Kim has a very high rating on Curiosity, and her daughter's score is almost as high.

Fig 3.25 Personality factor scores for Samantha and Elly



Samantha and her 6 year old daughter Elly both share fairly low Sociability scores. Samantha scores quite highly on Dominance and moderately on

Anxiety and Curiosity. Her daughter's very high score on Anxiety is interesting, and, unlike the other infants, Elly scores lower than her mother on Curiosity.

A comparison of the mother-offspring profiles across age groups shows some basic differences in younger and older offspring. Regardless of the profile of the mother, younger females have high Curiosity scores and low Dominance scores. Young males also have high Curiosity scores, but their Dominance scores are higher than for females of the same age, as would be expected in a species in which males are the dominant sex. Curiosity scores seem to decrease over time. This pattern of higher curiosity/playfulness scores for younger animals is one that has already been documented (e.g. McGuire *et al.*, 1994; Murray, 1995).

While the correlations between mother and offspring scores do not reach the required (corrected) level of significance, a closer consideration of the scores of individual mother-offspring pairs reveals some interesting patterns. For infants aged 1-5, their personality profiles closely mirror their mothers; for older infants and juveniles, the profiles are more disparate, though some older mother-offspring pairs have very similar profiles. It seems that the personality of young infants very closely resembles their mother's, but as they get older their temperament develops. Sociability scores for 1-5 year olds, for instance, are very similar to the mothers' scores, but they diverge more in older offspring. However, the Sociability scores for most of the mother-offspring pairs considered are still fairly close, even for adolescent offspring (e.g. Flo and Lara; Helga and Angela). Mother and daughter Sociability scores are slightly more similar than mother and son scores.

Dominance scores of mothers are also similar to those of offspring. In most cases, more dominant mothers had more dominant offspring, and less dominant mothers had less dominant offspring. However, this is only true of female offspring; males older than 5 years scored higher then their mothers on Dominance.

Anxiety scores of mothers were very similar to their offspring, and this was true for both male and female offspring. Again, scores were more similar for younger offspring. The similarity in Anxiety scores was more pronounced when the mother scored particularly high or low on this factor; this was almost always mirrored in very similar offspring scores (e.g. compare Rosie and Sally with Florin and Alice). This suggests that the mother's scores on Anxiety may be particularly important for the social development of her offspring. The extent to which this may be mediated by sex of the offspring needs to be considered with a larger sample.

The pattern of high Curiosity scores for infants has already been mentioned. In younger infants (particularly up to age 5), their Curiosity scores were high regardless of the mother's score on that factor. In older offspring, Curiosity scores were lower, and in the oldest offspring their Curiosity scores matched the mother's quite closely (compare the profiles for Helga & Austin and Jutta & Marco (both infants of 5 years) with the profiles of Kate & Kankan and Helga & Angela (adult/adolescent offspring respectively). An interesting aspect of the Curiosity scores is that they appear to be linked to Anxiety scores on some of the profiles. Younger offspring appear to score high on Curiosity regardless of their own or their mother's Anxiety scores, perhaps reflecting the pronounced activity of infants and juveniles. Older offspring and mothers, however, seem to show a pattern whereby high Anxiety scores are associated with low Curiosity scores. This seems only true for females though, in older male offspring high Anxiety scores are associated with high Curiosity scores. Differences in dominance patterns between the sexes may be an important factor here. For females, high levels of anxiety may lead to reduced rates of playful, investigative and exploratory behaviour. For males, the pursuit of dominance may engender more active, exploratory behaviour, regardless of levels of anxiety. Alternatively, high levels of anxiety in males may function to increase attempts to exercise social control through the acquisition of dominance rank.

Previous work comparing personality characteristics in nonhuman primate mother-offspring pairs is sparse. The only previous study to compare characteristics of captive chimpanzee mothers and offspring was that by Hemelrijk and de Kogel (1989). A small sample (N = 8) of m others and their infants (aged 1-3) were observed at the Burgers' Zoo in Arnhem. Summed ranks of four variables were used to define sociability of the mother: number of grooming partners; diversity index of grooming partners; support in conflicts; time spent in positive social interaction. Sociability of infants was defined as time spent in social play (excluding time spent with the mother). Interestingly, mothers rated as more sociable had infants that spent less time in social play. One maternal characteristic of these mothers is that they were less responsive to their infants. The authors suggest that, in large groups, the greater sociability of the mother results in less time spent with the infant, possibly resulting in infants who are less confident in exploring the social environment (Hemelrijk and de Kogel, 1989). It seems clear that, particularly in captive groups, individual personality must be considered within the context of the network of social relationships that characterise primate social structure, and that trait-behaviour relationships may not be comparable across captive groups.

In the present study, one pattern that emerged from comparing scores for individual mother-offspring pairs was the greater disparity between mother and son scores, compared to mother and daughter scores. This pattern has also been documented for monkeys. Stevenson-Hinde *et al.* (1980a) compared ratings of rhesus mothers with their infants. On a confident factor, mother and daughter scores were similar, but not mother and son scores. On a sociable factor, male and female offspring's scores were similar to their mothers'. For measures of excitability (which can be considered to measure anxiety), more excitable mothers had less confident offspring. In the present study, both mother and offspring scores on Dominance and Anxiety were closely related, i.e. mothers with low Dominance scores had higher Anxiety scores, and this pattern was reflected in their offspring. This was only true for females and younger males, however; older male offspring tended to have high Dominance scores and high Anxiety scores. Murray (1995) also found that immature male chimpanzees were rated as more dominant than females of the same age, though females were rated as more confident than the males.

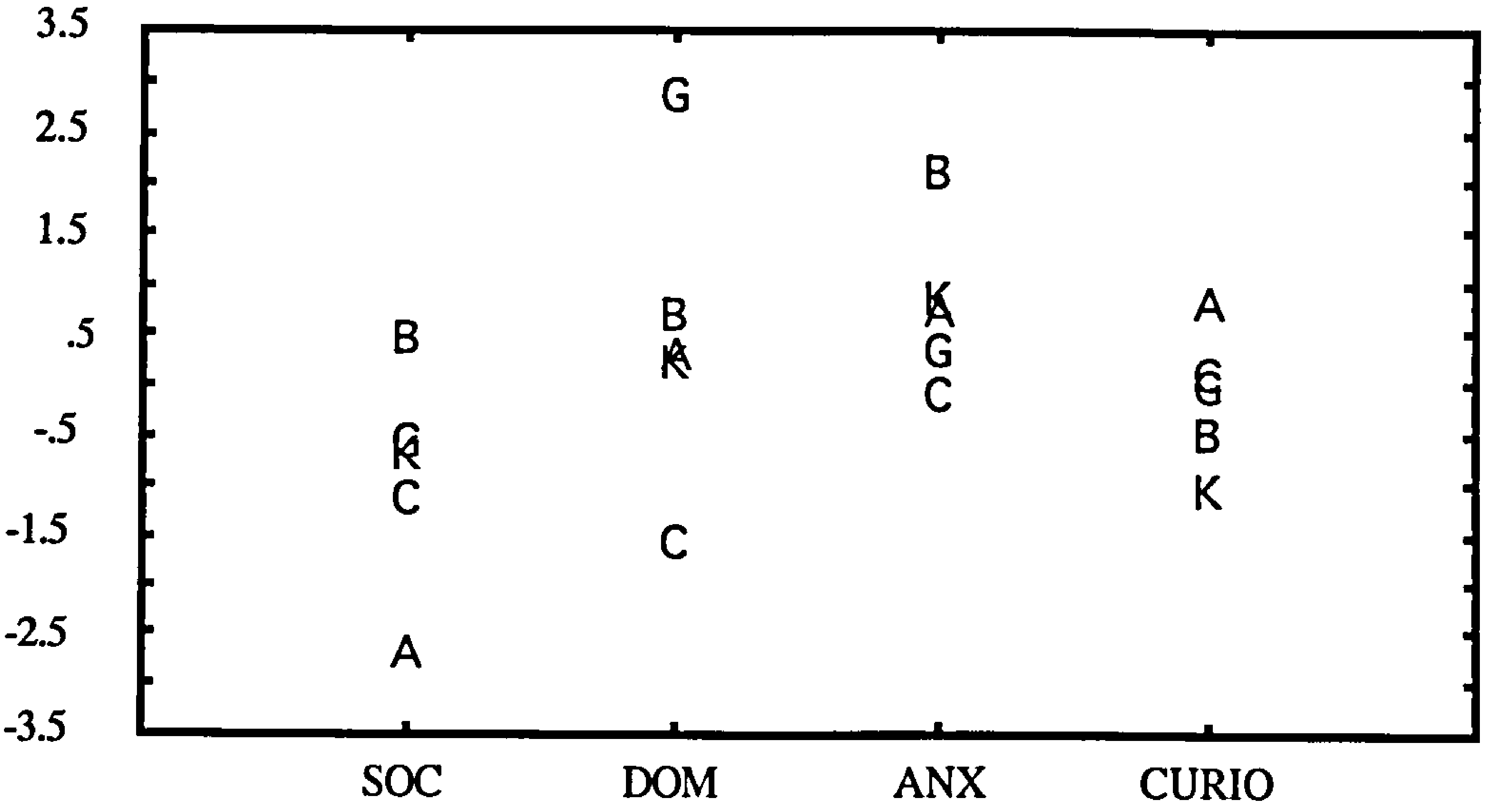
The extent to which the development of an individual's personality is influenced by early nurturant relationships is a difficult question, but one that appears to require a process-oriented view of personality, in which the quality and the dynamics of social relationships are seen as shaping the eventual personality (e.g. Hinde and White, 1974; Stevenson-Hinde and Hinde 1986). It is likely that a closer examination of the development of chimpanzee personality over time may highlight the ways in which the characteristics of the mother (and in particular the characteristics of the mother-infant *relationship*) influence the differing ways in which males and females integrate themselves into their social group. It seems likely that some of these processes may reflect human social development; for example, a greater tendency for females rather than males to more closely mirror the characteristics of the mother (e.g. Winnicott, 1957).

3.3.11 Personality profiles of animals with behavioural problems

There were five animals in the total sample whom the raters identified as having social or behavioural problems. Angus was removed from the Tygerberg group only one month after being introduced to the group, as he was unable to adapt to group life. Gerrit was removed from the same group after a year. He was described by one the raters as: "extremely ambitious and stubborn, unable to adapt to not being alpha...resulted in continuous aggressive encounters which turned group against him.....when [he was the] alpha, was unbending and excessively assertive." Clyde was described as experiencing problems in relating to other animals, the raters felt she had some kind of 'mental retardation'. Bustah was simply described as "neurotic". Both were also from Tygerberg. Kate is a Chester chimp, and her anxious behaviour, and unusual aggressive displays, have been discussed above.

Factor scores for each of these animals were plotted, below. All of the animals show moderate to low sociability and curiosity. Gerrit has a particularly high dominance score, and this would fit with his description of being aggressive and ambitious. All of the animals, particularly Bustah, have moderate to high anxiety scores. There seems to be a pattern of low dominance and high anxiety that was found for the mother-offspring pairs previously discussed, the exception here is Gerrit who shows high dominance and relatively low anxiety. For all the animals shown here, higher anxiety scores are associated with lower curiosity scores (again a pattern found in the earlier comparisons).

Fig 3.26 Personality factor scores for Angus, Bustah, Gerrit, Clyde and Kate



While it is difficult to draw any general conclusions from this plot without comparing profiles for all individuals, it does seem clear that at least some of the behavioural problems identified by the keepers are apparent in the personality profiles.

3.4 Discussion

The principal components analysis of trait ratings produced a four factor structure, identified as: Sociability, Dominance, Anxiety and Curiosity. This was a relatively clear factor structure characterised by high loadings, many of which were highly significant. The roles of sex, age and dominance rank were considered in relation to factor scores on each of these components. Within-zoo inter-rater reliabilities were examined for each of the 46 trait items of the personality rating scale. Reliabilities varied substantially between zoos, and between trait items. The highest number of significant reliabilities was found for raters at Belfast and Chester zoos. While a substantial number of moderate to high reliabilities were found for the other zoos, many did not reach the required stringent level of significance, when corrected for multiple testing. An examination of the median reliabilities for each trait item indicates two clear patterns: reliabilities were particularly high for items relating to dominance characteristics of behaviours, and were particularly low for those items describing more subtle behaviour involving complex mental characteristics (e.g. deception).

Previous work has identified characteristics of the animals themselves that may have an effect on reliability of ratings. Buirski *et al.* (1973) found that reliability of ratings of baboon personality was lower for those animals undergoing dominance changes. Bolig *et al.* (1992) suggested that ratings of rhesus macaques were affected by various social changes that animals were experiencing. In both of these situations, ratings might be expected to be unreliable as an animal adapts its typical behaviour patterns to cope with environmental stressors. Additional comments made on the questionnaire by raters in the present study indicate that they found it particularly difficult to rate males who were undergoing changes in status. The influence of status changes on personality ratings is discussed in more detail in Chapter 7.

In the factor analysis presented in this chapter, all items have been included, despite some showing low reliability. For these items, in most cases low reliabilities were characteristic of only one, or two, zoos, and such items often had high reliabilities when used by other zoos in the sample. In addition, the reliabilities for the Chester 1999 raters were very high, and it is these ratings on which the subsequent trait-behaviour analyses are based.

The findings of the present study echo similar findings across a range of studies of primate personality, and provide independent support for a common primate personality structure. For example, personality factors denoting sociable, fearful, dominant, and curious behavioural responses have been identified for rhesus monkeys (e.g. Bolig *et al.*, 1992), and sociable, dominant and curious factors identified for vervet monkeys (e.g. McGuire *et al.*, 1994). The only study of gorilla personality to date, that by Gold and Maple (1994) on captive gorillas, also found four similar factors (labelled 'fearfulness', 'understanding' 'extroversion' and 'dominance'). Two previous studies have identified personality factors for captive chimpanzees. Murray (1995) based her personality rating scale on that used by Stevenson-Hinde *et al.*, 1978, 1980a) and found similar factors to Stevenson-Hinde: 'confident', 'sociable' and 'excitable'. The most recent attempt to formally rate captive chimpanzees was by King and Figueredo (1997). A sample of 100 captive chimpanzees were rated on 43 adjectives, 41 of which were items taken from the Big Five taxonomy of trait terms (Goldberg, 1990). Factor analysis produced the Big Five factors of Surgency (or Extraversion), Dependability (or Conscientiousness), Agreeableness, Emotionality (or Neuroticism) and Openness, as well an additional factor of 'dominance'. As in the present analysis, high loadings were found for most of the items on the rating scale. It is interesting to note the highest and lowest loading items in King and Figueredo's study. The factor that accounted for most of the variance in their study (20.8%) was 'dominance', suggesting the central role this factor plays in judgements of chimpanzee personality. It is on this factor that the highest loadings are found, suggesting that, as in the present study, raters found items loading on this factor the most salient. As in the present study, the lowest loading items in the King and Figueredo study all refer to more subtle personality characteristics that are perhaps difficult to apply to chimpanzees: clumsy, autistic and manipulative all loaded below .52 and stingy and imitative, both loaded at .52.

The pattern of item loadings in the present study was compared to the nature of the Big Five factors (see section 3.3.5). The factors of Sociability, Anxiety and Curiosity seem similar to the Extraversion, Neuroticism and Openness to Experience factors of the human Big Five factors, so it seems clear that these aspects of temperament are shared by the primates. The factor of Dominance seems more important for nonhuman primates than it does for humans, in this study Dominance explained almost as much variance as Sociability. In humans, individuals do vary on dominance, but it seems to be an aspect of Extraversion rather than a separate factor. The appearance of Dominance as a clear factor in nonhuman primate studies reflects the important role that dominance relationships have in many primate societies. A comparison of simple dominance rank scores with the personality factor scores showed a strong positive relationship between rank and the Dominance factor, with low or moderate (nonsignificant) correlations between rank and the other three factors. This indicates that high ranking animals score highly on the Dominance factor, and are more sociable, less anxious and more curious.

A comparison of the structure of the Dominance factor in different nonhuman primate studies would be useful. In nonhumans, this factor seems to be composed of a combination of items that relate to other factors, rather than being composed of a unitary selection of trait terms. The composition of this factor, and individual profiles of dominance scores might reflect the differing dominance structures of various species of primate. In species with more rigid dominance structures, for instance, this factor may be composed of fewer behaviours, or ones which specifically relate to dominance interactions. In chimpanzees, this factor seems to encompass a wide range of behaviour patterns. The dominance factor in chimpanzees, then, does not appear to be structured like a human factor trait, but it may be more 'trait-like' than in monkeys, or non-primates.

This study attempted to briefly examine the relationship between age and personality ratings, and between sex and ratings. Point-biserial correlations between sex and the four factors showed a highly significant difference between males and females on the Dominance factor, with very small (nonsignificant) differences on the other factors. On all the factors, males scored higher than females. The influence of sex on personality ratings is one which is complex, and likely to be confounded by age. A comparison of personality of 20 mother-offspring pairs indicated some similarities between personality profiles of animals in different age classes, and suggested that these profiles were sex-specific. In addition, the relationship between personality profiles of mothers and offspring seems to depend upon the sex of the offspring.

A comparison of age with personality factor scores showed that younger animals scored more highly than older animals on the Curiosity factor, and lower on the Dominance factor. This pattern was also mirrored in the comparisons between mother-offspring pairs. Younger males and females are more curious than older animals (with infants and young juveniles the most curious). Curiosity scores decrease with age, and appear to be linked with Anxiety scores. Highly anxious individuals seem less curious, and this is particularly true for older animals. This effect, however, may depend upon the sex of the animal; the data for male offspring suggest that highly anxious males are also highly curious, so curiosity may only decrease in females, not in males.

To summarise, this study identified four personality factors in chimpanzees. There appear to be clear sex and age differences in scores on the four factors, but scores are likely to reflect age, sex, and dominance rank in a complex way. A consideration of all of these characteristics is necessary to adequately understand how personality ratings may reflect individual responses. In addition, it seems clear that the role of environmental events (e.g. birth of an offspring, change in dominance status) has to be considered to achieve a full understanding of an individual's temperament.

CHAPTER FOUR

Understanding individual differences and relationships

4.1 Introduction

From an ethological perspective, the identification of a common number of personality dimensions in nonhuman primates is of little use without an adequate explanation of the conceptual status of traits, and a practical notion of how they relate to behavioural measures. This chapter examines the utility of the trait concept as a tool for describing individual variation among nonhuman primates, and then considers whether trait ratings can provide additional information to traditional behavioural measures. Hinde's (1976, 1979a, 1979b) conceptual framework for analysing social structure is considered in relation to a study of individual differences. The effects of age and sex differences on proximity, grooming, play and dominance behaviours are briefly discussed as a background to the use of these measures in the following studies. The rationale for the following studies is outlined, and some predictions made concerning individual differences in social behaviour patterns.

4.2 Traits as explanatory concepts

More recent attempts to clarify the epistemological status of the trait concept have focused upon the genetic and evolutionary basis of individual differences. Indeed, one of the characteristics of the concept of temperament is that it is largely inherited. Buss and Plomin (1975) for example, extended the early conceptualisation of Diamond (1957), who had suggested four basic components of temperament, thought to be common to all social mammals: fearfulness, aggressiveness, affiliativeness and impulsiveness. Buss and Plomin (1975) put forward the components of emotionality, activity, sociability, and impulsiveness (the latter dropped from their later models) as the basic units of temperament. Their criteria for this classification rested upon the description of these temperaments as stable, appearing early in development, and heritable (Buss and Plomin, 1986).

The relationship of basic temperament to the personality concept is an uneasy one, and the two concepts have been distinguished less clearly in nonhuman than in human studies (Clarke and Boinski, 1995). Clarke and Boinski (1995) define temperament as an expression of basic reactivity level; that is, how the organism reacts to novel stimuli or situations. By contrast, personality refers to specifically social ways of responding, often described by using human trait terms. While there have been fruitful attempts to relate temperamental dimensions like 'highly reactive — unreactive' to individual variation in physiology (e.g. Suomi, 1991), or to differences between populations (e.g. Martau *et al*., 1985), ultimate (and even proximate) explanations for more complex trait ratings have not been easy to identify. While personality trait terms appear useful in describing individual variation, the adaptive value of particular traits has not been clearly identified.

One of the main reasons for this problem lies with the explanatory status of traits; more specifically, the level of explanation at which traits exist. Within psychology, trait names are used to refer to 'dispositions'; i.e. tendencies to behave in particular ways. At one extreme, dispositions or traits may simply be hypothetical concepts that happen to be useful for summarising patterns of behaviour. Thus Mason (1971) defines traits as "dispositions to display behaviors that appear to be functionally similar." (p. 6). For Mason, trait terms "refer to hypothetical processes that are inferred from differences between entities along some dimension.....such differences will be consistent across time and situations." (p.6). At the other extreme, traits may be afforded causal status (e.g. Allport, 1961). From this perspective, variation between individuals is caused by latent underlying dispositions. The validity of this position is problematic. As Harré (1998) points out, dispositions are (logically) unobservable properties of an object. Thus higher order dispositions like traits may be classificatory, but they cannot be explanatory. Harré describes traits as 'taxonomic concepts'; relegating them firmly to a descriptive, rather than an explanatory status (Harré, 1998, p.80).

4.3 The relation between personality ratings and behavioural observations

The complex theoretical status of trait ratings does not necessarily detract from their utility in human and nonhuman studies. Both formally and casually, many people who work with animals already utilise personality trait terms. The relationship between personality ascriptions and behavioural observations is therefore important, and the investigation of how the two domains interact is likely to clarify both types of procedure.

One of the problems with earlier personality work was the assumption that there would be a clear linear relationship between trait scores and measures of discrete behaviours, fuelled by the notion of traits as causal entities (Waters, 1981). Early criticisms of the trait concept focused upon poor cross-situational consistency in ratings (Mischel, 1968), but later work began to identify some of the personal and contextual factors that affect behavioural consistency (e.g. Bem and Allen, 1974). The more sophisticated interactionist approach that resulted attempted to describe the complex ways in which situational factors influence the expression of personality (e.g. Endler and Magnusson, 1976).

However, the precise nature of environmental influences on development, and the interplay between contextual and individual characteristics, may be difficult to identify. Even apparent discontinuities in behavioural development, e.g. the sudden appearance or disappearance of a behaviour pattern, may be difficult to interpret in terms of underlying structure (Bateson, 1981; Hinde and Bateson, 1984, but see Pereira's (1995) analysis of growth patterns and dominance). Internal characteristics of the organism may find expression in many ways, and may be 'masked' by environmental changes. As Hinde and Bateson express it:

> "The importance of context suggests that the concept of psychological structures more or less isomorphic with behaviour is misleading. We are concerned not with static entities whose effects (or images) appear as invariant action but with *propensities whose interactions with each other depend on conditions operating at the moment.*" (1984, p. 137, emphasis added)

What this means for the study of individual differences is that we must expect complex correlations between different behaviours, or between the same behaviours at different times. In the words of Sroufe (1979) we must search for "coherence across transformations" rather than expecting simple relationships between discrete behaviours and the kind of global, holistic estimations of behavioural style that raters typically provide. Identification of psychological continuity underlying different behaviour patterns may only arise through a consideration of different levels of social complexity (Hinde, 1992).

It is clear that an adequate account of individual differences requires a rationale for linking ratings to behaviours, and an acceptance of the potential complexity of this relationship. It is therefore important to understand the processes of interpretation that characterise both ratings and observations. Traditionally, personality theorists have distinguished between implicit theories of personality, and explicit personality theories. One criticism of rating scales is that they merely reflect the raters' implicit theories; that is, they are subjective, biased estimates of personality differences. Observational ratings, by contrast, have often been assumed to be less prone to bias, and better estimates of individual differences. The relationship between the two sources of information may be more complex however.

One important comparison between the two sources of information is the extent to which they reflect different sources of variation (Cairns and Green, 1979). For instance, ratings may be affected by biases and dispositions of the raters, but the rating process also requires complex judgements regarding which characteristics of the subject are stable and which are temporary. In addition, raters must attempt to provide a global estimate of personality based upon many disparate sources of information, and make appropriate decisions about the quality of that information. For example, it is assumed that the rater will base his/her ratings upon relevant aspects of behaviour, and that individual ratings are produced by comparison with an appropriate population. In contrast, behavioural observations are assumed to rely less on processes of judgement than on accurate recordings of actual behaviours. In addition, the initial stages of observational recording typically do not distinguish between aspects of behaviour that may be stable or temporary, or between behaviours that might be idiosyncratic or representative of the group (Cairns and Green, 1979).

There are thus important differences in how the rater/observer filters and interprets information during the process of rating/observing individuals. As Cairns and Green point out, however, the two processes do share some important aspects. Thus observations can also be subject to the bias of the observer, and ratings may also incorporate interpretations of behaviour and intentions. What is clear is that both processes depend upon recognition and interpretation of contextual sources of variation that may be important sources of influence upon behaviour. Cairns and Green suggest that observations and ratings may in fact be ends of a continuum, rather than qualitatively separate processes. Constructivist approaches to personality (e.g. Kelly, 1955) emphasise that personality ratings incorporate multiple sources of information, including rater biases, memories of behaviour patterns, and contextual information. However, personality judgements should be considered as more than an amalgamation of 'subjective' and 'objective' information. To the extent that an individual's personality is 'constructed' from diverse sources of information, reflected in traits at one end of the continuum and behaviour at the other, then personality may best be understood as an expression of relationships.

4.4. A relationships approach to personality differences

It is clear that trait ratings and behavioural observations, though interdependent, may actually reflect different aspects of the individual, and can involve qualitatively different processes of estimation. If this is the case, then meaningful correlations between the two procedures may only appear if the appropriate measures are compared. That is, trait-behaviour correlations may be weak if the 'wrong' measures are correlated.

The extent to which several different measures of an individual's personality and behaviour should relate is not necessarily easy to determine. Personality ratings often involve a consideration of the 'behavioural style' of the individual, and this may relate more to the perceived/assumed function of behaviour (as well as the motivation behind that behaviour) than to the actual content of the behaviour. Thus assessments of personality are likely to involve many different types of variables, or measures, and the relationships between these measures may change over time (McCall, 1986).

Within this context, the conceptual framework suggested by Hinde (1976, 1979a, 1979b) may prove to be useful. Hinde outlined several interdependent levels of analysis which together comprise the social structure of a species. Hinde and his colleagues have successfully analysed individual differences within the context of this framework, and a brief outline of the approach is provided here.

4.4.1 Hinde's levels of analysis

In a number of papers, Hinde and his colleagues suggested the utility of a multilevel conceptual framework to understand social behaviour of primates (e.g. Hinde, 1976, 1979a; Hinde and Stevenson-Hinde, 1976). The framework encompasses three levels: interactions, relationships and social structure. These levels are mutually interdependent, but provide distinct ways of conceptualising and analysing social behaviour.

The most basic components of social structure are interactions (dyadic or polyadic) between individuals. Important characteristics of interactions include the content of the interaction (what individuals do together), the diversity of the interaction (how many different things they do together) and the quality of the interaction (e.g. do they play gently or roughly) (Hinde, 1976). The frequency, and type, of interactions that individuals perform may be influenced by a number of factors. For instance, some types of interactions may occur in only some classes of individuals (e.g. suckling behaviour is only apparent in mother-infant interactions). An important aspect of the study of interactions, therefore, is a consideration of the relationship within which those interactions occur.

Relationships describe a series of interactions between individuals over a time period. In addition to the content and quality of the interactions, their temporal patterning is considered (Hinde, 1976). Thus, the meaning of a particular interaction may involve not only what each animal does (content), and how they do it (quality), but when, and in what context, each behaviour is performed. This can often be understood only by a consideration of the long-term relationship between the participants, particularly where more subtle behaviours are concerned. For example, the "separating interventions" described by de Waal (1982) in which one chimpanzee repeatedly interrupts proximity between a rival and his partner, can only be understood within the framework of status relationships (and possibly also a model of primate social cognition) (de Waal, 1982; see also Kummer, 1974).

One important characteristic of relationships is that of dynamic stability (Hinde and Stevenson-Hinde, 1976). Since relationships are comprised of relatively long-term interactions, behavioural indices of relationships may remain stable or they may change progressively over time (Hinde and Stevenson-Hinde, 1976). In fact, one way of viewing the notion of relationships is as intervening variables, describing patterns of interactions, or potential patterns of interaction. In this sense, a relationship between two individuals may change over time to include many different behaviours, whilst still retaining some aspect of continuity.

Hinde's notion of social structure incorporates the conceptual levels of interactions and relationships. Just as a study of relationships involves principles that arise from interaction data, a consideration of social structure must focus on the characteristics of the relationships within a group, including the interactions that constitute those relationships. Thus the study of social structure focuses on the content, quality and patterning of relationships (Hinde, 1976), and on the processes that determine those relationships (Hinde, 1995).

4.5 Personality differences and social relationships

Research suggests that the social interactions of nonhuman primates may involve complex memories for previous interactions, an understanding of at least some aspects of relationships like status (de Waal, 1986b; Dasser, 1988; Cheney and Seyfarth, 1990) and an ability to manipulate the social relationships of others (Whiten and Byrne, 1988). Thus the complexity of chimpanzee social behaviour suggests that a focus on relationships, as a context within which to study social behaviour, may be useful.

Stevenson-Hinde has suggested that behavioural measures may in fact lie on a continuum, with one end of the continuum relating more to individual characteristics like temperament, and the other end relating more to characteristics of relationships (Stevenson-Hinde, 1985; Stevenson-Hinde and Hinde, 1986; Hinde, 1992). This is a useful perspective from which to consider personality, as it avoids the problematic notion of invariant aspects of the individual (e.g. inherent traits) and the expression of these in discrete behaviours. In fact it may be more useful to hypothesise a range of personality characteristics that relate in different ways to aspects of relationships. For example, the characteristic of 'activity' may be more an aspect of the individual, whereas 'negative mood' may relate more to aspects of a relationship (Stevenson-Hinde, 1985). While particular aspects of temperament (e.g. activity, fear) may be clearly linked to genetic components (e.g. Suomi, 1981), in primates it is likely that variation in other personality characteristics may be more influenced by social context, and expressed most clearly in the context of social relationships.

The process of examining individual differences within the framework of social relationships has a number of specific advantages. Firstly, it is likely that in neotonous social species individual development is closely tied to the nature of the individual's early social relationships. For instance, infant Japanese macaques were found to develop greater independence from their mothers at an earlier age the more close kin they had. This was particularly the case when the mothers were low-ranking or old (Gouzoules and Gouzoules, 1987). In humans, the development of a number of important abilities, and their subsequent expression, have been linked to the nature and quality of social relationships, from social competence and joint attention (Butterworth, 1995) to communication (Bateson, 1981), self-awareness and complex thought itself (Mead, 1934/1974; Vygotsky, 1930/1978). We can thus expect the individual's personality development to be similarly affected by its social relationships (Hinde, 1995).

Secondly, it is arguable that many personality descriptions are at root social characteristics. Buss, for instance, has argued that personality dispositions reflect social tactics and strategies (Buss, 1991). On a more pragmatic level, even trait terms which describe nonsocial characteristics or activities (e.g. tidiness) are still judgements that are made by a rater based upon their perception of the ratee. This means that the process of personality ascription involves at the very least the social relationship between the rater and ratee.

Finally, it is important to emphasise that, if personality is studied concomitant with social relationships, the enterprise of measuring individual differences becomes more tractable, through the identification of some important sources of variation. For example, the acknowledgement of the mutuality of behavioural interactions in a given relationship may make it easier to relate cross-situational or cross-temporal changes/continuities in behaviour to continuities/changes in the relationship (Auhagen and Hinde, 1997). This then provides an explanatory framework in which to study changes within the relationship, and their effects upon individual responses.

The dialectic between the individual and the relationship means that examining a number of relationships that an individual is involved in may illustrate a number of different aspects of personality (since a single relationship may only provide information regarding particular types of interactions/ behaviours) (Stevenson-Hinde and Hinde, 1986). In addition, the nature and content of a social relationship will be affected by the other relationships with which the participants are involved, such that social behaviour within a relationship is dynamic. The dynamic nature of an individual's social life, and the influences of age, sex and status need to be examined and understood before the nature and significance of stable individual characteristics can be identified.

4.6 Personality differences and relationship measures

The expression of personality characteristics within a relationship may involve some aspects of the relationship and not others. It may be more meaningful, for instance, to consider the quality and patterning of interactions within a relationship, rather than to focus on content (Stevenson-Hinde and Hinde, 1986). In terms of measurement, this suggests that simple frequency measures may be less informative than relative frequencies, the proportion of events in relation to other events, and sequential relations between different types of interaction (Hinde, 1979b).

There are several aspects of behavioural interactions that can be considered to be aspects of relationships, and which may provide relatively subtle indices of personality differences of interactants; the outlines below are based on Hinde (1995).

1. The diversity of the interactions within a relationship, i.e. the types of activities that the participants do together, illustrates the nature of the relationship. The more diverse the interactions, the more information is provided about the personalities of the interactants.

2. The relative frequency and patterning of interactions is an important estimate of the nature of the relationship. One aspect of this is the relative frequency with which individuals initiate actions, and the patterning of interactions over time. For example, knowing the frequency with which an animal is aggressive is less useful than knowing how often that individual initiated the aggression, and what sort of behaviour, if any, the aggression was a response to.

3. The reciprocity and complementarity of the relationship. In reciprocal relationships, both participants do similar things, in complementary relationships the interactants behave in different, but complementary ways. Some relationships are mostly reciprocal (e.g. playmates); others are mostly complementary (e.g. mother-infant; dominant-subordinate). Many relationships involve both aspects, and to the extent to which principles like dominance organise behaviour, reciprocity and complementarity are important aspects of a relationship.

4. All of the relationship characteristics described above can be seen to be indications of the quality of a relationship. Relationship quality is a somewhat ephemeral concept to operationalise, but the indices above may provide useful tools. What is clear is that assessment of the quality of a relationship may be difficult using simple behavioural measures. In addition, it is likely that such assessments involve attributions of motivation and intention, and so the inter-observer and temporal reliability of such evaluations of relationship quality may be complex. For this reason, however, behavioural data that relates to quality of the relationship may be more suitable for comparison with trait ratings. Even though such ratings may not explicitly incorporate aspects of relationships (Stevenson-Hinde, 1985), such information may be implicit within rater judgements. Therefore,

the complexity inherent in personality ratings may be better reflected in measures of social relationships.

4.7 Sociodemographic variables and personality

The effects of important sociodemographic variables like sex and age are often seen as constraints upon the expression of personality. However, if personality differences are described and explained within the context of social relationships, then these factors must be seen as partly responsible for shaping the development of the individual's personality over time. Thus, certain aspects of the personality may be a function of age/sex/status specific behavioural interactions. If individual differences are adaptive they should be expected to relate to these life history variables in meaningful ways (Clark and Ehlinger, 1987). Thus Altmann's (1980) study of maternal 'style' in baboons highlighted the relationship between individual behavioural strategies and status. The 'restrictive' baboon mothers she described were more likely to have infants that were not predated or kidnapped at an early age, whereas the infants of more 'laissez-faire' mothers ran the risk of these dangers. The infants of laissez-faire mothers, however, achieved independence more quickly than those of restrictive mothers. The status of the mothers was seen to interact with the mothering style; the infants of high status mothers were less likely to be kidnapped or predated, so for high ranking mothers a laissez-faire style would be more adaptive, as it would allow their infants to develop more quickly. For low status females, a more restrictive mothering style would be more adaptive.

Relationships between mothers and their infants are useful in highlighting the ways in which life history variables might interact with personality, as such relationships are typically long-lasting. It is in such studies that the effects of sex, age and status can be closely studied within the dynamics of a close relationship. In addition, detailed study of such relationships can help to determine the relative contribution of the individual characteristics of both participants to the relationship. Hinde and White (1974) examined differences in ventro-ventral contact between rhesus mother-infant pairs. Their data suggest that differences between pairs are not necessarily due to differences in mothers, or differences in infants.

Rather, individual characteristics of mothers and infants interact in complex ways, and their observed effects depend on the behaviour studied, and on the age of the infant. For instance, for young infants, it is the mother who is primarily responsible for the amount of ventro-ventral contact; as the infant gets older he/she becomes more responsible for contact. Thus early on, we might expect contact to be more affected by individual differences between mothers. However, the personality of the mother is itself affected by the relationship with her infant. A mother may behave differently towards a male infant than towards a female infant; Stevenson-Hinde and Hinde (1986) found that in humans, ratings of 50 month old girls on the characteristics 'active', 'intense' and 'shy' were more closely related to mother-infant interactions than the same characteristics in boys, although this was not the case for ratings of 'moody'.

The extent to which particular behavioural measures relate to personality ratings may therefore be influenced by the effects of variables like sex, age and status. In order to assess the extent and importance of individual differences in behaviour, species-typical behaviour patterns for different age/sex classes need to be considered. In addition, these behaviour patterns must be seen as relationship measures, since they derive their structure, patterning and meaning from the relationships in which they are expressed.

4.8 Behavioural measures of personality differences: variation in behavioural strategies

The dynamic nature of personality and social relationships necessitates detailed, ideally longitudinal, observation of many aspects of social behaviour. This is something that personality researchers are rarely able to provide for large numbers of individuals; often the emphasis is placed upon obtaining less detailed data for larger numbers of individuals, in order to develop models of personality that can generalise to larger numbers. However, where an emphasis on relationships has structured personality work, as in the studies on personality characteristics of children at home and at school (e.g. Stevenson-Hinde and Hinde, 1986; Hinde and Tobin, 1986) the findings have yielded more sensitive measures of individual characteristics and their interaction with environmental effects.

In order to further examine personality differences between individuals in the Chester group, a focus on the characteristics of relationships detailed by Hinde was adopted. A range of behavioural measures were used to study the content, the quality and the patterning of a number of social relationships, and these measures were compared to the trait ratings previously collected. The following section summarises the research literature on the social behaviours of interest in this study: proximity, grooming, play, and conflict. The aim is not to provide a comprehensive overview of each of these research areas, but to highlight the basic patterns of behaviour involved, and to outline how these behaviours interact with age and sex differences. The behavioural measures derived from these descriptions are then presented in section 4.9, together with an indication of how personality trait ratings might be expected to relate to behavioural differences.

4.8.1 The role of social structure

The nature and properties of both interactions and relationships are a result of two dialectics: one with the characteristics of the individuals, the other with the nature of the social situation (Stevenson-Hinde and Hinde, 1986). The network of relationships that comprise the social structure of a primate group are thus determined and limited by that structure itself. Each relationship is embedded within a network of other relationships, and its nature must be analysed within this larger context to be fully apparent. Similarly, the interpretation of a behavioural interaction must refer to the behavioural propensities of the participating individuals as members of particular age/sex classes (Hinde, 1976). In fact, one way of describing individual differences is as limitations to the flexibility an individual can show (Clutton-Brock and Harvey, 1976; Caro and Bateson, 1986; Auhagen and Hinde, 1997).

The specific age, sex or status of a given individual may therefore function to, at least partially, explain individual differences in behaviour across these sociodemographic categories. Within these categories, however, there may be substantial individual variation, that may or may not be adequately explained as alternative behavioural strategies. However, the extent and function of individual differences in social behaviour becomes clearer as a result of a relationship perspective, as individual responses can be compared to the norm for specific sociodemographic groups. Thus the nature of the social structure acts as a framework within which to describe and explain differences in relationship characteristics, just as these relationships contextualise the nature of the behavioural interactions that signify them.

4.8.2 Patterns of association

A basic characteristic of social relationships concerns the amount of time individuals spend in each other's proximity. In wild chimpanzees, the fusion-fission structure of the society means that individuals spend most of their time travelling and foraging in small, temporary parties and the whole group may only meet at certain times, e.g. when a particular food source is available (Goodall, 1986). Captivity obviously places constraints upon these natural association patterns; even in large enclosures, captive individuals are likely to experience at least a greater opportunity to interact more, and with a larger number of individuals.

The variation in basic sociality levels, and in number of social relationships formed, may thus be a function of age/sex class. For instance, association indices of male and female chimpanzees in the wild and in captivity suggest very different patterns of interaction for the sexes. Adult females spend much of their time with dependent and juvenile offspring, and interactions between adult females in the wild are typically infrequent (Wrangham and Smuts, 1980; Goodall, 1986). Adult males, however, associate mostly with other adult males and cycling females. While these association patterns remain unchanged for captive males, rates of proximity and grooming in females are much higher in captivity than in the wild (de Waal, 1994). The artificial nature of the captive colony increases sociability levels for females and permits the formation of strong adult female-female relationships; in addition females in captivity are more likely to form coalitions and to influence male status relationships (de Waal, 1994; Baker and Smuts, 1994; see also section 4.8.5).

Age also has an effect upon sociality patterns. Infants and juveniles of both sexes spend most of their time with their mothers, and at this stage the sociability levels of the mother can have an important influence on the developing levels of sociality of the offspring (Stevenson-Hinde *et al.*, 1980a), particularly in the wild when infants and juveniles may spend large amounts of time away from other group members if the mother is relatively asocial (Goodall, 1986). The presence of sibling relationships, however, can have an important effect upon the infant's social development. For instance, infant Japanese macaques with more close kin were found to develop much greater independence from their mothers at an earlier age, especially if the mother was old or low-ranking (Gouzoules and Gouzoules, 1987).

In adolescence, sex differences in association patterns become more striking; adolescent males gravitate towards the company of adult males and cycling females, while adolescent females continue to spend large amounts of time with their mother unless they are cycling (Pusey, 1990). The oestrus cycles in a group, particularly in captivity, can thus have a significant effect upon proximity patterns, with cycling females spending more time with adult males than anoestrus mothers, while adult and adolescent males both associate with, and compete for, females in oestrus.

An important aspect of any relationship is the extent to which it is reciprocal or complementary (Hinde, 1979b). One measure of the quality of a relationship is the extent to which various interaction measures are reciprocal. The nature and quality of the time that two individuals spend together will be affected by how much proximity is sought by both individuals (i.e. is reciprocal) rather than maintained by one or other partner (i.e. is complementary).

4.8.3 Grooming relationships

It is likely that grooming among primates serves a variety of functions, including removal of ectoparasites, reduction of social tension and maintenance of social bonds (Seyfarth, 1980). In both wild and captive populations, the variety of contexts in which social grooming occurs makes it likely that grooming patterns can provide an important source of information regarding the structure of groups and the nature of their social relationships.

As with most other social behaviours, study of grooming patterns shows interesting variation relative to age, sex and relatedness. In addition, the complexity of social grooming is revealed in comparison of a range of grooming measures, including the distribution of grooming between individuals in a group, the relative frequency and duration of grooming, and the patterning of grooming sequences.

Among Old World monkeys and apes, grooming tends to be distributed preferentially among kin (Gouzoules and Gouzoules, 1987), though in many species the status of potential grooming partners is also important. Thus any functional explanation of grooming may have to include the operation of alternative grooming strategies. For instance, Seyfarth (1976, 1977) examined the relative effects of status and kin relationships on the distribution of grooming in baboons, geladas, rhesus and stump-tailed macaques. In these species, it seems likely that two optimum strategies may underlie grooming patterns, such that animals may direct more grooming to close kin, but direct 'remaining' grooming to high ranking individuals (Sade, 1972; Stammbach, 1978; Dunbar, 1980; Fairbanks, 1980; Seyfarth, 1980, 1983; Silk, Samuels and Rodman, 1981). Thus individual variation in grooming may be related to basic relationship parameters like relatedness, although adequate functional explanations for such individual differences may remain incomplete due to the numerous aspects of relationships that may affect social primates (Simpson, 1973).

In chimpanzees, grooming occurs most frequently between mothers and offspring, adult males, and adult males and females (Goodall, 1968, 1986; Pusey, 1990). In the wild, levels of grooming between adult females are much lower than for adult males. A number of studies of wild chimpanzee and bonobo groups have identified differences between the sexes in both frequency and duration of grooming sessions. Adult male chimpanzees groom more frequently, for longer duration and have more grooming partners than adult females (Muroyama and Sugiyama, 1994). Higher male-male grooming in the wild may result from the need to forge cooperative bonds to manage intergroup and intragroup competition (Nishida, 1979; Goodall, 1986; Muroyama and Sugiyama, 1994). This is supported by the finding that grooming patterns among males may vary depending on levels of tension within the group (de Waal, 1982; Goodall, 1986; Muroyama and Sugiyama, 1994). In females such cooperation produces fewer benefits, so female grooming should be expected to be less variable (Muroyama and Sugiyama, 1994, but see Baker and Smuts, 1994). Instead, female rates of grooming may depend more on kin relations, although grooming among non-related females may be higher in captivity, as captive females have greater opportunity to form long-term associations (Goodall, 1986).

In addition to sex, the age of the individual can also influence the nature of his/her grooming relationships, although as Pusey (1990) points out, such differences in grooming behaviour may simply reflect differing opportunities to groom within age/sex specific social groupings. In wild groups, for instance, the fission-fusion structure of the group means that juvenile offspring and adolescent females in particular spend long periods of time with their mother, with less opportunity to groom other members of the group. In captivity, therefore, the artificial proximity of the whole group may increase both the variety of grooming partners and rate of grooming.

In both male and female chimpanzees, the nature and function of grooming appears to be associated with status, and the relative ranks of grooming partners may affect the incidence, duration, distribution and reciprocity of grooming bouts. In chimpanzees, most grooming occurs between adult males, and both adolescent and adult males preferentially groom older, high ranking males (Simpson, 1973; Pusey, 1978, 1990; Goodall, 1986; Kawanaka, 1990). Older and more dominant males are thus groomed more frequently, and for longer durations than adolescent males (who tend to be of lower status), and are more involved in grooming clusters than more peripheral adolescent males (Simpson, 1973; Pusey, 1978, 1990). However, frequency and duration measures of grooming amongst males are not always correlated, suggesting complex interactions between a number of factors. Thus Simpson's detailed study of male grooming relationships at Gombe suggested that competition between adolescent males may occur for grooming access to higher ranking males; so for some adolescents their grooming of dominant individuals was infrequent but was of long duration when it did occur. High status males, by contrast, manage to groom other high status males frequently, but the duration of their grooming sessions is shorter (Simpson, 1973), although Kawanaka (1990) found that the alpha males at Gombe associated most with males of declining rank, and groomed these males for long periods.

What Simpson's (1973) study also highlighted was the importance of the reciprocity of the grooming relationship, and he suggests that some differences between grooming pairs may depend more on characteristics of the individual, while other aspects relate more to characteristics of the pair. For instance, the median durations for which individuals groom appeared to be consistent, regardless of their grooming partner at the time. However, within these parameters the duration for which an animal groomed did vary according to how long their partner groomed in a particular session, i.e. reciprocal grooming sessions are longer than non-reciprocal sessions (Simpson, 1973; Goodall, 1986). The relative importance of individual differences to grooming behaviour may therefore depend upon an analysis of the interaction between basic measures like frequency and duration, as well as a focus upon the more subtle aspects of the grooming sequence (e.g. initiation, termination and patterning of grooming).

While the grooming relationships of juvenile and early adolescent females may centre around their family group, in older females their oestrus cycles bring them into closer contact with adolescent and adult males (Goodall, 1968; 1986). Late adolescent and adult females are groomed most by adult males, and for these females high ranking adult males seem to be the preferential grooming partners (Pusey, 1990). The effects of a female's oestrus cycle may be apparent in both male-male and male-female grooming relationships. Females may be groomed more by males just before, or during, their maximally tumescent period, and male-male grooming may increase at this time due to competition between males (Goodall, 1986; de Waal, 1986; Shefferly and Fritz, 1992).

The effects of dominance interactions on female grooming are less clear. Dominance relationships among females are less pronounced than between males (de Waal, 1982, 1993b; Goodall, 1986), though in unstable social groups, and in captivity, female-female relationships may resemble those of males' more (Baker and Smuts, 1994; see section 4.8.5 below). The increase in proximity among females in captivity may be associated with higher rates of grooming, since these two measures are usually related (e.g. Simpson, 1973; Seyfarth, 1980). In addition, changes in social structure in captivity, such as fluidity in the male hierarchy, may be expected to affect the relationships between females (discussed further in Chapter 7).

4.8.4 Social play

Among chimpanzees, there can be substantial variation between individuals in the frequency with which they play, and in the nature of their play behaviour. Some of this variation is due to age differences. In chimpanzees, play occurs most frequently between mothers and offspring, and between juveniles, particularly between individuals of the same sex and age (Goodall, 1986). The frequency and duration of peer play increases as the infant gets older, and peaks between two and four years of age (Goodall, 1968). The nature of play behaviour also changes with age; older infants and juveniles and adolescents engage in rougher, more aggressive play sessions (Pusey, 1978, 1990; Goodall, 1986).

By the time individuals reach adolescence, the amount of time spent in play declines, even when these figures are corrected for the possibility that older individuals spend less time with potential play partners (Pusey, 1990). As with social grooming, the frequency with which individuals initiate interactions varies. Pusey (1990) notes that adolescents ignore play invitations more than animals of other age classes. Among adults, play between males and females may be initiated more by males, and may be more frequent than female-female play (Goodall, 1986), although this pattern may be different for captive groups. Lee (1983) noted similar sex differences in vervet play, but suggests that the difference may be because the age decline in play occurs earlier in females than in males.

There has been much debate about the precise function of social play (e.g. Bekoff and Byers, 1985; Rosenberg, 1996), but it is likely that the development of social play is an important indication of the nature and quality of social relationships (Dolhinow and Bishop, 1970; Lee, 1983). The more aggressive play patterns used by males may help to develop the skills used in dominance behaviours; the more gentle 'approach-withdrawal' play in females may be useful in later development of caretaking skills (Cheney, 1978; Lee, 1983). For both sexes, however, the timing of the development of play behaviour and the responsiveness of an individual to others in play sessions may be an important part of the ability of an animal to manage social relationships (Lee, 1983; Goodall, 1986). As such, the development of play behaviour may be related to the development of other social skills, and may be expected to show individual variation.

4.8.5 Dominance relationships

Among group-living primates, dominance relations play an important role in the structure and functioning of the group. The attainment and possession of social dominance may lead to increased reproductive potential by the acquisition of resources such as food and mates (e.g. Fedigan, 1983). However, in many primate species the complexity of the interactions between social, demographic and ecological factors make it difficult to identify simple functional relationships between rank and resource acquisition (de Waal, 1989a; Pereira, 1995).

De Waal (e.g. 1986a, 1986b, 1989a, 1989b, 1992, 1996) has emphasised the importance of a 'relational' approach to social dominance in primates, that moves beyond an explanation of dominance as simply a means to acquire resources. From a relational perspective, dominance hierarchies function to ensure the cohesiveness of the group in the face of conflicting interests between individuals. Social conflict, within the bounds of hierarchical relationships, thus becomes a means of managing social relationships. In chimpanzees, a relatively egalitarian dominance hierarchy exists which incorporates a substantial amount of flexibility (de Waal, 1989a). For instance, subordinate individuals can often dominate higher ranking animals in certain contexts, or in the presence of specific others (e.g. kin, non-related allies).

The complexity of primate dominance relationships, particularly in species like chimpanzees, who form symmetrical social relationships, necessitates an awareness of the heterogeneous nature of social conflict. The dominance relationship between two individuals can be expressed through a variety of proximate mechanisms: including formal dominance, agonistic dominance, coalitions, social tolerance, reassurance, reconciliation and appeasement (de Waal, 1982, 1986a, 1986b, 1989b, 1996; de Waal and van Roosmalen, 1979). Descriptions and explanations of dominance relationships in chimpanzees probably also should incorporate motivational and cognitive factors (e.g. de Waal, 1982, 1989b) for a complete account. Where social relationships are complex, such assumptions are often inherent in their explanations. Thus an awareness of dominance relationships, and an expectation of what others might — or should — do, may suggest that chimpanzees 'negotiate' their relationships, conflictual or otherwise (Hinde, 1976; de Waal, 1996). That is, behaviour towards a conspecific may be structured within the constraints of the relationship, as when a dominant animal displays tolerance to a subordinate in a competitive feeding situation (e.g. de Waal, 1989a).

If dominance behaviour functions according to the demands of particular relationships, then these relationships must be described and understood in order to chart the dynamics of dominance hierarchies. Indeed, while the concept of dominance may usefully summarise the patterning of both affiliative and agonistic interactions between a dyad (e.g. by relating the direction of grooming to their relative dominance ranks), these interactions are often the product of a relatively long history of association and must be understood within the larger context of the patterning of social structure (Hinde, 1978).

Perhaps more than with any other behaviour, then, the analysis of dominance merits a multi-level approach. The multi-faceted nature of the dominance concept is probably the main reason that it has proved so difficult to understand. While dominance has been shown to influence, and be influenced by, social structure and life history variables (e.g. Pereira, 1995), the reproductive advantages of high rank vary across, and even within species, and in some species these advantages can be affected by factors such as alternative mating strategies and coalitions (Smuts, 1987). On the level of dyadic social relationships, the relative status of each individual affects the incidence and quality of almost all of their interactions, including affiliative ones like grooming and play (e.g. Simpson, 1973).

The patterning of dyadic interactions also affects, and is affected by, the identity and relationships of others in the group (Hinde, 1976). For instance, the presence of kin can significantly affect both the outcome of dominance interactions and the nature of long-term dominance relationships between individuals, most conspicuously in those species of Old World monkeys where females form matrilines (Gouzoules and Gouzoules, 1987). While dominance relationships in chimpanzees are not completely dependent on the support of kin, related individuals do support each other in agonistic encounters (Goodall, 1986). Pusey (1990) noted that chimpanzee adolescents of both sexes showed an increase in aggression directed towards others, but in females aggression occurred most when the female's mother was present. Goodall has documented the supportive relationship between two adult males at Gombe, which resulted in the younger male, Figan, achieving alpha position with the help of his brother Faben (Goodall, 1986).

Dominance interactions in both sexes can also be affected by female oestrus cycles. Conflict levels between males may be exacerbated by the presence of oestrus females, particularly if these are adult females, who are more popular mating partners (Goodall, 1986). Shefferly and Fritz (1992) found increases in male agonistic behaviours when greater numbers of females were maximally tumescent. In addition, increases in affiliative behaviours such as grooming, proximity and play were found, presumably as a means of reducing tension between the males (Shefferly and Fritz, 1992; see also de Waal, 1989b).

In any consideration of chimpanzee dominance behaviour, differences between males and females in the nature and quality of dominance relationships become apparent. De Waal (1982, 1989a, 1989b) has distinguished 'formal dominance' and 'agonistic dominance'. The latter refers to the actual outcome of agonistic encounters. The former concept describes the expression of uni-directional ritualised signals, in the form of bowing, bobbing movements and pant-grunts, directed by a subordinate individual to a dominant animal (de Waal, 1986a). Formalised dominance 'greetings' are often expressed in the context of group reunions in the wild (Goodall, 1986). These two measures of dominance may, or may not, covary. However, there tend to be stable differences between the sexes in both measures. Male chimpanzees are dominant to females, and engage in more agonistic encounters than females. Dominant males engage most in dominance displays, and receive most greetings from others. Females rarely perform dominance displays, and incidences of greeting rituals between females are rare (Goodall, 1986; de Waal, 1989a).

The central importance of the dominance hierarchy for males has been emphasised by many researchers (e.g. Bygott, 1979; Nishida, 1979; de Waal, 1982, 1989b, 1993b; Goodall, 1986). While the dominance hierarchy among males is not necessarily transitive it appears much more clear-cut than the female hierarchy. In addition, the incidence of agonistic coalitions and the frequency of conflict resolution mechanisms such as reconciliations are lower in females (de Waal, 1984, 1989b, 1993a). These differences may be explained by differences in life history strategies. Intragroup competition for females would lead to the development of agonistic dominance relations between males (Goodall, 1986; Wrangham, 1986; de Waal, 1989a, 1993b; Baker and Smuts, 1994). In addition, intergroup aggression requires that males also form strong bonds and manage conflict effectively. Females in the wild, by contrast, forage more widely than males and so experience less competition and have less need for a formalised hierarchy (de Waal, 1978, 1993b; Goodall, 1986).

While the effects of captivity may increase sociality of both males and females, for females captivity also appears to increase the tendency to form bonds and coalitions with other females, although frequencies of reconciliation behaviour are still more common among males than females in captivity (de Waal, 1989a). In addition, female dominance relationships of captive animals remain less hierarchical than those of males, with some females simply never engaging in social interactions (de Waal, 1989a, 1993b). However, it does appear that female dominance relationships possess the plasticity to adapt to changing social circumstances. Baker and Smuts (1994) compared female-female relationships in the Arnhem zoo colony with a recently established colony at Detroit zoo. The differences between male and female dominance relationships reported by de Waal for the Arnhem group were not apparent in the newly formed Detroit colony, which was characterised by a unstable social structure. In this group, females were found to engage in more conflicts over status than the Arnhem females and to reconcile more after conflict. The Detroit females also formed more coalitions (Baker and Smuts, 1994).

Baker and Smuts suggest that stable alliances usually exist between females in the wild in order to protect their core areas from younger immigrant females. Thus it pays females to form stable social bonds with other females, whereas the relationships between males are more fluid (e.g. Kawanaka, 1990). When the social structure is unstable, however (as in the Detroit colony) females will use the competitive strategies typically associated with males to forge a place in the competitive order. Even in stable groups, however, the effects of resource competition in the wild may be apparent in differences in the quality of conflict management displayed by females. Thus the nature, as well as the frequency, of coalitions may differ between the sexes in captive groups, with male alliances being more opportunistic and fluid, while those between females more stable (Baker and Smuts, 1994). It seems that dominance strategies are just as important to females as to males, but are structured by different competitive payoffs. There is thus a possibility that factors such as personality and personal preferences may feature more largely in female-female relationships than those of males (Baker and Smuts, 1994).

The importance of the quality of social relationships in understanding conflict behaviour has also been noted in research on reconciliations. This behaviour refers to the tendency for individuals to seek contact with each other following a conflict episode (de Waal and van Roosmalen, 1979; de Waal, 1989b, 1993a; Kappeler and van Schaik, 1992), and is not unique to primates (Castles, Aureli and de Waal, 1996). The frequency with which individuals reconcile after conflict has been explained by reference to the quality of their relationship (de Waal and Yoshihara, 1983; Aureli, van Schaik and van Hooff, 1989). In addition to the 'relationship quality' hypothesis, variation in the tendency to reconcile has been linked to rates of grooming, intensity of aggression and directionality of approach behaviour: the 'systematic variation' hypothesis (de Waal and Luttrell, 1988; de Waal, 1989a). What is clear is that the quality and patterning both of dyadic relationships and group structure is important to an understanding of this complex behaviour. Moreover, the relationship between these two levels can vary even within a particular species. Castles *et al.* (1996) examined the systematic variation and relationship quality hypotheses by comparing rates of reconciliation across two groups of captive pigtail macaques: one group was newly formed, while the other group was formed in 1963. In both groups, rates of reconciliation occurred most between individuals with stronger affiliative bonds, while other social variables, such as approaches, allo-grooming and aggression, did not vary between groups. Affiliative bonds differed, however, between groups. Individuals in the older group focused their affiliative behaviour (including reconciliations) among a smaller number of animals than did individuals in the newly formed group, suggesting that affiliative ties in the older group were more intense (Castles *et al.*, 1996).

4.9 Behavioural definitions and derived measures

The aim of the studies presented in Chapters 6 and 7 is to determine relationships between personality ratings and social interaction patterns. The analyses presented in Chapter 3 identified four personality factors: Sociability, Dominance, Anxiety and Curiosity, and factor scores for each of the chimpanzees have been derived from these. Ten focal individuals have been chosen for comparison, in order to examine their affinitive and agonistic social interactions in some detail and to place these interactions in the context of specific relationships.

The aim is to attempt to show how personality ratings relate to the content, quality and patterning of an individual's social relationships, and the measures appropriate to these levels of interaction are briefly outlined below.

4.9.1 The content of the relationships

At this level of analysis, each individual's social interactions will be summarised by reference to its levels of proximity, grooming, play and conflict. Since the interactions that an animal engages in may differ according to the identity of the interaction partner, these data will be placed in the context of each animal's social relationships using sociograms and other related measures.

4.9.2 The quality of the relationships

According to Hinde (1976) it is the more detailed assessments of the quality and patterning of social interactions that more easily relate to personality differences. The quality of a relationship is difficult to measure, and may relate less to a single measure and more to the covariance of a number of different characteristics, like timing and reciprocity (Hinde, 1995).

In Chapters 6 and 7, measures related to the quality of each individual's affinitive and agonistic interactions are presented; these include the reciprocity of grooming and play bouts, and the role of the focal individual in initiating and terminating interactions.

4.9.3 The patterning of the relationships

As well as measures of diversity and reciprocity of interactions, measures of the patterning of interactions can be an important source of information about the quality of the relationship, and the relative role of each individual. In Chapter 7, data are presented on conflict episodes. Each conflict interaction is described with reference to the role of each focal individual. Agonistic dyads involving the focal animals were analysed to show the role of each animal in the escalation and de-escalation of the conflict.

4.10 Predictions of trait — behaviour relationships

Although factor scores on Sociability, Dominance, Anxiety and Curiosity are expected to relate in meaningful ways to the behavioural measures, these correlations are not likely to be simple. For example, although scores on Sociability might reasonably be expected to relate to the amount of time an animal associates with others, the extent to which the target animal initiates those interactions may be a more useful indicator. Inevitably, predictions of behaviour from trait ratings entail difficult questions about the causal status of traits. It is tempting to conceptualise trait ratings in terms of motivational differences between individuals, e.g. Dominance factor scores might be assumed to reflect individual differences in the 'drive' to dominate others. This assumption may lead to simplistic predictions, however; variation in dominance behaviours may be due instead to differences in more generalised temperamental modes of responding to stressful events (Mason, 1993), and so may relate more (or at least as) closely to Anxiety scores. Thus trait scores may relate to more than one situation and be expressed in a variety of disparate, though functionally related, behaviours. The trait-behaviour correlations presented are thus interpreted as suggestive of the relationships between personality ratings and social behaviour patterns, rather than as constituting any explicit evidence of causal, underlying traits or mechanisms.

Chapter 5 presents details of the sampling and recording methods used to collect the behavioural data and definitions of the behaviours recorded. Chapter 6 compares patterns of affiliative behaviour (proximity, grooming and play) with personality factor scores. Chapter 7 discusses individual differences in agonistic interactions within the context of the dominance relationships in the group.

CHAPTER FIVE

Observational methods and behavioural definitions

5.1 Study site and selection of sample

The behavioural data were collected from the Chester zoo group of chimpanzees. Details of the site and housing conditions have been given in Chapter 2. Biographical details of the Chester group can be found in Appendix II.

Eleven individuals were originally chosen as observation targets, from a possible 28 individuals. A relatively small sample was chosen in order to focus in detail on the social relationships of each individual. Each of the males in the group were observed, as there are only five of them (although this is an usually large sample of males in a captive group). To select the female focal animals, several things were taken into consideration. It was decided that adults and adolescents, rather than infants and juveniles, would provide the widest range of behaviours to relate to the trait ratings. In addition, the personality profiles of each animal were examined and those individuals with interesting profiles were favoured as focal targets.

The final sample consisted of eleven individuals. After the first few weeks of observation, one adult female, Halfpenny, was dropped from the sample, leaving ten focal animals. Initial observations indicated that Halfpenny's behaviour was significantly altered as a result of her care of her infant Kiki, who suffers from cerebral palsy. In particular, her involvement in conflicts, and her general sociability levels, have dropped since the birth (see 3.3.9).

Observations took place in the indoor hall and the outside island, depending upon the time of year and on the weather. For most of the time, the animals have free access to both areas. If the weather is exceptionally cold they are restricted to the indoor area. In the summer months, most individuals spend the majority of their time outside, and in the winter months they spend much of the time inside. Since the study period covered nine months of the year, each focal animal was observed for approximately equal amounts of time in both areas.

Ideally, it would have been useful to compare data on behaviour patterns collected inside with data collected outside. Rates of grooming and aggression, for instance, might possibly be higher when animals were restricted to the inside enclosure. Times when animals were restricted to only the inside/outside enclosure were, however, rare during the study period, and when they happened the entire group was restricted in the same way. In addition, changes in rates of behaviour due to environment were not expected to significantly affect the overall rates recorded, since this was essentially a longitudinal study. Because this factor was not expected to affect overall rates of behaviour, reliable records of whether observation periods were inside or outside were not necessarily kept for all observations (though were noted for some). A possible problem may have arisen in comparing behaviour patterns for focals if specific individuals were observed exclusively in one environment. However, as discussed above, there were no obvious preferences for individual animals to spend more time either inside or outside, so all focals were observed for approximately equal amounts of time in both environments. In addition, weather patterns often influenced the behaviour of individual animals in a similar way; when it was warm the entire group was outside for most of the day, and conversely they all tended to stay inside in cold or wet weather. On the only occasion where one chimpanzee was separated from the rest of the group and restricted to the sleeping area, all data collection was suspended.

5.2 Study periods and observational methods

The ten individuals were observed for nine months from November 1998 to July 1999. Each individual was observed for a total of 20 hours, over three daily observation periods: 9.45am - 12.30pm, 12.30pm - 2.30pm and 2.30pm - 5.00pm. Each animal was observed for almost an equal amount of time in each period.

Focal animal sampling was used, and behaviours were recorded on checksheets. Each focal session lasted for a minimum of 20 minutes, and a maximum of three hours in any one day. The mean number of observation sessions for each focal animal was 24.6, and the mean duration of observation sessions was 50 minutes. Target individuals were selected semi-randomly before arrival at the zoo, and a different animal observed during each time period throughout the day. If an animal was asleep, or out of sight, then another was chosen. In the summer months, observation sessions were sometimes interrupted by public feeding of the animals. During these times, and when the animals were disturbed by other activities such as cleaning of the enclosures, focal observations were suspended until the disturbance was over. Towards the end of the study, preference for focals was given to animals who had been observed for the least amount of time. Throughout, observation sessions were allocated as evenly as possible for each animal, so that most of the time, all focal individuals were observed each week.

In addition, video recordings (a total of approximately 30 hours) were obtained of the whole group at two points in each day: during feeding time (2.00pm - 2.45pm) and before the chimpanzees went into the sleeping area in the evening (4.15pm - 5.00pm).

5.2.1 Sampling methods

Focal animal sampling was used together with all-occurrences and time sampling to record a number of social behaviours in the ten target animals. The measurement protocols can be summarised as follows:

Proximity	instantaneous time sampling (point sampling) all-occurrences of approach, leave and avoidance behaviour
Grooming	instantaneous time sampling all-occurrences of initiation, termination and invitation
Play	instantaneous time sampling all-occurrences of initiation, termination and invitation
Conflict	all-occurrences of conflict episodes

For the instantaneous time sampling, a small sample interval was chosen, as this is most likely to approximate continuous records (Martin and Bateson, 1995; Lehner, 1998). In order to determine the most appropriate sample interval for the behavioural states (proximity, grooming, play and time spent alone) a short video sample of each of the behavioural states was used to calculate duration using a continuous record. This was then compared to the measures of duration obtained using 15, 30 and 60 second sample intervals (Martin and Bateson, 1995). An interval of 30 seconds was chosen as the interval best approximating the continuous record.

5.3 Definitions of recorded behaviours

5.3.1 Proximity to others

The focal animal was classed as being in proximity to another animal if it was within one arm's reach of the other in the indoor house (Goodall, 1986). When the animals were observed on the outdoor island, however, the proximal distance was defined as two arm's reach. Outside, the distances between animals tended to be greater in general; thus, two animals who were clearly in proximity might not be within one arm's reach. All animals within proximity to the focal animal were identified on each sample point.

Approaches by other animals to within the proximal distance of the focal animal were recorded, and the identity of the individuals noted. Approaches by the focal animal were also recorded, together with the identity of the individual approached. Approach behaviour was defined as one animal moving within one arm's reach (or two arm's reach if outside), while the approached animal remains still. Instances where the focal animal left the proximity of another were noted, as were instances where another individual left the proximity of the focal animal. If the focal animal avoided another animal, or was avoided by another, this was also recorded. An animal was considered to have avoided another if the avoider left immediately (within one second) of being approached within one arm's reach (or two arm's reach if outside). Generally, it was easy to determine when an animal was deliberately avoiding another, and this usually occurred in the context of dominance interactions.

5.3.2 Alone

If there were no other individuals within these proximal distances of the target animal, then the animal was considered to be alone.

5.3.3 Grooming

Allo-grooming was characterised by a variety of grooming patterns and techniques, involving the searching and removal of dry skin and parasites. This process was often accompanied by grunting noises, tooth-clacking, lip-smacking and 'raspberrying'. The identity of the focal animal's grooming partner(s) and the directionality of grooming was recorded on each sample point. In addition, the initiator and terminator of each grooming session were noted, and grooming invitations, and who they were directed to, were recorded. Invitations involved presenting (of back, arm, or rump), scratching and 'head-bobbing'.

The criterion interval to define independent grooming bouts was 2 minutes (after Goodall, 1986). Pauses of less than two minutes were considered to be within-bout intervals, and pauses of more than two minutes were considered to constitute separate bouts. The exception to this definition was if a bout had been interrupted for a clear reason, for example, if a grooming dyad had ceased grooming to monitor an event such as a conflict, and the same partners had then resumed grooming. On these occasions the reason for the interruption was noted.

5.3.4 Play

Social play between individuals was characterised by behaviours such as chasing, tickling, nuzzling, biting and wrestling, including 'finger-wrestling'. These movements were accompanied by the 'play-face' and panting, 'laughing' vocalisations. The identity of the focal animal's play partners was noted, and the initiator and terminator of each play session. Play invitations were also recorded; these usually took the form of a play-walk toward the desired play partner, or head bobs accompanied by the play-face.

Play bouts were considered to be independent if they were separated by intervals of 30 seconds or more (after Goodall, 1986).

5.3.5 Conflict

A variety of agonistic behaviours was recorded and used to classify each conflict interaction. As de Waal and van Hooff (1981) note, the categorisation of agonistic behaviour patterns is not straightforward, since some behaviours may be emitted in more than one context; e.g. biting can be aggressive, or can be playful. The behavioural elements used here, and their definitions, are based upon van Hooff's (1974) factor analysis of chimpanzee social behaviour, and his subsequent definitions of agonistic behavioural elements.

Conflict episodes involving any of the focal individuals, or involving any other individuals in the group, were recorded ad libitum. When the conflicts involved other individuals, the behaviour of the focal animal was usually altered, or interrupted, during the episode. Pauses of less than 2 minutes were classed as interruptions in the conflict interaction. Where pauses were more than 2 minutes, this was defined as constituting separate conflict episodes.

During the focal observation sessions, conflict episodes were classified as they occurred according to whether they were Low-intensity (1), Moderate-intensity (2) or High-intensity (3) level conflicts.

- Low-intensity level conflict usually involved threat or very mild aggression. This definition included a variety of gestures, postures and vocalisations, including:

arm-raise threat	the arm is raised towards the target of the threat
hand-flap	brief hitting/slapping movement in the direction of the target
flailing	with a branch/other object toward the target
hunch	in either a sitting or quadrupedal position
bipedal swagger	swaying from one position, facing toward the target
brief chase	chases target for only a short way, often uttering grunt-barks or shrill-barks
vocal threat	grunt or grunt-barks (called cough-threat or soft-barks by Goodall (1968, 1986))

Threats would be accompanied by a low-closed grin, or a full-closed grin

(Goodall, 1986), or a compressed-lips face (in the case of the bipedal swagger or chase). Bristling of the hair might also occur in this context.

- Moderate-intensity level conflict was defined as a full chase, or bluff-over, or 'light physical assault' (Noë *et al.*, 1980). Sub-behaviours included:

tugging or hitting	when this behaviour is relatively mild, or evokes a brief response from the target
charging	usually performed as part of the charging display. During the vocal charging display, the charger displays towards, or through, one or several individuals, often uttering pant-hoots (Bygott, 1974, 1979). The display may incorporate stamping and slapping the ground or trees, and the dragging, flailing and throwing of branches, soil or other objects. The charger may hit others as he passes, but these attacks usually consist of mild slaps and are not sustained for any length of time. Alternatively, the charger may bluff over other individuals, or perform an 'arm-bluff' (where just the arm, and not the whole body, is thrown briefly over the target individual). Before and during a charging display, autonomic arousal produces bristling of the body hair.

- High-intensity level conflict was defined as attacks involving 'heavy physical assault' (Noë *et al.*, 1980).

hitting, trampling, kicking, dragging, slamming, biting, scratching, and wrestling	behaviours were deemed to constitute high-intensity conflict when performed in an agonistic, rather than play, context and when their performance elicited an intense response from the target.

charging	These behaviours were sometimes performed following a non-vocal charging display, where the charger would target a specific individual and direct an attack at them (Bygott, 1974, 1979). Such a display was often accompanied by the compressed-lips face.

Targets of mild, moderate or high intensity aggression would either retaliate with aggression, or exhibit submissive responses. Mild submissive responses included fear-grins or pant-grunts ('rapid oh-oh', Goodall, 1968, 1986) to a dominant individual. Moderate submissive responses included crouching, flinching and shrinking. Highly submissive responses to aggression included screaming, fleeing or throwing temper tantrums.

In addition to classifying the intensity of each conflict, the identity of all individuals involved in the conflict was recorded, and the initiator of the conflict (where apparent). Where the cause of the conflict could be determined this was also noted, and any explanatory notes that helped to elucidate the situational context.

During the afternoon feeding time, and before the evening feed, video observations were made of the group. At these periods, the levels of conflict in the group were usually high so these were good opportunities to obtain detailed behavioural records of agonistic interactions. During the afternoon feeding session, the main possible cause of aggression was competition over food. In the period leading up to feeding time, the anticipation within the group often led to high levels of social excitement, during which charging displays by the males were frequent. Similar levels of social excitement and displaying were observed during the second video recording period, before the evening feed.

One possible disadvantage of recording conflicts at these periods is that they do not represent the full range of social contexts within which conflict can occur. However, what they do provide is an opportunity to compare behaviour of each individual in a standard situation. In addition, it was found that most of the conflicts did occur in these periods; a large proportion of chimpanzee aggression seems to occur in the context of previous aggression (de Waal and Hoekstra, 1980), and these periods featured a large proportion of the polyadic conflict interactions observed.

5.3.5.1 Between-observer reliability of conflict behaviour

Inter-observer reliability was tested using a sample of the video-recorded data. It was thought to be important to test for reliability of the codings of conflict behaviour due to the large number of, often subtle, conflict categories used in this study. In addition, the categorisation of agonistic and submissive behaviours into different levels of intensity needed to be examined for reliability. Nine tapes were randomly selected, giving a total of nearly five hours of observation (295 minutes). Each tape was treated as a separate 'recording session'. Prior to recording, the second observer was given written definitions of each behavioural category, and shown a visual example of each behaviour from a separate tape that was not included in the subsequent reliability exercise. During each session, the frequency of low, moderate and high level conflicts was recorded by each observer, as well as the frequency of mild, moderate and highly submissive behaviour (see definitions of these categories above). In addition, both observers coded all instances of the following conflict-related behaviours: agonistic intervention, side-directed communication, semi-agonistic intervention, non-agonistic intervention, redirection and multiple initiation (see 7.3.1 for definitions of these).

Recorded frequencies of each of these categories across the nine recording sessions were compared using Pearson's product-moment correlation coefficient for a one-tailed test (N=9). Ten such comparisons were made (neither observer recorded any frequencies for the categories of redirection and multiple initiation). The Bonferroni correction for multiple testing was applied to the criterion alpha level of 0.05. The corrected alpha level was 0.005. Value's of Pearson's r for each behavioural category are shown in table 5.1.

Assuming that a Pearson correlation of 0.7 or above shows an acceptable level of reliability (Martin and Bateson, 1995), nine of the above correlations indicate good inter-observer reliability. With the exception of the category of side-directed communication, all values of r were significant at or below the corrected alpha level of 0.005.

The lower level of agreement found for side-directed communication is interesting. This is probably one of the most difficult set of behaviours to perceive without a great deal of experience, and the examples of this behaviour that occurred in this sample of video tapes were actually quite subtle. However, even for this category, a correlation of .66 indicates that nearly 44% of the variance is shared between the two sets of scores.

Table 5.1 Inter-rater reliabilities for agonistic behavioural categories*

Behavioural Category	Pearson's *r*
Low level conflicts	.84
Moderate level conflicts	.84
High level conflicts	.89#
Mild submissive responses	.99
Moderate submissive responses	1.00#
Highly submissive responses	1.00#
Agonistic intervention	.85
Side-directed communication	.66#
Semi-agonistic intervention	.77
Non-agonistic intervention	.88

*Scores on which these reliabilities are based are in Appendix X

It should be noted that the recorded frequencies were low for these relatively infrequent behaviours. These values have been included for the sake of completeness.

5.4 Additional recorded behaviours

During focal observations, all occurrences of pant-grunts between any of the individuals in the group were recorded as seen, and the directionality of these was noted. Any attempted matings or successful copulations that were seen were recorded, and the location of these matings noted (e.g. if they occurred out of sight of the other males). Where focal females were observed in proximity of their infants, suckling, carrying and ventro-ventral contact was noted.

CHAPTER SIX

Personality differences and affiliative relationships

6.1 Introduction

This chapter presents data on the affiliative behaviour patterns for the ten focal chimpanzees, and compares patterns of association, grooming and play with personality factor scores for Sociability, Dominance, Anxiety and Curiosity. A number of different social measures were employed, as it seems apparent that the variation that is captured in trait ratings involves global perceptions of many different facets of social life (Kelly, 1955; Hinde, 1976). For each behaviour pattern, a number of different quantitative measures were used. The complex ways in which social species interact with their (social) environment make it unlikely that simple trait-behaviour correlations will be found (Sroufe, 1979; Hinde and Bateson, 1984). Instead, individual differences are likely to be expressed most clearly in a range of relationship characteristics, including the content, diversity and patterning of specific social relationships (Hinde, 1976, 1979a, 1979b). In this sense, the 'personality' of an individual acquires meaning as one aspect of the way in which that individual conducts his/her social relationships. Thus, changes in personality over time and situations can more easily be understood as expressions of the dynamic nature of social relationships (Hinde and Stevenson-Hinde, 1976; McCall, 1986).

The range of behaviour, and its expression within particular social relationships, depends heavily upon an individual's age and sex. The relation of these factors to social behaviour is discussed in this chapter. Such factors should not be seen as constraints on the expression of personality; rather, they serve to focus and shape the development of an individual's personality over time, and they may provide important clues to the adaptiveness of particular personality differences (Clark and Ehlinger, 1987).

In addition to examining the content of each focal individual's dyadic interactions, this chapter attempts to analyse the quality of such interactions. Within an individual's nexus of social contacts, the diversity and reciprocity of social interactions can be important indices of relationship quality (Hinde, 1979a, 1979b, 1995; Stevenson-Hinde and Hinde, 1986). It is these latter aspects of relationships that may reveal more about personality differences, as they may be less constrained by the social limits on particular relationships.

6.2 Personality profiles

Factor scores for each of the focal animals are shown in Table 6.1. (These were derived from the factor analyses described in Chapter 3; see 3.3.4 for definitions of factor scores).

Table 6.1 Personality factor scores for focal chimpanzees

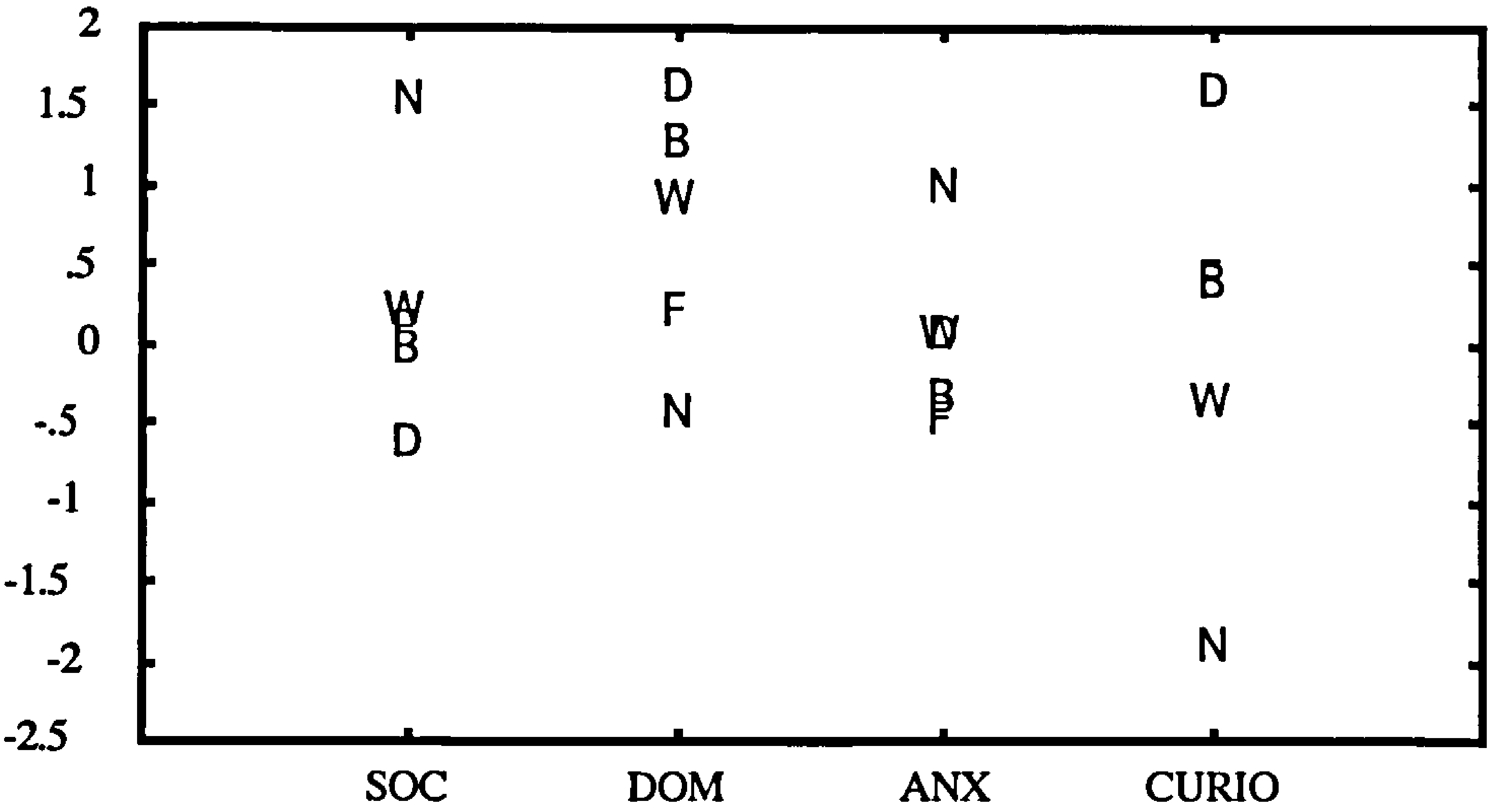
	Sociability	Dominance	Anxiety	Curiosity
Boris	-0.031	1.272	-0.333	0.403
Wilson	0.202	0.923	0.072	-0.352
Nicky	1.551	-0.443	1.002	-1.916
Friday	0.100	0.212	-0.462	0.437
Dylan	-0.618	1.634	0.084	1.587
Cleo	1.348	0.277	-1.347	0.196
Florin	-1.069	0.429	-0.591	1.403
Mandy	0.996	-1.369	0.408	0.226
Kankan	0.118	-0.092	-0.227	-0.522
Wanda	-1.081	1.097	-0.706	0.728

Some similarities between the personality profiles for the males are apparent from initial inspection of the factor scores. The Dominance factor scores are high for all of the males, although Nicky scores lower than most of the focals on this factor. Nicky's personality profile differs from the other males in two other respects: he shows a relatively high level of sociability and a low level of anxiety compared to the other four males. The similarity between the profiles of Boris and Dylan is interesting in the context of dominance relationships. Boris is the dominant male at the moment, but is under serious threat from Dylan for his alpha position. Both males score low on Sociability, and high on Curiosity and Dominance, though Boris has a lower Anxiety score than that of Dylan. The relation of personality to dominance is discussed more fully in Chapter 7.

Examining the factor scores for the females, it can be seen that the animals who score highest on Sociability are Cleo, Mandy and Kankan, while Florin and Wanda have relatively low scores on this factor. The animals who score highest on Dominance are Cleo and Florin; Cleo is actually the dominant female in the group at this time. Cleo also has the lowest Anxiety score, with Mandy scoring the highest of the females on this factor. All of the females except Kankan score reasonably highly on the Curiosity factor.

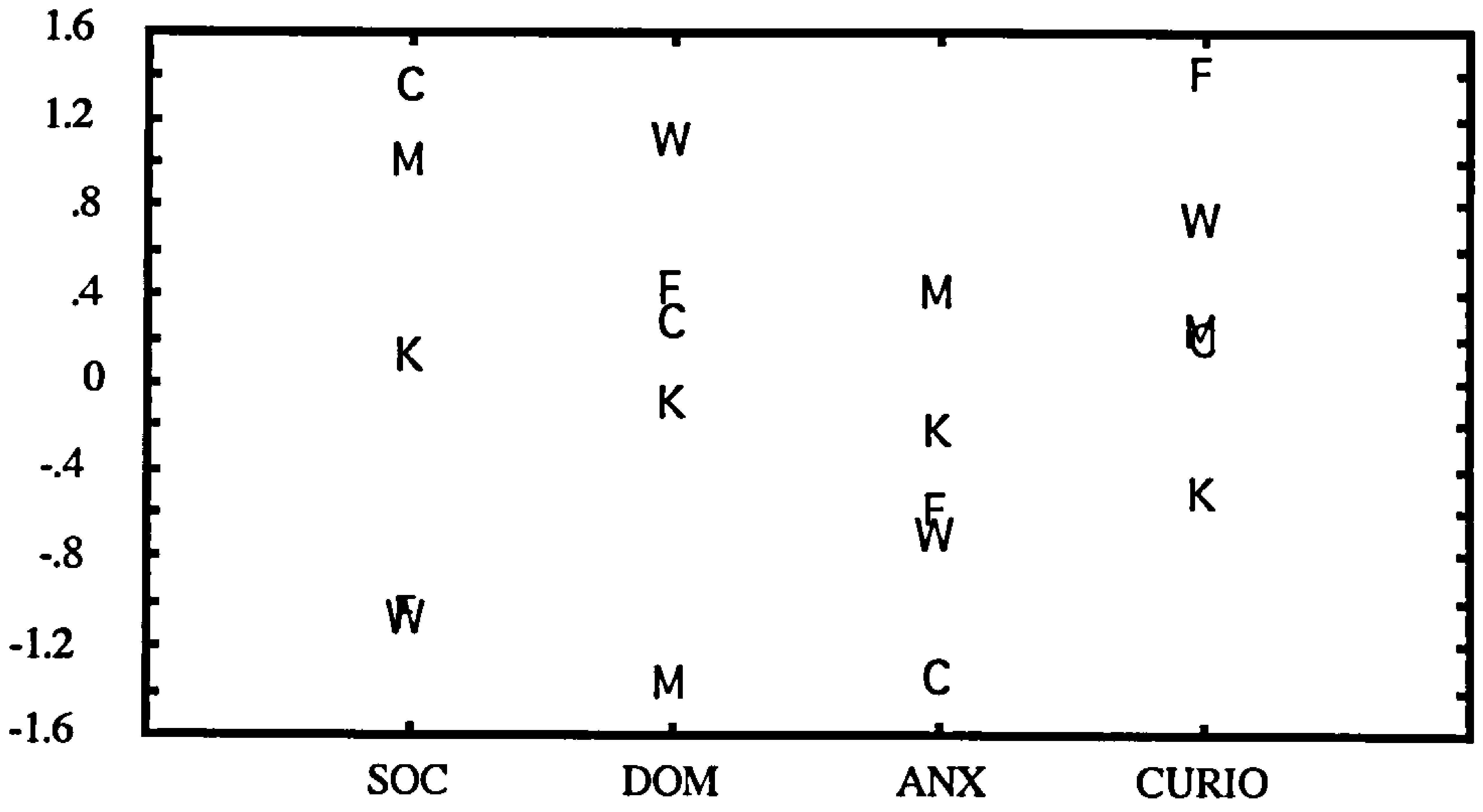
6.2.1 Comparison of focal male and female personality profiles

Fig 6.1 Factor scores for focal males



An examination of the male profiles using the same axes highlights the animals who score in a similar way on the four factors. Boris, Wilson and Friday show similar Sociability scores, while adolescent Dylan is somewhat less sociable, and Nicky much more sociable. On the Dominance factor, Dylan is actually rated highest, with Boris and Wilson next most dominant, respectively. Nicky is rated as the least dominant. Whilst Boris, Wilson, Friday and Dylan are rated similarly on Anxiety, Nicky again scores more extremely, with a relatively high Anxiety rating. The factor scores between the males are much more disparate for Curiosity. Boris and Friday are rated very closely on this factor, with Nicky and Dylan providing the most extreme scores: Dylan is rated as much more curious than the other males, and Nicky as much less curious.

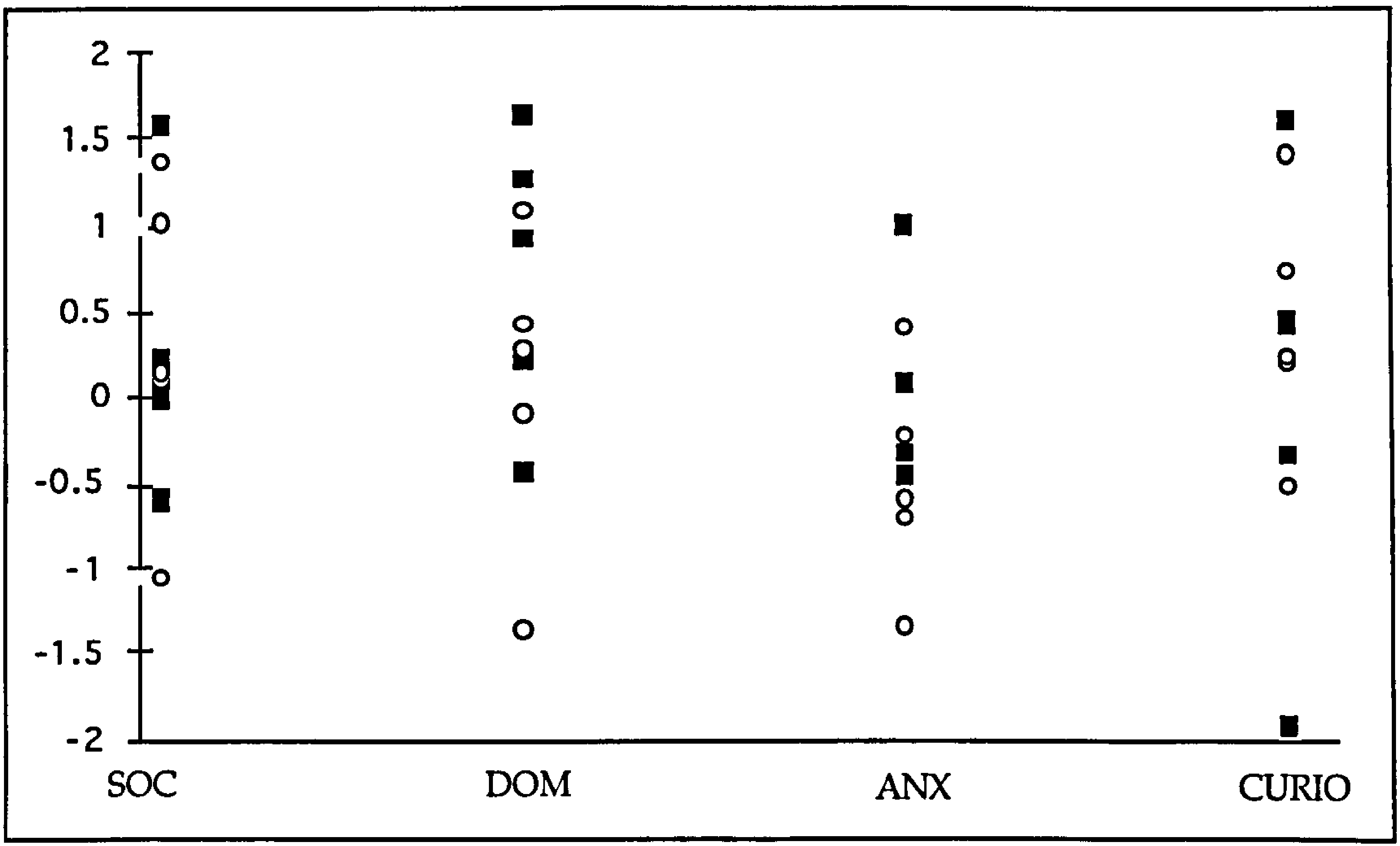
Fig 6.2 Factor scores for focal females



The scores of the females are somewhat more widely dispersed than those of the males. There are large differences, for instance, on Sociability, with Cleo and Mandy rated as much more sociable than Florin and Wanda. Kankan occupies an intermediate position between these two extremes. On the Dominance factor, the high scoring of Cleo, Florin, and in particular Wanda, is in contrast to the very low dominance score of Mandy. Mandy is again placed at one extreme on Anxiety; the highest anxiety rating is occupied by her, while the lowest score belongs to Cleo. Cleo and Mandy share similar Curiosity scores, with Florin and Kankan occupying the highest and lowest scoring positions, respectively.

Figure 6.3 plots factor scores for the five focal males and five focal females, to compare general scoring patterns between the sexes. The clearest difference between the sexes is on the Dominance factor, with males rated higher than females on this factor. Indeed, this was the only significant difference between the sexes on the personality factors, although males score slightly higher than females on Sociability, Anxiety and Curiosity (point-biserial correlations reported in chapter 3, section 3.3.7).

Fig 6.3 Factor scores for focal males and females



Filled squares represent males; open circles represent females

6.3 Representation of proximity, grooming and play data

In the sections below, several measures of association are presented. The number of point samples the animal was observed in proximity to others, grooming and playing are shown, together with proportionate scores (i.e. proportion of total sample points on which the behaviour occurred). While neither the number nor the proportion of point samples give true durations, the latter can give a good approximation of the proportion of time a behaviour occurred, if the sample interval is short relative to the duration of the behaviour (Dunbar, 1976; Martin and Bateson, 1995). The 'estimated time' uses the number of sample points (30-second interval) to give an approximation of the number of minutes spent performing a particular behaviour. In this and the following chapter, Spearman's *rho* was used for all (two-tailed) trait-behaviour comparisons due to the small sample size, and the fact that not all factor scores were normally distributed. To assess significance, Bonferroni corrections were applied to the standard alpha level of 0.05. There is some disagreement in the literature over the appropriate level at which corrections for multiple testing should be applied (e.g. should correction be applied to all tests performed in a single study, or to all tests performed in an entire research program?). In this thesis, a conservative estimate was used to correct for multiple testing: all trait-behaviour comparisons in the thesis were considered as testing the hypothesis that there would be a relationship between personality trait scores and behavioural measures. The total number of such comparisons was 196, and this was used to calculate the corrected level of significance as $p \leq 0.0002$.

A consequence of this stringent level of correction is that most trait-behaviour comparisons, while often substantial, are not significant at the corrected level. Indeed, for those correlations involving a sample of only 5 (i.e. involving only male focals, or only female focals) only a near perfect correlation would be significant at the 0.0002 level. In the discussion of results below, correlations which are substantial (though nonsignificant) have been presented and commented on, and for completeness those correlations are identified which, though nonsignificant at the required corrected level, would have been significant at an uncorrected alpha level of 0.05 or below. Many of the correlations here are actually higher than those typically found in comparisons of human personality ratings and behaviours, which are usually in the order of 0.3 (Kline, 1993a).

While it is likely that the correlations found here would be significant given a larger sample size, the level of statistical significance does not necessarily give a good estimate of the importance of a result, and many authors suggest the importance of considering the magnitude of the effect, such as the amount of variance explained by a correlation coefficient (Cohen, 1988; Martin and Bateson, 1985).

Differences between trait-behaviour correlations for focal males and focal females.

Correlations between personality ratings and behavioural measures were performed for the complete group of focal chimpanzees (N=10) but separate correlations were also carried out for focal males (N=5) and focal females (N=5). In some of these comparisons, large differences between the magnitude and direction of correlations for each sex were apparent. These differences were tested for significance using the following formula:

$$z = r_1' - r_2' / \sqrt{1/N_1 - 3 + 1/N_2 - 3}$$

where r_1' and r_2' are the values of the correlations, and N_1 and N_2 are the sample sizes.

In this chapter and the next, 44 comparisons were made between male and female correlations, therefore the criterion alpha level of .05 was corrected for multiple testing, to produce a corrected value of p = 0.001. To be significant at the required level, z_{obt} must be larger than $z_{0.0005} = \pm 3.50$ for a two-tailed test (Howell, 1982). Significant differences between correlations are highlighted and discussed in the text.

6.4 Time spent alone

For each focal animal, the number and the proportion of point samples that each individual was recorded as being alone was calculated. The number of bouts spent alone was determined and the median length of each bout calculated. Table 6.2 shows these data for each focal individual. Each chimpanzee was observed for 20 hours.

Table 6.2 Number of point samples, proportion of point samples, estimated duration, estimated percentage time, number of bouts and median bout length of time spent alone for the focal animals

	No. of sample points	Prop. of sample points	Estimated time (mins)	Estimated % time	Number of bouts	Median bout length (mins)
Boris	457	0.19	228.5	19.0	70	3.00
Wilson	1030	0.42	515.0	42.9	86	2.50
Nicky	951	0.39	475.5	39.6	51	4.50
Friday	907	0.37	453.5	37.7	58	3.00
Dylan	1071	0.44	535.5	44.6	76	4.50
Cleo	720	0.30	360.0	30.0	71	2.00
Florin	1126	0.46	563.0	46.9	90	3.25
Mandy	936	0.39	468.0	39.0	69	3.50
Kankan	411	0.17	205.5	17.1	72	1.50
Wanda	1031	0.42	515.5	42.9	53	5.50

The proportion of point samples was correlated with personality scores for each of the four factors. There was little correlation between proportion of point samples spent alone and Anxiety scores ($r_s = .07$). Moderate, though nonsignificant, correlations were found, however, between time spent alone and Sociability scores ($r_s = -.43$), between time spent alone and Dominance scores ($r_s = .34$) and between time spent alone and Curiosity scores ($r_s = .57$).

The correlations between time spent alone and factor scores varied between the sexes (though they were mostly nonsignificant at the corrected level). For Sociability the correlation was low for males (-.10), but much larger for females (-.60). For males, high scorers on Dominance spent less time alone (-.30), but the pattern was reversed for females (.60). The correlation between Anxiety and time spent alone was much higher when males and females were compared separately; for males .60 and for females -.10. The correlation with Curiosity was low for males (-.20), but perfect for females (1.00). The difference between these two correlations was not significant at the corrected level of $p = 0.0005$, but approached significance at $p = 0.0006$.

The correlation between age and time spent alone was also non-significant, but of a moderate size ($r_s = -.37$). This suggests that younger animals spend more time alone. In this sample, the youngest individuals are Dylan and Wanda, both adolescents. As an early adolescent, Dylan spends little time with his mother, Farthing, and is attempting to integrate himself with the other adult males. His interactions with adult females are often brief, and aggressive, as he attempts to dominate them. Wanda associates frequently with her mother Heidi, and with the adult female Cleo, but has relatively few strong social partners apart from these two. With no offspring, Wanda spends much more time alone than the females closest to her in age, Kankan and Sarah, who both have offspring.

The correlations between time spent alone and the factor scores are suggestive. As might be expected, both male and female animals rated higher on Sociability spent less time alone, though this relationship was much stronger for females. The direction of the relationships between Dominance scores and time spent alone also varied between the sexes. For males, those individuals rated highly on Dominance and Curiosity spent more time alone. Comparing the factor scores of Boris and Dylan is interesting in this respect. Boris and Dylan are actually rated as the least sociable males, and both are among the four highest scoring chimps on Curiosity. It may be that the Curiosity factor expresses a type of social vigilance, rather than a simple object-based curiosity. The two highest scorers on Curiosity are Dylan and Florin. Both spend a great deal of time monitoring others, and their environment. In Dylan's case, this is almost certainly linked to his persistent efforts to challenge the alpha male, Boris, and most of his monitoring is directed toward the other males. A different relationship between Dominance and time spent alone is suggested for females, with those females rated as most dominant spending *more* time alone. Similarly, the direction of the relationship between time spent alone and Anxiety is different for males and females; with a small negative relationship for females (more anxious females spend less time alone) and a more substantial positive relationship for males.

6.5 Association patterns

For each focal animal, the number of point samples spent in proximity to others was calculated, and the proportion of point samples spent in proximity. This was expressed simply as:

Time A + B spent together / Total time available to spend together

In practice, the availability of all possible proximal partners was constant, since the animals were housed together at all times. The one exception to this occurred in June 1999 following the loss of an infant to Rosie. For four days Rosie and her adolescent daughter Sally remained in the sleeping area. During this period, observations were suspended until the whole group were re-united.

The number of bouts spent in proximity to others was determined, and the median duration of each bout. The total number of approaches, leaves and avoidances (performed by the focal animal and by others) was used to calculate responsibility for proximity according to the index suggested by Hinde and Atkinson (1970):

$$\text{Responsibility for proximity} = Ua \,/\, (Ua + Ub) - Sa \,/\, (Sa + Sb)$$

Ua is the number of occasions A and B were united by A's movements, and *Ub* is the number of times they were united by B's movements. *Sa* is the number of times the pair were separated by A's movements, and *Sb* the number of times the pair were separated by B's movements. The resulting index ranges from -1.0 (indicating that B was totally responsible for maintaining proximity) to +1.0 (indicating that A was totally responsible for maintaining proximity. If the value is zero, this indicates that both were equally responsible for maintenance of proximity.

6.5.1. Proportion of time spent in proximity

Table 6.3 (p.185) shows the estimated percentage of time (out of the entire observation period) that each focal animal spent with each of the other individuals in the group. Also shown is the median of these percentage association times. Grooming and play bouts were included in this estimation of proximity.

Because of her infant's disability, Halfpenny is always in close proximity to Kiki; therefore, the time that each focal spent with Halfpenny necessarily included Kiki. However, Kiki is also represented separately in this table as sometimes individuals clearly approached Kiki herself, usually to hold or to play with her.

6.5.2. Sex, age and personality differences in association time

Age was positively correlated with proportion of point samples spent in proximity ($r_s = .31$), although this is not significant. This suggests that older animals are more sociable.

The correlations between three of the personality factors and proportion of point samples spent in proximity were moderate, though mostly insignificant. As might be expected, animals rated higher on Sociability spent more time in proximity ($r_s = .38$), but this is a stronger relationship for females (.60) than males (.10). For the focals considered as a group, animals rated highly on Dominance spent less time in proximity (-.34). Again, the stronger relationship here was for females (-.60) compared

Table 6.3 Percentage association times and median percentage association times for focal individuals

	BS	WN	NK	FD	DY	CL	FL	MD	KN	WD
Boris		8.87	5.12	1.45	2.16	12.50	1.91	0.66	3.33	3.83
Wilson	6.50		4.29	9.37	4.95	2.58	1.04	1.75	0.37	4.54
Nicky	0.29	2.79		2.79	4.54	3.20	1.66	2.50	4.79	2.08
Friday	1.62	5.62	4.37		8.33	4.12	3.45	4.12	3.91	3.70
Dylan	1.62	1.41	6.16	8.62		3.41	2.16	1.33	1.20	1.75
Cleo	4.83	7.25	13.0	4.95	2.75		3.87	5.79	10.16	18.91
Florin	0.75	0.33	0.58	5.16	1.25	1.16		0.66	1.70	2.25
Mandy	1.08	0.75	3.33	4.08	0.87	0.91	2.37		0.20	0.91
Kankan	7.29	0.66	1.29	4.91	2.75	9.58	3.70	5.95		1.95
Wanda	3.12	0.83	3.20	6.37	7.08	7.08	0.25	1.83	2.12	
Meg	1.66	0.41	1.75	2.91	0.70	3.58	0.58	6.87	2.08	1.29
Kate	0.62	1.20	6.16	3.70	1.04	3.54	1.00	2.58	7.37	2.12
Heidi	18.20	7.08	8.29	4.62	2.66	8.70	1.79	1.54	2.25	8.91
Rosie	11.33	5.83	8.16	9.04	0.58	1.00	2.50	4.54	0.04	0.08
H'penny	4.79	1.29	4.29	8.83	4.62	0.58	4.95	1.41	2.66	4.04
Farthing	1.12	10.50	2.87	1.50	2.00	3.0	1.87	2.91	2.37	0.70
Sarah	0.50	1.20	1.50	6.12	3.33	3.25	4.00	0.91	0.87	0.83
Sally	1.25	2.50	0.33	2.37	1.08	1.75	0.58	0.75	1.75	2.20
Kaylie	1.87	0.00	1.25	2.16	1.50	0.79	1.33	0.00	1.37	3.91
Layla	0.41	4.04	1.04	0.08	2.79	2.04	2.79	1.00	2.20	0.25
Alice	0.25	0.79	0.79	1.62	3.41	1.37	6.70	1.00	2.45	0.50
Whitney	0.58	0.62	1.00	0.87	1.79	1.75	2.00	2.04	22.16	1.20
Zeezee	2.37	1.58	4.75	0.29	0.25	4.87	0.37	23.5	0.62	1.04
Lizzie	0.33	0.41	2.16	0.95	0.08	2.95	0.54	1.37	0.50	0.20
Holly	0.33	0.54	0.16	1.87	1.79	0.33	1.79	0.20	0.37	0.75
Kiki	0.08	0.00	0.08	1.45	2.45	0.00	0.29	0.04	0.33	0.33
Chrissie	0.04	0.33	1.04	0.66	1.29	0.29	21.91	0.08	2.20	0.66
Patti	0.25	1.75	1.08	0.33	2.62	10.54	1.41	0.41	42.50	0.54
Total	73.08	68.58	88.04	97.07	68.66	94.87	76.81	75.74	121.8	69.47
Median	1.12	1.20	2.16	2.79	2.16	2.95	1.87	1.41	2.12	1.29

to males (-.30). Those scoring higher on Curiosity spent less time in proximity (for all focals -.51; for focal males -.20; for focal females -1.00

(significant at 0.0002)). The difference between these two latter correlations was not significant at the corrected level of $p = 0.0005$ (but was significant at an uncorrected level of 0.002). Since it is the youngest animals who scored highest on Curiosity, this suggests that the relation between Curiosity and time spent in proximity may be an effect of age. There was a very small correlation between Anxiety scores and time spent in proximity (-.11), suggesting that more anxious animals spend less time in proximity to others. However, this correlation was large when males were considered separately (-.60), and in the opposite direction for females considered separately (.10).

To summarise: the basic measure of time spent in proximity relates substantially to some of the personality factor scores, but this pattern of relationship is different for males and females. Those females who spend more time in proximity are rated as highly sociable and anxious, but less dominant and curious. Males who spend more time in proximity are rated as highly sociable, but less dominant, curious and anxious. This suggests that personality-behaviour relationships are expressed differently in males and females, as would be expected from their differing opportunities for social interactions, and their different life history strategies.

6.5.3. Diversity of association patterns

To examine affiliative behaviour patterns in more detail, the distribution of affiliative behaviour was examined for each focal, using the Shannon-Weaver index of diversity (Shannon and Weaver, 1949). Shannon's H expresses the extent to which an individual's affiliation is distributed evenly throughout the group. The proportion of scan samples that each focal spent in proximity, grooming or playing with each other member of the group was calculated. These were summed for all partners of the focal, then Shannon's H calculated for each focal:

$$H = -\sum pi \ln pi$$

with pi as the proportion of scan samples the focal affiliated with an individual i. H ranges from 0 to 3.29 ($H_{max} = \ln S = 3.29$).

Shannon's equitability was then calculated for each focal:

$$EH = H / \ln S$$

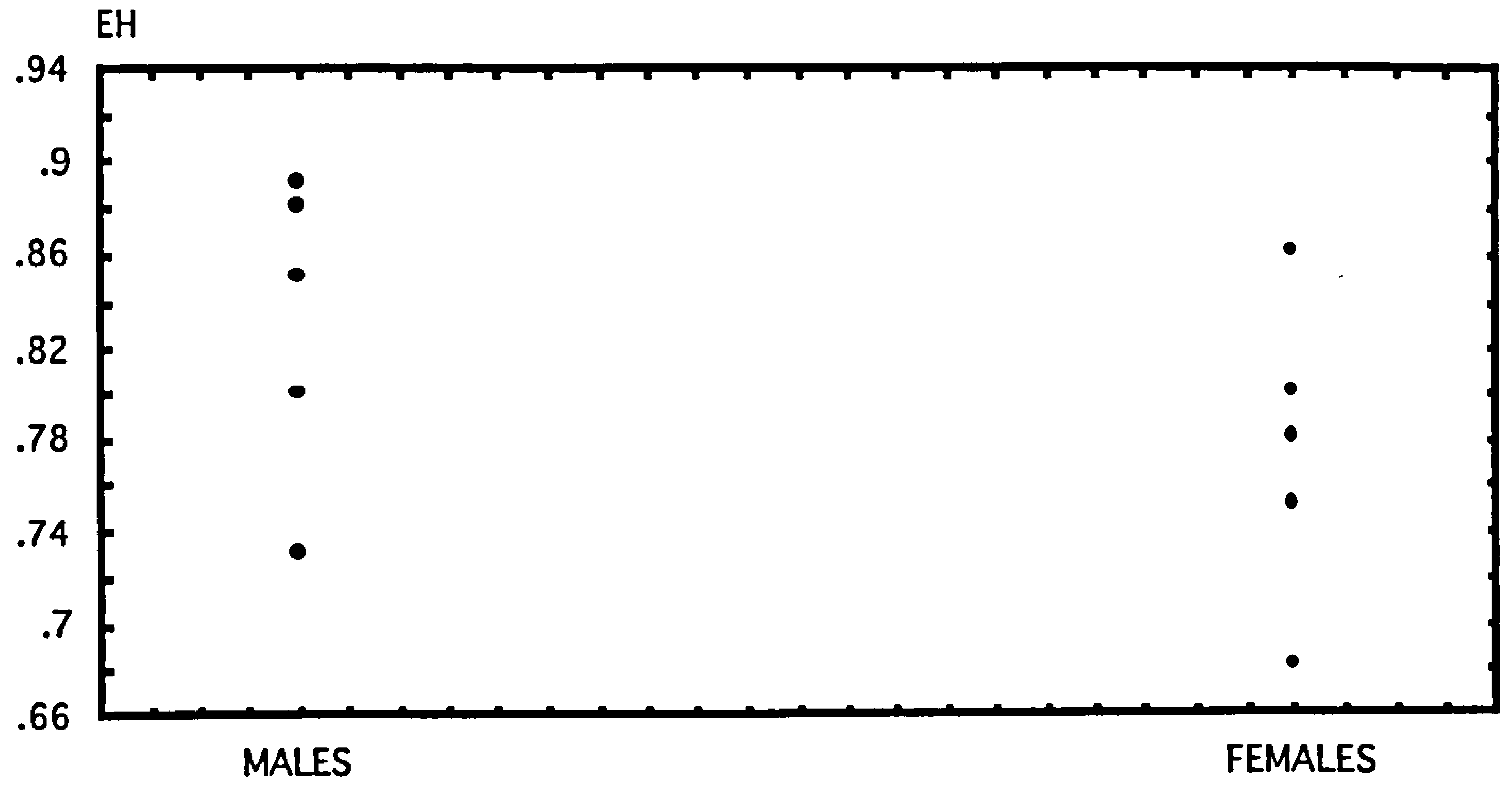
S is the total number of individuals in the group. EH produces a value between 0 and 1, with a score of 1 indicating that affiliation is distributed evenly. Table 6.4 shows *H* and *EH* for each focal.

Table 6.4 Distribution of affiliation for focal males and females

	Males			Females	
	H	*EH*		*H*	*EH*
Boris	2.42	0.73	Cleo	2.83	0.86
Wilson	2.63	0.80	Florin	2.65	0.80
Nicky	2.82	0.85	Mandy	2.48	0.75
Friday	2.90	0.88	KanKan	2.27	0.68
Dylan	2.94	0.89	Wanda	2.57	0.78

The indices show that all the focals distribute their affiliation quite evenly, though scores for focal males are slightly higher than for focal females (Fig. 6.4, below). This differences is, however, not significant (U = 6.50, p = .250).

Figure 6.4 Shannon's equitability *(EH)* for focal males and females



Each focal's factor scores were compared to their diversity indices using Spearman's correlation, and this was calculated separately for males and females. None of the correlations were significant at the corrected level of significance, though some were substantial. For males, the correlation between *H* and Sociability = -.30; *H* and Dominance = .10; *H* and Anxiety = .20; *H* and Curiosity = .60. For females the correlation between *H* and Sociability = .20; *H* and Dominance = .50; *H* and Anxiety = -.80; *H* and Curiosity = .40. The strongest relationships here suggest that more curious males, and less anxious females, distribute their affiliation more evenly.

The proportion of time that each focal spent with every other member of the group was examined to more closely analyse the identity of close affiliates, and the intensity of these relationships.

Figures 6.5 and 6.6 below illustrate the patterning of each focal's social relationships in the form of sociograms, representing the proportion of time spent with other members of the group. Males are shown at the top of each sociogram, and are outlined in bold. Adult females are ranged around the base of each diagram, adolescents and juveniles on the left, and infants on the right.

In the following discussion of association patterns, relationships are referred to as 1st-degree, 2nd-degree, etc, in reflection of the above proximity scale (e.g. a relationship where the dyad spent 20% — 50% of time together would be referred to as a 6th-degree relationship). It is assumed that the most intense relationships are characterised by a larger amount of affiliation. The discussion below focuses upon those affiliation partners who are in the top quartile of each focal's affilation scores (defined as proportion of scan samples spent with each group member (c.f. Cords and Aureli, 1993, cited in Castles *et al.*, 1996)).

Scale for proximity:		
	—	Less than 1%
	—	1% — 4%
	—	4% — 6%
	—	6% — 10%
	—	10% — 20%
	—	20% — 50%

The diversity indices range from 0.73 to 0.89 for the focal males, with Boris showing the least affiliative diversity and Dylan the most. While Boris affiliates with every other group member, only a small number of those affiliates could be classed as intense. Boris has only one strong male relationship (with Wilson) and only three strong relationships with the females Heidi, Rosie and Kankan. However, those relationships are intense (5th degree with Heidi and Rosie and 4th degree with Kankan).

Wilson has the next lowest diversity index (0.80), and also has a small number of close relationships. He shares a 5th degree relationship with Farthing and 4th degree relationships with Heidi and Cleo. However, Wilson also has a number of moderately intense relationships: with Boris (4th degree) and with Friday, Rosie and Farthing's adolescent daughter Layla (all 3rd degree).

The highest scorer on Sociability, Nicky has a number of high and moderately intense relationships with a substantial number of group members (*EH* = 0.85). He has moderately strong relationships with all of the other males: 3rd degree with Boris, Wilson and Friday, and 4th degree with Dylan. His strongest relationship among the females is with Cleo (5th degree), but he has strong (at least 3rd degree) relationships with a number of other females (e.g. Rosie, Kate, Heidi and Halfpenny).

Friday has the second largest diversity index (0.88). Among the males, he associates mainly with Wilson and Dylan (both 4th degree). Among the females, Friday's strongest bonds are with younger and lower-ranking animals: Halfpenny, Rosie, Sarah, Mandy, Kankan and adolescent Wanda.

Dylan has the largest diversity index (0.89) but is the lowest scorer on Sociability (among the males). In contrast to the other males, he has no 5th degree relationships. His strongest relationships are with Friday and the adolescent female Wanda (both 4th degree).

There are clear differences between the focal males in the distribution of affiliation. The older adult males, Boris, Wilson and Nicky, typically exhibit small numbers of intense social relationships, and the most intense of these bonds are with other adult males and females. By contrast, the young adult Friday, and adolescent Dylan, distribute affiliation more evenly but have few intense relationships. In addition, they spend more time with adolescent and juvenile animals. This pattern would suggest a negative relationship between the number of significant relationships and their intensity (c.f. Castles *et al.*, 1996).

The association patterns of the males seem to reflect sex-specific reproductive strategies. Chimpanzee males typically associate largely with other adult males and cycling females (Wrangham and Smuts, 1980; Goodall, 1986). This pattern is observed for the focal data presented here, with each male's most intense relationships concentrated among these 2 groups. However, the young males Friday and Dylan distribute their affiliation more evenly between the females, which would suggest competition for access to cycling females by the older males.

The affiliation patterns of these two younger males are interesting to compare. Both show a relatively even distribution of affiliation, but of the two it is Friday who has the greater number of strong relationships (particularly among the females). Dylan's only strong relationship among the females is with Wanda, herself an adolescent.

The diversity indices range from 0.68 to 0.86 for the focal females; with Kankan showing least diversity, and Cleo the most. Cleo, the highest scorer on Sociability among the females, enjoys a number of strong relationships. Her most intense relationships are with Boris and with Kankan's infant Patti (both 5th degree). Cleo also has a strong relationship with Kankan, and with Heidi and Heidi's daughter Wanda (all 4th degree). Another infant whom Cleo spends time with is Mandy's daughter Zeezee (whom Cleo allo-parents). She also has a good number of 2nd and 3rd degree relationships with other adult and adolescent males and females.

Florin is one of the lowest scorers on Sociability but has the next highest diversity score among the females (0.80). Florin's strongest relationships are with her offspring; with infant Chrissie (6th degree) and adolescent daughter Alice (4th degree). Florin has only two other moderately strong relationships (3rd degree), one with her sister Halfpenny and one with Halfpenny's daughter Sarah, but she has a number of 2nd degree relationships with other adult males and females.

Figure 6.5 Distribution of proximity for the five focal males

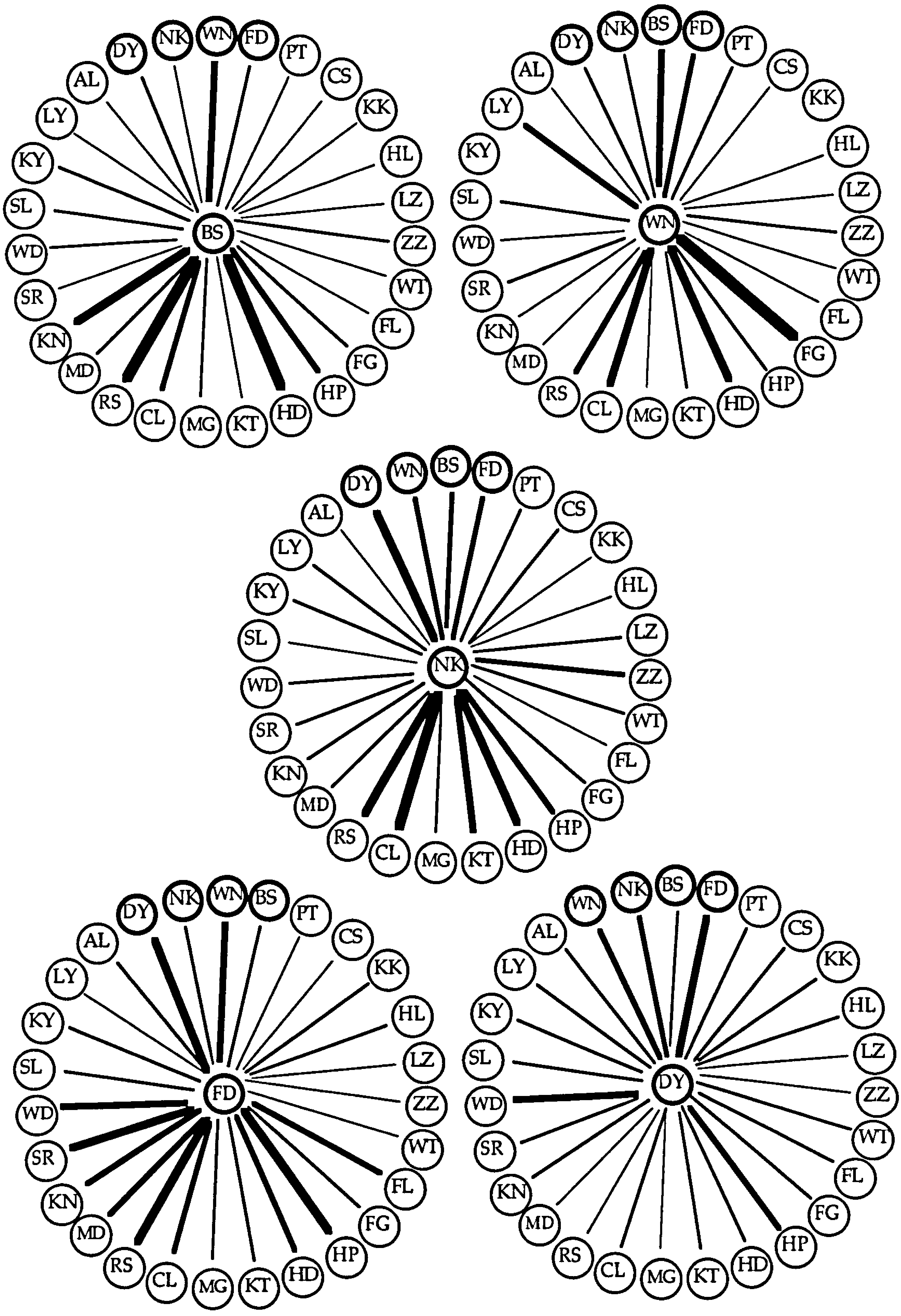
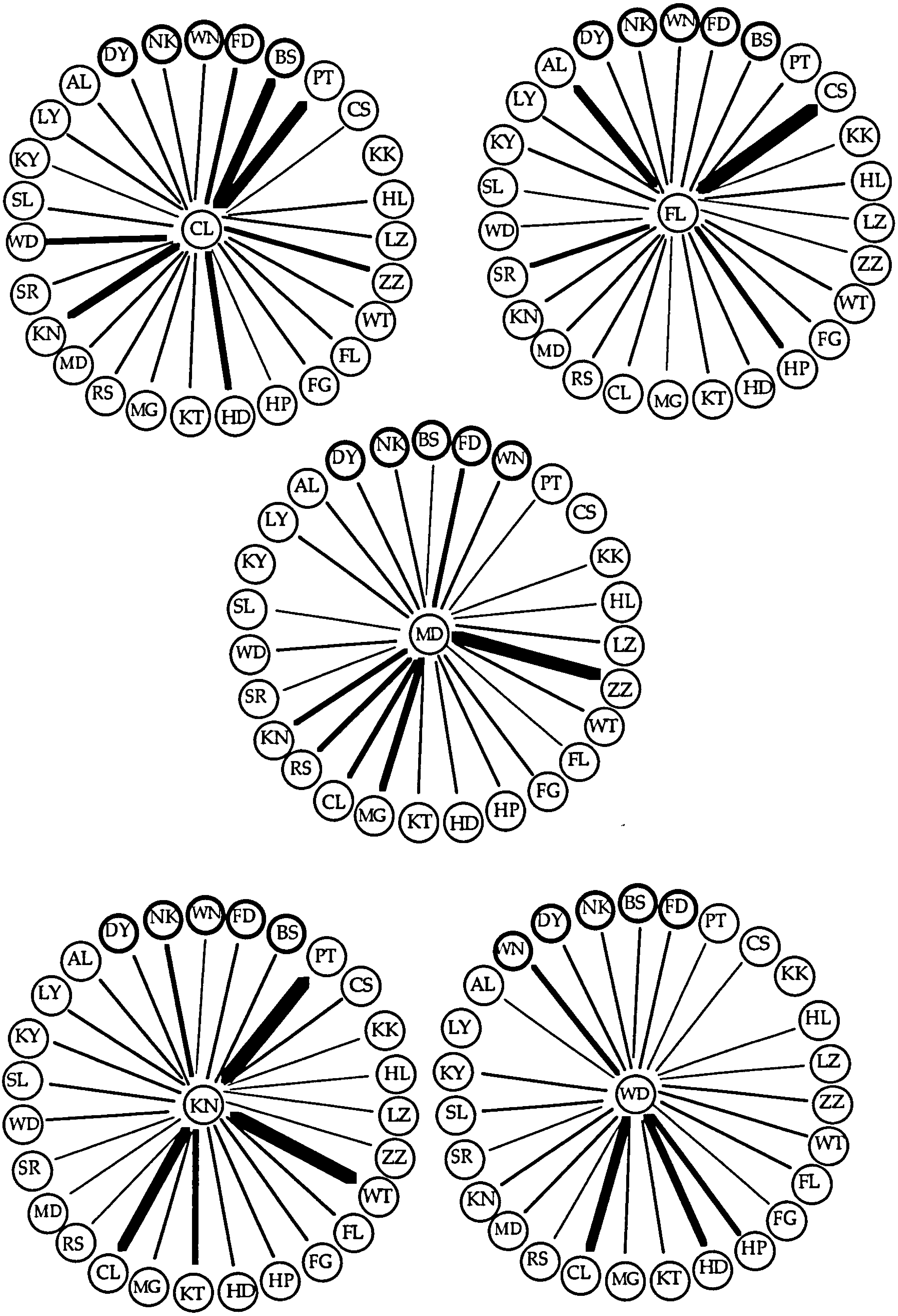


Figure 6.6 Distribution of proximity for the five focal females



Wanda, also a low scorer on Sociability, has a similar diversity index to Florin's (0.78). Wanda has a particularly strong relationship with Cleo (5th degree) followed in intensity only by that with her mother Heidi (4th degree). Wanda has moderately strong relationships (3rd degree) with Wilson and with Halfpenny.

The strongest association for Mandy is with her offspring. She has a 6th degree relationship with her infant Zeezee. She also has a strong relationship with the old female Meg (4th degree) and 3rd degree bonds with Friday, Kankan, Rosie and Cleo.

Kankan has the lowest diversity score of the focal females. Her most intense relationships are with her daughters Whitney and Patti. She has only three other relationships of 3rd degree or more: with Cleo, with Nicky and with her mother Kate.

The distribution of affiliation for focal females clearly reflects sex-specific social patterns. Cleo, widely considered to be the dominant female and with no offspring of her own, shows the most evenly distributed pattern of affiliation. Florin, Mandy and Kankan show lower scores for distribution and typically intense relationships with offspring and other kin (Pusey, 1990). Adolescent Wanda shows few strong bonds with other adult females (with the exception of Cleo), and spends most time with her mother Heidi.

6.5.4 Responsibility for proximity

The nature and quality of a particular relationship often depends not just on how long two individuals spend together, but to what extent each is responsible for the association. Examining a large number of social relationships is likely to provide the most complete account of an individual's personality (Hinde, 1976) and the quality of an individual's social relationships may be an important expression of their personality (Hinde, 1995). However, the extent to which a relationship is reciprocal is also influenced by the dominance and reproductive strategies each individual is pursuing, and so reciprocity may be expected to vary (for a given individual) depending upon which relationship is considered. For example, the relationship between a dominant and a subordinate animal may well be complementary rather then reciprocal. However, within these limits, a given dominant may well choose to operate in a tolerant or a despotic way, thus affecting the 'quality' of that social relationship (e.g. Castles *et al*., 1996). This variation in behaviour may best be conceptualised as individuals choosing between alternative reproductive strategies, although such variation seems an implicit part of raters' accounts of dominant animals.

Responsibility for proximity was calculated for each focal, based upon observed approaches, leaves and avoidances during each focal observation. Table 6.6 shows the responsibility indices calculated for each dyadic association. Note that these data are based upon a smaller number of interactions than the general proximity data, as it was not always possible to determine who was responsible for each proximity bout, and in some cases the start of a proximity bout appeared to be mutual.

The discussion of the responsibility indices focuses upon each individual's strongest dyadic associations, i.e. those of 3rd-degree or more. Particularly large indices are commented upon and interesting relationships with these association patterns and the factor scores suggested. Responsibility for proximity was considered for those relationships characterised by more than 5 occasions of contact. Table 6.5 shows the number of relationships for each focal that the focal was more responsible for (A), the number of relationships that other partners were responsible for (B), and the number that were reciprocal (R).

In terms of the balance of reciprocity, Table 6.5 shows that for Boris, Nicky and Dylan, their affiliative partners are more responsible for the relationships, while Friday and Wilson are more responsible for the majority of their relationships. It is notable that Boris and Dylan are the highest scorers on Dominance, while Nicky is among the lowest scorers on this factor. In almost all of Boris' relationships, others take more responsibility for proximity. This is true for his strongest relationship among the males (with Wilson) and for his strong female relationships. The indices for both Heidi and Rosie are highly negative, suggesting that Boris is responsible for very few interactions in these relationships. The index for Kankan is lower but still indicates that Kankan is more responsible for her proximity with Boris.

Table 6.5 Distribution of reciprocity for focal relationships

	Responsibility for proximity		
	A	B	R
Boris	1	19	1
Wilson	9	6	2
Nicky	5	9	8
Friday	9	8	2
Dylan	9	14	1
Cleo	4	14	2
Florin	7	14	1
Mandy	10	7	2
Kankan	7	12	1
Wanda	10	9	2

The pattern of reciprocity for Wilson's relationships is very different. Wilson is more responsible for his relationships with his strongest male associates (Boris and Friday), and he is also more responsible for his strong relationships with the females Cleo and Heidi, but in his relationship with Farthing it is she who is more responsible.

The majority of Nicky's relationships are maintained by others, but almost an equal number are reciprocal. In his strong relationships with the females Cleo, Kate and Rosie it is the females who are more responsible for proximity. Nicky's strong relationships with Heidi and Dylan are reciprocal, as is his relationship with Friday. Nicky is more responsible for his relationships with Boris and Halfpenny.

Friday's strongest relationship among the males is with Wilson and this is a reciprocal relationship. In his relationship with Dylan, Wilson is more responsible. Of his strong female relationships (with Wanda, Sarah, Halfpenny and Rosie) the first is reciprocal, while the latter three take more responsibility. In his relationships with females Cleo, Heidi, Florin and Kankan, Friday is more responsible.

Dylan's strongest relationships are with Friday and Wanda, and it is these other animals who are more responsible for the contact. Dylan has moderate relationships with Wilson, Halfpenny and Nicky, and for the latter two Dylan is more responsible.

Cleo has strong relationships with both Boris and Friday. She is more responsible for her relationship with Boris, but the relationship with Friday is reciprocal. Among the females, Cleo has strong links with Heidi and Wanda, and it is Cleo who is most responsible for these bonds. She also has strong relationships with Kankan and Kankan's infant Patti, but the latter two are more responsible for these relationships.

Florin's strongest relationships are with her daughters Alice and Chrissie. In her relationship with Alice, Florin is more responsible, but infant Chrissie is more responsible for their relationship. Florin also has links with Halfpenny and Sarah, and it is the latter two who are more responsible for these relationships.

Mandy's strongest relationship is with her infant Zeezee, for which Zeezee is more responsible. Among the females Mandy is responsible for her relationships with Meg, Rosie and Kankan, and for her relationship with Friday. In her relationship with Cleo, it is Cleo who is more responsible.

Kankan's closest associations are with Cleo (Cleo more responsible) and her daughters Whitney and Patti; her offspring are more responsible for their proximity to her. However, Kankan is more responsible in her relationship with her mother Kate. In her relationship with adult male Nicky, it is Nicky who is more responsible for proximity.

Wanda's strongest bonds are with her mother Heidi (a reciprocal relationship) and with Cleo (for which Cleo is more responsible). She has moderate relationships with Halfpenny (Wanda more responsible) and with Wilson (Wilson more responsible).

Table 6.6 Responsibility for proximity for focal dyadic associations. (Empty cells indicate that no actual approaches, leaves or avoidances were observed between that dyad. Figures in brackets are the number of occasions that the indices are based upon) (see page 197)

	BS	WN	NK	FD	DY	CL	FL	MD	KN	WD
BORIS		0.19 (39)	0.42 (9)	0.20 (10)	-0.09 (22)	0.45 (17)	-0.38 (12)	0.17 (13)	0.58 (14)	0.30 (17)
WILSON	-0.19 (40)		-0.19 (23)	0.00 (30)	-0.33 (27)	-0.25 (15)	0.60 (8)	-0.37 (16)	0.00 (5)	-0.18 (15)
NICKY	-0.34 (5)	0.09 (10)		0.12 (12)	0.07 (22)	-0.33 (6)	-0.20 (11)	0.00 (8)	-0.58 (14)	-0.09 (7)
FRIDAY	-0.44 (19)	0.06 (33)	0.00 (11)		-0.15 (40)	0.00 (11)	0.20 (15)	0.10 (9)	-0.50 (7)	-0.60 (8)
DYLAN	-0.07 (13)	-0.04 (17)	0.00 (30)	0.03 (26)		-0.36 (11)	-0.27 (13)	0.66 (12)	0.17 (15)	0.15 (17)
MEG	-0.39 (20)	-0.55 (9)	0.00 (18)	-0.16 (5)	0.33 (6)	-0.32 (18)	1.00 (3)	0.16 (19)	0.13 (12)	0.42 (14)
KATE	-0.05 (13)	0.10 (7)	-0.08 (7)	-0.05 (14)	-0.17 (5)	-0.60 (10)	1.00 (1)	0.35 (9)	0.05 (24)	0.00 (8)
CLEO	-0.38 (10)	0.19 (27)	-0.37 (12)	0.55 (9)	0.30 (18)		-0.23 (16)	-0.11 (29)	-0.01 (22)	-0.41 (31)
HEIDI	-0.89 (55)	0.14 (28)	0.00 (20)	0.46 (15)	0.10 (20)	0.31 (29)	-0.05 (14)	0.25 (8)	0.34 (8)	0.00 (14)
ROSIE	-0.96 (63)	0.19 (26)	-0.66 (10)	-0.15 (18)	-0.39 (19)	-0.67 (7)	-1.00 (3)	0.39 (17)		1.00 (1)
HPENNY	-0.61 (30)	1.00 (4)	0.30 (7)	-0.04 (16)	0.15 (23)	0.00 (3)	-0.17 (30)	-0.50 (3)	-0.55 (9)	0.04 (11)
FARTHING	-0.25 (9)	-0.08 (30)	-0.20 (9)	1.00 (2)	-0.07 (8)	-0.02 (13)	-0.18 (19)	1.00 (3)	-0.04 (11)	-0.80 (7)
MANDY	-0.44 (11)	1.00 (4)	-0.08 (14)	-0.17 (10)	0.00 (1)	-0.40 (18)	-0.27 (8)		-0.67 (4)	0.06 (17)
FLORIN	-0.66 (6)	0.00 (5)	0.14 (16)	0.05 (19)	0.08 (17)	-0.16 (10)		-0.07 (11)	-0.51 (21)	0.27 (11)
KANKAN	-0.20 (15)	0.75 (5)	0.25 (7)	0.25 (8)	-0.36 (23)	-0.36 (19)	0.10 (30)	0.25 (6)		-0.33 (4)
SARAH	-0.40 (10)	-0.33 (5)	0.05 (9)	-0.60 (9)	-0.07 (9)	-1.00 (3)	-0.01 (20)	-0.16 (7)	0.00 (3)	-0.66 (6)
WANDA	-0.11 (18)	0.00 (9)	-0.25 (9)	0.00 (15)	-0.50 (28)	0.95 (49)	0.03 (12)	-0.64 (17)	0.08 (14)	
SALLY	-0.34 (10)	-0.07 (11)	-1.00 (3)	-0.66 (8)	-0.57 (19)	0.00 (4)	-0.20 (8)	0.25 (5)	-0.66 (9)	-0.59 (14)
KAYLIE	-0.28 (10)	-1.00 (2)	-0.25 (8)	0.27 (8)	-0.20 (10)	0.00 (9)	-0.46 (15)	0.00 (2)	-0.20 (13)	0.18 (12)
LAYLA	-0.50 (10)	0.25 (10)	0.00 (10)		0.00 (8)	0.16 (10)	-0.25 (16)	0.00 (4)	-0.23 (13)	1.00 (2)
ALICE	0.00 (1)	-0.50 (3)	0.00 (8)	0.60 (8)	0.11 (25)	0.50 (4)	0.28 (33)	0.00 (12)	-0.13 (8)	0.32 (12)
WHITNEY	1.00 (5)	-0.06 (8)	0.00 (4)	-0.33 (4)	-0.25 (14)	-0.50 (5)	-0.07 (17)	0.33 (7)	-0.05 (45)	0.50 (6)
ZEEZEE	0.00 ((10)	0.00 (4)	0.00 (10)	-1.00 (2)	1.00 (3)	-0.16 (27)	-1.00 (2)	-0.08 (52)	0.00 (1)	0.33 (6)
LIZZIE		-1.00 (2)	0.00 (7)	-0.50 (6)	0.00 (1)	-0.33 (6)	0.00 (5)	-0.34 (10)		-0.17 (5)
HOLLY		-1.00 (3)	0.00 (4)	0.00 (3)	0.07 (13)		0.34 (5)		-1.00 (1)	-0.17 (9)
KIKI					1.00 (7)		-1.00 (1)	0.00 (1)		0.00 (2)
CHRISSIE		0.00 (3)	-0.33 (5)	0.00 (4)	-0.16 (12)	0.00 (4)	-0.14 (81)		0.40 (8)	0.40 (10)
PATTI	0.00 (3)	1.00 (4)	0.00 (4)	0.00 (1)	-0.03 (18)	-0.10 (15)	0.55 (9)	0.50 (4)	-0.40 (82)	0.50 (3)

6.6 Grooming relationships

The number and proportion of point samples observed grooming were calculated for each focal chimp. The responsibility for initiating and terminating each bout was noted. Table 6.7 shows these figures and the estimated time spent grooming, as well as number of bouts and median bout length.

Table 6.7 Number of point samples, proportion of point samples, estimated duration, estimated percentage time, number of bouts and median bout length of time spent grooming for the focal animals

	No. of point samples	Prop. of point samples	Estimated time (mins)	Estimated % time	No. of bouts	Median bout length (mins)
Boris	811	0.33	405.5	33.7	77	2.75
Wilson	348	0.14	174.0	14.5	61	2
Nicky	328	0.13	164.0	13.6	43	2
Friday	804	0.33	402.0	33.5	102	3
Dylan	407	0.16	203.5	16.9	62	2.5
Cleo	702	0.29	351.0	29.2	51	4.75
Florin	337	0.14	168.5	14.0	54	2
Mandy	457	0.19	228.5	19.0	66	2.5
Kankan	696	0.29	348.0	29.0	60	3.5
Wanda	541	0.22	270.5	22.5	34	3

6.6.1 Sex, age and personality differences in proportion of time spent grooming

The proportion of point samples spent grooming, the frequency of grooming bouts and the median bout length were examined separately, as frequency and duration measures are not necessarily correlated (e.g. Simpson, 1973; Dunbar, 1976). As expected, none of the correlations are significant at the corrected alpha level of 0.0002 due to the stringent level of correction applied, though some are substantial, given the small sample size.

The proportion of point samples spent grooming was moderately correlated with the frequency of grooming bouts ($r_s = .47$). Proportion of point samples spent grooming was highly correlated with the median bout length ($r_s = .81$, significant at an uncorrected alpha level of 0.003), but median bout length was unrelated to frequency of grooming bouts ($r_s = .006$).

There was a moderate correlation between amount of grooming given and received (-.43); those animals who groomed the least tended to receive more grooming. Correlations between these measures and the factor scores were small to moderate. The largest correlations were between grooming given and age (-.35), Dominance (-.26) and Anxiety (.21), suggesting that older, more dominant animals gave less grooming, and more anxious animals groomed more. However, examining the sexes separately, it seems that it is more dominant females who groom less (-.60); for males the correlation was positive (.10). For Anxiety it is more anxious females who groom more (.90, significant at an uncorrected alpha level of .03); more anxious males actually groom less (-.70). The difference between these correlations was not significant at the corrected level of $p = 0.0005$ (but significant at an uncorrected level of $p = .009$).

For grooming received the largest correlations were with age (.20), Curiosity (.33) and Dominance (.16), suggesting that older, more dominant and more curious animals received more grooming. Again, the dominance effect seems to be limited to the females (.60); more dominant males receive less grooming (-.30). When the sexes were examined separately, high correlations were apparent between Anxiety and grooming received; -.60 for both sexes, suggesting that more anxious animals receive less grooming. There were no significant differences between males and females in these measures.

Mann-Whitney *U* tests showed no significant differences between males and females in the proportion of point samples spent grooming, the number of grooming bouts and the median bout lengths. Age was correlated slightly (though not significantly) with these measures: with proportion of point samples spent grooming $r_s = .06$, with number of grooming bouts $r_s =$

.26, and with median bout length $r_s = -.22$.

Spearman's *rho* was calculated for personality factor scores and proportion of point samples spent grooming, number of grooming bouts and median bout length (Table 6.8).

Table 6.8 Correlations between personality factor scores and grooming measures

	Prop. point samples spent grooming	Number of bouts	Median bout length
Sociability	-.17	-.04	-.02
Dominance	.10	.05	-.02
Anxiety	-.49	-.23	-.58
Curiosity	.12	.21	-.03

None of the correlations in Table 6.8 are significant at the criterion value of 0.0002, but there are moderate relationships between the grooming measures and Anxiety scores, suggesting that more anxious animals spend less time grooming, and have fewer, and shorter, grooming bouts.

If males and females are considered separately, however, a different pattern emerges. While none of the following correlations are significant at the corrected level, some are substantial, and suggestive. For males there is a substantial correlation between proportion of point samples spent grooming and Sociability scores (-.66), suggesting that more sociable animals groom less. This relationship is reversed for females (.41). While grooming and Dominance scores are minimally related for females (-.15), they are moderately, and positively, correlated for males (.41), suggesting that more dominant animals spend more time grooming. Correlations between Anxiety and time spent grooming are negative for both males (-.87, significant at an uncorrected alpha level of .05) and females (-.35), but higher for males. The correlation between time spent grooming and Curiosity, while low when the focals are considered as a group, is substantially higher when males and females are considered separately. Males who score highly on Curiosity spend more time grooming (.66), while females who score highly on Curiosity spend less time grooming (-.87, significant at an uncorrected alpha level of .05). The difference between these correlations was not significant at the corrected level of p = 0.005 (but significant at an uncorrected level of p = 0.01).

Table 6.9 illustrates the amount of time each focal spent grooming, being groomed and in mutual grooming sessions with males, females and infants (infants are defined as animals under the age of five). Figures in cells are the number of (estimated) minutes observed in each type of grooming session. Note that the totals for each individual are higher than grooming totals in Table 6.9, as they include figures for polyadic grooming sessions.

If the three types of grooming session are collapsed into time spent grooming and being groomed, then clear differences emerge between the focal animals. All of the males spend more time grooming and being groomed by females than by males. The exception is Dylan, who grooms other males more than he grooms females, but is groomed by females more than he is groomed by males.

Table 6.9 Distribution of different types of grooming between focal animals and males, females, and infants

	Males			Females			Infants		
	Given	Rec'd	Mutual	Given	Rec'd	Mutual	Given	Rec'd	Mutual
Boris	8	9	3	96	244	570	2	0	0
Wilson	43	11	19	175	50	39	14	0	0
Nicky	4	95	14	16	82	144	1	6	0
Friday	52	72	118	166	219	253	20	1	0
Dylan	145	24	51	39	101	76	1	1	0
Cleo	59	26	223	40	75	298	0	3	1
Florin	26	47	9	68	59	46	90	1	0
Mandy	34	7	10	56	68	86	170	17	32
KanKan	8	8	51	278	56	257	70	1	0
Wanda	73	56	25	40	38	340	2	0	3

All of the females except Wanda spend more time grooming and being groomed by other females. Of the females, Cleo spends the most time grooming, and unlike the other females, almost half of her grooming time is devoted to grooming sessions with males. She is also the animal who is groomed the most by males and females. An examination of the male-male grooming relationships shows that Boris, Nicky and Friday are groomed by other males more than they groom males themselves, while Wilson and Dylan groom other males more than they are groomed. All of the males except Wilson groom other females less than they are groomed, while Wilson grooms females more than twice the amount of time he is groomed by them.

Strong grooming relationships are typical between adult males and females, and between adult males (Goodall, 1968, 1986; Pusey, 1990). The high amount of grooming Dylan gives to males is interesting here, as it suggests that as an adolescent he may be spending more time trying to integrate himself into the male group. As might be expected, the highest figures for grooming given to infants are for mothers Florin, Kankan and Mandy. Among the females, Cleo and Wanda groom males more than they groom females. However, a large proportion of Cleo's grooming time is spent in mutual grooming with males (this is not so for Wanda). While adult males are popular grooming partners for females (Pusey, 1990), it seems clear that Cleo, herself a dominant and popular grooming partner, enjoys stronger bonds with the adult males than does adolescent Wanda.

6.6.2 Distribution of grooming

Both Shannon's *H* and Shannon's Equitability *(EH)* were calculated for each focal animal, using the proportion of point samples spent grooming with each of the other members of the group (Table 6.10).

The indices show that all the focals distribute their grooming relationships fairly evenly. There were differences in distribution between focals but these were not large. The highest diversity was shown by Dylan, and the lowest by Wanda.

Each focal's factor scores were compared to their diversity indices for grooming using Spearman's *rho*, and this was calculated separately for males and females. None of the correlations were significant at the corrected level of significance, though some were substantial. For males, the correlation between *H* and Sociability = -.30; *H* and Dominance = .40; *H* and Anxiety = .20; *H* and Curiosity = .50. For females the correlation between *H* and

Sociability = .60; *H* and Dominance = -.10; *H* and Anxiety = -.40; *H* and Curiosity = -.20. The strongest relationships here suggest that more curious males, and more sociable females, distribute their grooming more evenly.

Table 6.10 Distribution of grooming for focal males and females

	Males			Females	
	H	*EH*		*H*	*EH*
Boris	1.66	0.50	Cleo	2.17	0.66
Wilson	2.26	0.68	Florin	2.16	0.65
Nicky	1.82	0.55	Mandy	1.66	0.50
Friday	2.13	0.64	KanKan	2.05	0.62
Dylan	2.27	0.69	Wanda	1.49	0.45

The directionality of grooming was examined in order to more closely analyse the quality of grooming interactions between the focals and specific other members of the group. Figures 6.7 and 6.8 show the estimated proportion of time each possible dyad was observed grooming with each group member.

Scale for grooming:

─	5 — 20 minutes
─	20 — 60 minutes
━	60 — 120 minutes
▬	> 120 minutes

Figure 6.7 Distribution and directionality of grooming for five focal males

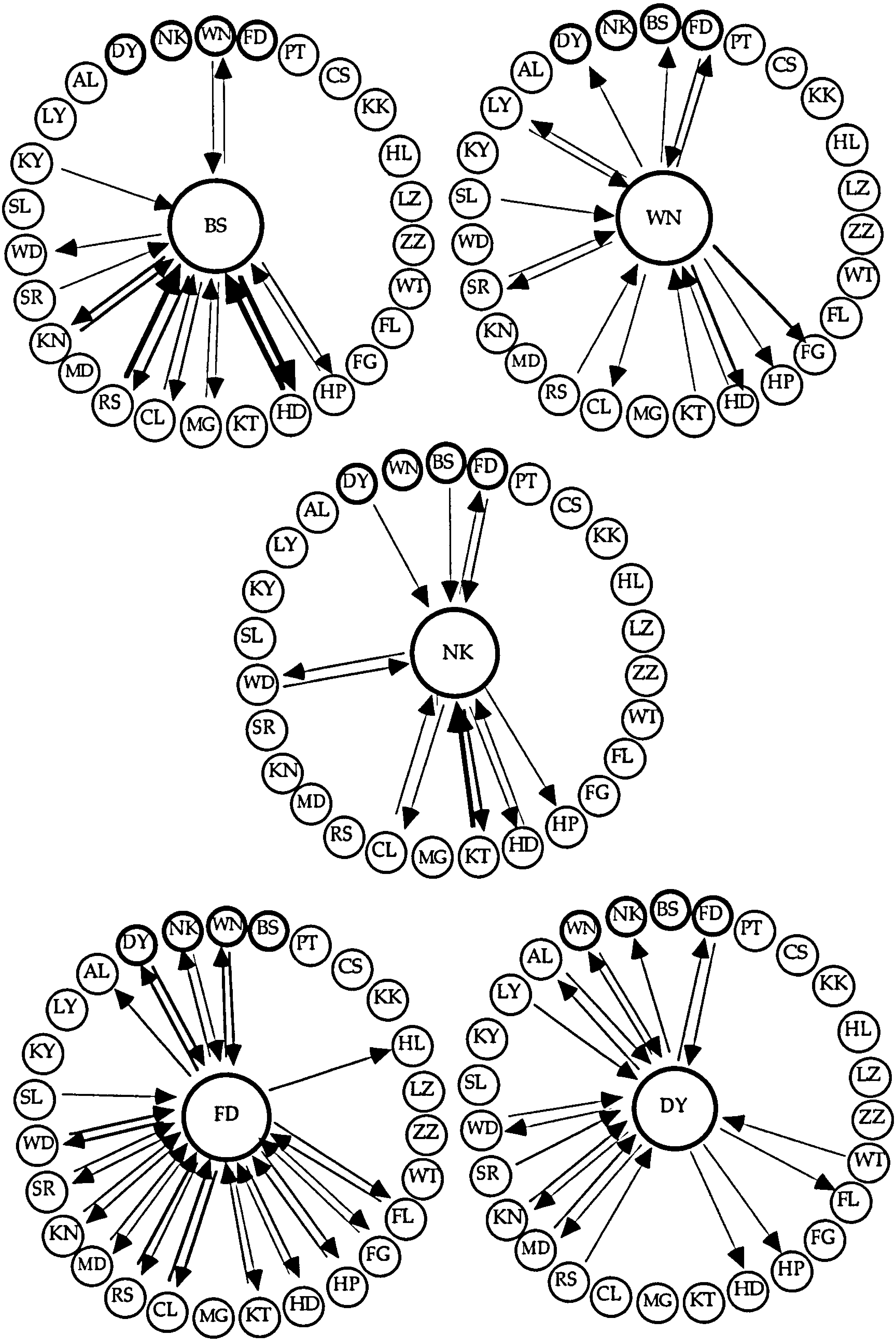
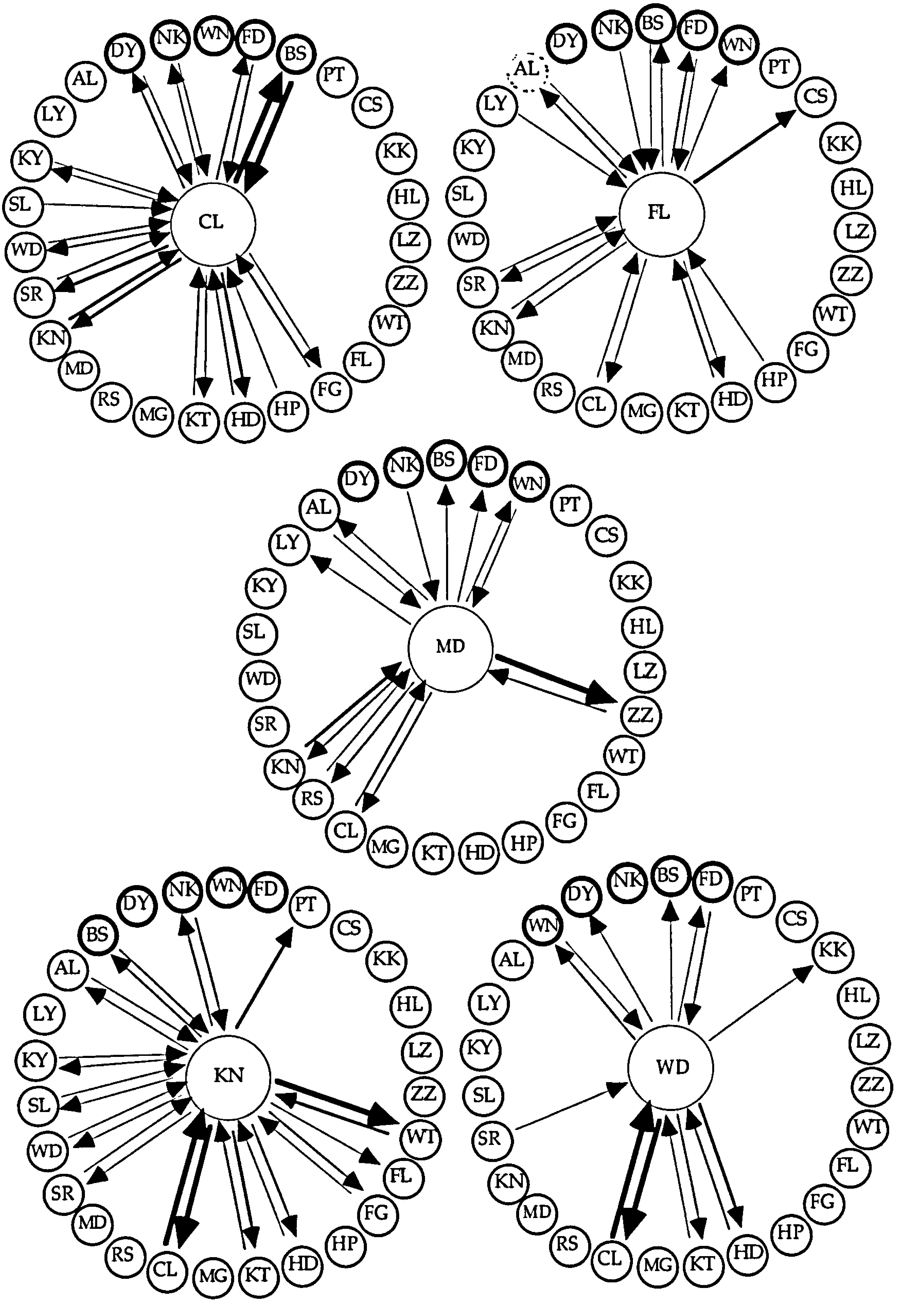


Figure 6.8 Distribution and directionality of grooming for five focal females



As with the proximity indices, Boris shows the least even distribution of grooming, and Dylan the most. The majority of Boris's grooming interactions take place with the adult and adolescent females. In most of these grooming relationships, reciprocity is more or less equal, or Boris receives slightly more grooming than he gives.

Compared to Boris, Nicky has fewer intense grooming relationships apart from his strong relationship with Kate. Along with Boris, Nicky's grooming is less evenly distributed than that of the other males. In most of his grooming relationships, Nicky received more grooming than he gave; the exceptions were Halfpenny and Heidi who received slightly more grooming from Nicky than they gave. No grooming was observed between Wilson and Nicky, but he received grooming from Friday, Dylan and Boris. Apart from his grooming relationship with Wanda, Nicky grooms mostly with the adult females Kate, Cleo, Heidi and Halfpenny.

Friday, Dylan and Wilson show wider distribution in their grooming relationships, but compared to Boris and Nicky have no intense grooming relationships. Wilson tends to give more grooming than he receives, particularly in the case of his grooming interactions with Boris, Farthing and Heidi. Unlike the other males, Wilson appeared to direct much of his proximity exclusively to females in oestrus, and Cleo, Heidi and Farthing received much of this attention.

Friday grooms with all of the other males except Boris, and with most of the adult and adolescent females. Among the males, Friday grooms most with Wilson and Dylan, and in both of these relationships he is groomed slightly more than he grooms them. He grooms with Nicky for a much shorter period of time, and it is Friday who is responsible for most of this grooming. Among the females, his strongest grooming relationships are with Cleo, Wanda and Wanda's mother Heidi. Reciprocity is almost equal in his relationships with Wanda and Cleo, but it is Friday who grooms Heidi more. Friday also has moderate grooming relationships with the younger adult females Florin, Rosie and Mandy, and with adolescents Kankan, Sarah and Alice. Among the males, Friday (along with Nicky) has the largest number of mutual grooming interactions.

Dylan's most significant grooming relationships are with Friday (whom he grooms almost three times more than Friday grooms him), with Nicky and with Wilson, both of which he grooms more than they groom him. His grooming among the females is distributed largely among adolescents and young adults; he spends most time grooming with Kankan, Alice and Wanda, and the latter two groom Dylan more than he grooms them.

Of the females, Cleo, Florin and Kankan show the most evenly distributed grooming relationships. Cleo has strong grooming relationships with all the males except Wilson. She spends the most time grooming with Boris, and this relationship appears almost reciprocal, with Cleo grooming Boris slightly more. Cleo also grooms Friday slightly more than he grooms her, but Dylan and Nicky groom her more than she grooms them. Cleo's strongest relationships among the females are with Heidi, Kate, Sarah, Wanda and Kankan. All of these relationships are characterised by almost equal amounts of grooming given and received.

Florin's grooming is distributed among a limited number of partners. Her strongest relationships are with Chrissie, her infant, and Alice her adolescent daughter. Florin grooms Alice more than twice the amount of time Alice grooms her. As is usual in a mother-infant relationship, it is Florin who provides all of the grooming in her relationship with Chrissie. Florin grooms for a small amount of time with the four adult males; with Boris and Wilson, Florin grooms more than she is groomed but the reciprocity is reversed with Friday and Nicky. Florin grooms for only small amounts of time with the other females. Her strongest relationships are with Heidi, Cleo and Sarah.

Kankan shows the third highest value for diversity of grooming. She directs most grooming towards her juvenile daughter Whitney, receiving about a third of this amount from Whitney in turn. Her infant daughter Patti receives another large amount of grooming. Kankan has moderate grooming relationships with only two males, Boris and Nicky; in both relationships grooming is reciprocal. Among the adult females, Kankan's strongest relationship is with Cleo, and she spends far more time grooming with Cleo than with any other female. The amount of grooming she gives and receives from Cleo is almost equal. Kankan's other significant grooming partner is her mother Kate, but she grooms Kate more than twice the amount of time that Kate grooms her. Other moderate grooming relationships are with Heidi, Sarah and Farthing.

Grooming relationships are much less evenly distributed for Mandy and Wanda. Like Florin, much of Mandy's grooming is directed towards her infant Zeezee, with Mandy receiving a small amount of grooming in return. Among the males, Mandy directs most of her grooming to Friday, receiving none in return. Among the females, Mandy grooms Cleo, Rosie and Kankan the most. She receives a similar amount of grooming from Cleo, but receives more grooming than she gives from Kankan.

The diversity index for Wanda is the lowest for all the focals. Her strongest grooming relationship is with Cleo, and this relationship is almost entirely reciprocal. Wanda also spends a moderate amount of time grooming her mother Heidi, and she grooms Heidi slightly more than Heidi grooms her. The only other female Wanda spends a moderate amount of time grooming is the adult female Kate. Among the males, Wanda grooms Boris and Dylan more than she is groomed by them, but she spends most time grooming with Wilson (who grooms her more than she grooms him) and Friday (whom she grooms more than she is groomed by him).

Several conclusions can be drawn from the data for the distribution of grooming. For males, those individuals who spread their grooming less evenly seem more likely to have intense grooming relationships with a selected number of partners. The males Wilson, Friday and Dylan, while showing greater diversity in grooming distribution, have few close grooming partners. This pattern may suggest the importance of status in determining both overall distribution of social interactions and identity of social partners. The young adult Friday and adolescent Dylan spend more time grooming other males than do Boris, Wilson and Nicky. Older higher ranking males are preferential grooming partners for both adolescent males and females (Simpson, 1973; Pusey, 1978, 1990; Goodall, 1986; Kawanaka, 1990). However, neither Friday nor Dylan direct any grooming towards the most dominant male Boris. This raises questions about the nature of the status relationships within the group. In the case of Dylan, the observed lack of pant-grunting towards Boris, and the absence of grooming between them, may indicate a status relationship that is currently undergoing change; in such situations lack of contact between the protagonists may be a useful strategy to avoid conflict (de Waal, 1982).

Friday and Dylan both direct a large amount of grooming towards adult and adolescent females, and Dylan also spends more time grooming with young and low-ranking females than do the other males, perhaps indicating a lack of strong well-developed bonds to dominant more popular females, and competition for access to them.

While previous work suggests that male chimpanzees groom for longer and have more grooming partners than females (Muroyama and Sugiyama, 1994) the present data do not show this pattern. This may be due to the effects of captivity, which may serve to intensify relationships among females, particularly during times of instability in the male hierarchy (Baker and Smuts, 1994).

The relationship between distribution of grooming and intensity of grooming relationships is different for the female data. While there are differences in distribution of grooming between the focal females, all of them have strong grooming relationships. The dominant female Cleo is the only female to have a strong grooming relationship with a male, and this is with the dominant male Boris. Cleo also has a strong grooming relationship with Wanda. As previously noted, Wanda shows the least diversity of grooming among the females; this may indicate that Wanda, as an adolescent, has yet to acquire strong bonds within the group. However, the older females Kankan, Mandy and Florin also have only one or two strong grooming relationships, and these are kin-based. While status is less of a consideration for females, it seems likely that personality differences, or personal preference may influence social relationships more than for males. While kin relationships feature largely in the distribution of female proximity and grooming, Kankan, Cleo and Wanda have at least one strong grooming relationship with non-kin.

The females Florin and Mandy show no intense grooming relationships with non-kin. Yet the personality profiles for these animals are dissimilar. Mandy scores highly on Sociability, and Florin low. Mandy is highly anxious and scores low on Dominance, while Florin scores high on Dominance and low on Anxiety. It is of course possible (and highly likely in nonhuman primates) that different personality tendencies may produce similar behaviour. Mandy's high anxiety may be important in restricting the number of close social relationships she cultivates, while Florin's low sociability may result in the same social patterning.

6.6.3 Reciprocity of grooming

The number of times each individual initiated grooming sessions was briefly examined. Table 6.11 shows the proportion of grooming bouts initiated by each focal. Figures are based only upon bouts where a clear initiator could be determined; the total number of bouts the percentage is based upon is shown in the table.

Table 6.11 Responsibility for initiating grooming bouts

	% initiations	Total no. bouts
Boris	22.2	63
Wilson	71.9	57
Nicky	21.8	32
Friday	44.5	74
Dylan	44.6	56
Cleo	45	40
Florin	67.3	52
Mandy	70	60
KanKan	60	50
Wanda	57.1	28

Boris, Nicky and Friday initiate the least number of grooming bouts, with Wilson, Florin, Mandy and Kankan initiating the most. The correlations between factor scores and percentage initiations were extremely low, but age correlated -.22. While insignificant, the direction of this effect suggests that older animals initiate less grooming bouts than younger animals.

The percentage of initiations was correlated with factor scores separately for males and females. Sociability correlated low to moderately for both males (-.30) and females (-.10), suggesting that more sociable animals initiated slightly less grooming bouts. Dominance was moderately related for both sexes; for males, more dominant animals initiated more grooming (.50), while more dominant females initiated less (-.50). The correlation between Anxiety scores and grooming initiations was low for males (-.20), but much higher for females (.90, significant at an uncorrected alpha level of .03), suggesting that more anxious males initiate less grooming, but more anxious females initiate more. The correlations for Curiosity were in the same direction for the sexes, but slightly higher for males (.40) than for females (.30).

The differences between the sexes in the relationship between anxiety and grooming initiation is interesting here. The male scoring highest on Anxiety is Nicky, and he initiates the least grooming out of all the focals. The highest female scorer on Anxiety is Mandy, and of the females she initiates the most grooming bouts. This raises issues concerning the differential expression of personality in males and females. If personality is an aspect of an individual's social relationships, we might expect that the usual sex-specific patterning of those social relationships may be differentially affected by personality. For instance, the present data suggest that anxiety may affect grooming relationships in females more than in males. An anxious female may find it more difficult to establish strong social bonds with higher-ranking animals and may expend greater effort in initiating grooming with desired social partners. In males rates of anxiety may affect grooming much less, as an anxious male may have normal amounts of grooming directed towards him (particularly from females). The expression of anxiety may have much more of an impact in male status relationships.

6.7 Play

The total number and proportion of point samples observed in play was calculated for each focal, and the identity of play partners. Table 6.12 shows these figures, the estimated time spent playing, as well as the number of bouts and the median bout length of each play session.

For most of the animals, play occupied only a small percentage of the total 20 hours observation time. Wilson and Dylan were the males who played the most, and most of their play sessions were with infants. Wilson played the most with infants Holly and Patti, and with adolescent Alice. Dylan, who is the highest scorer on Curiosity, spent the most time playing with infants Kiki, Holly, Chrissie and Patti. Kiki's mother Halfpenny is one of Dylan's strongest associations. In their play relationships, both males are responsible for the majority of the play bouts observed.

Table 6.12 Number of point samples, proportion of point samples, estimated duration, estimated percentage time, number of bouts and median bout length of time spent playing for the focal animals

	No. of point sample	Prop. of point samples	Estimated time (mins)	Estimated % time	No. of bouts	Median bout length
Boris	7	.002	3.5	0.2	4	1
Wilson	53	.022	26.5	2.2	11	1
Nicky	6	.002	3	0.2	3	1
Friday	12	.005	6	0.5	4	2
Dylan	110	.045	50.5	4.2	11	2
Cleo	40	.016	20	1.6	9	2
Florin	15	.006	7.5	0.6	4	1.5
Mandy	55	.022	27.5	2.2	10	1
KanKan	31	.012	15.5	1.2	7	1
Wanda	13	.005	6.5	0.5	8	1

Of the females it is Mandy, Kankan and Cleo who spend the largest amount of time playing, and these females are the highest scorers on Sociability. Cleo plays most with Lizzie and Zeezee; she often acts as 'auntie' to the latter. Kankan plays most with her daughter Whitney. Mandy is the most playful of the females, playing most with Whitney, her own daughter Zeezee, Kiki and her brother Wilson. Both Cleo and Kankan are responsible for the majority of their play sessions, while Mandy is responsible for about half.

There was a moderate, though non-significant relationship between age and proportion of point samples spent playing ($r_s = -.34$), suggesting that older animals play less. Correlations between proportion of point samples spent playing and the factor scores were very low (and not significant at the required level), but were higher when the sexes were considered separately. More sociable males played less (-.46) but more sociable females played more (.90, significant at an uncorrected alpha level of .03). The difference between these two correlations was not significant at the corrected level of p = 0.0005 (but significant at an uncorrected level of p = 0.025). More dominant males played more (.56), while more dominant females played less (-.90, significant at an uncorrected alpha level of .03). The difference between these two correlations was not significant at the corrected level of p = 0.0005 (but significant at an uncorrected level of p = 0.01). The relationship between play and Anxiety scores was very low for males (.05) but moderate for females (.40), suggesting that more anxious females play more. The correlations for Curiosity were in the opposite direction for the sexes; more curious males played more (.61), but more curious females played less (-.50).

6.8 Discussion

The data presented in this chapter indicate that the relationship between behaviour and personality ratings can vary substantially according to which measures of social behaviour are utilised. The attempt here was to examine both broad measures of sociality and more detailed analyses of social relationships, and an attempt will be made in this section to summarise the main findings and to highlight the utility of the various measures in the understanding of personality differences. Due to the small sample size, few of the relationships discussed here proved to be significant when the probability level was corrected for multiple tests. However, some of the reported correlations are moderate or high, suggesting that there may be interesting relationships between some behavioural measures, and personality factor scores (though these would have to be confirmed with a larger sample).

6.8.1 The relationships between the behavioural measures

Some of the measures of proximity, grooming, play and time spent alone were strongly related (though these correlations were mostly nonsignificant at the corrected level). As expected, time spent alone was negatively related to time spent in proximity ($r_s = -.99$, significant at the corrected alpha level of .0002) and to time spent grooming ($r_s = -.71$, significant at an uncorrected alpha level of .02), but positively related to time spent playing (.32). Several measures of grooming were used and these were generally correlated: e.g. proportion of point samples spent grooming was positively correlated with the median grooming bout length (.81, significant at an uncorrected alpha level of .003) and number of grooming bouts (.47). Time spent grooming was not related to time spent in proximity (excluding play and grooming): $r_s = .01$. Amount of grooming given was positively related to time spent in play (.49) but the amount of grooming received was negatively related to time spent in play (-.57). Play was negatively related to proximity (excluding grooming and play): $r_s = -.22$.

6.8.2 Personality differences in primary measures of behaviour

The difficulty of determining straightforward relationships between the behavioural measures is reflected in the complexity of the relationships between the behaviours and the factor scores. In many instances, the magnitude, and sometimes the direction of these relationships changed when males and females were considered separately. Correlations involving only five individuals should be treated with caution, but for completeness all of the correlations are summarised and discussed here.

For some of the measures, absolute levels of behaviour correlated reasonably well with personality scores. For example, more sociable animals spent less time alone and more time in proximity to others. More dominant and more curious animals, by contrast, spent more time alone and more time in proximity, although this was only true for females. More dominant males spent *less* time alone and less time in proximity. There were poor relationships, however, between absolute levels of grooming and play and the factor scores when data were included for all the focals. Although proportion of time spent grooming and playing correlated moderately with age (older animals groom more, and play less), these measures did not relate strongly to the personality factor scores. When the sexes were considered separately, however, correlations were much stronger. For males, animals who groom the most are rated highly on Dominance and Curiosity, and low on Sociability and Anxiety. The pattern is almost the reverse for females: females who groom the most are rated highly on Sociability, but low on Dominance, Anxiety and Curiosity.

When grooming was considered in terms of amount given and received, there was a moderate relationship with personality when scores for males and females were grouped. Animals rated as more dominant gave less grooming and more anxious animals gave more. Those rated as more dominant and more curious received more grooming. When considered separately, however, the patterns for males and females differ. Males who give more grooming are more dominant and curious, and less sociable and anxious. Females who give the most grooming are highly anxious, but low on Sociability, Dominance and Curiosity. Males who receive the most grooming are curious, but less sociable, dominant and anxious; females who receive the most grooming are rated highly on Dominance and Curiosity, but low on Sociability and Anxiety.

The relationship between play and personality scores also varies for males and females. Males who play most are rated highly on Dominance, Anxiety, and Curiosity, but low on Sociability. Females who play the most are highly social and anxious, but less dominant and curious.

The directions of the interactions between the personality ratings and behavioural measures can be summarised as follows:

Sociability

For both males and females, more sociable animals spend less time alone and more time in proximity to others. More sociable males spent less time engaged in grooming and had fewer, and shorter, grooming bouts. More sociable females groomed more, and had more, and longer, grooming bouts. For both sexes, more sociable individuals initiated fewer grooming bouts. More sociable males were found to play less, but more sociable females played more.

Dominance

More dominant males spend less time alone and less time in proximity to others. More dominant females spend more time alone, and less time in proximity to others. More dominant males groom more, have more grooming bouts, and have longer grooming bouts. More dominant females groom for less overall time, have fewer grooming bouts, and shorter grooming bouts. While more dominant males play less, more dominant females play more.

Anxiety

More anxious males spend more time alone, and more anxious females spend less time alone. More anxious males spend less time in proximity to others, while more anxious females spend more time in proximity. More anxious males groom less, have fewer grooming bouts, and those bouts are of a shorter duration. More anxious females groom less, have more grooming bouts, but these are of a shorter duration. More anxious males and females play more (although the correlation between play and Anxiety is very low for males: .05).

Curiosity

More curious males spend less time alone, and less time in proximity, while more curious females spend more time alone and more time in proximity. More curious males spend more time grooming, have more grooming bouts and have bouts of a longer duration. More curious females groom less, have fewer bouts and these bouts are of a shorter duration. More curious males play more, while more curious females play less.

6.8.3 Personality differences in relationship measures: Association patterns

As indicated above, the relationship between personality ratings and behavioural measures differed greatly between the sexes, and this was also true when the quality of their social relationships was considered. Examining the basic measure of proportion of point samples spent in proximity, the strongest relationships between personality ratings and proximity were found for females, with proximity being positively correlated with Sociability and Anxiety scores, and negatively with Dominance and Curiosity scores. A similar pattern was found for males (except that Anxiety was negatively, not positively, related to proximity). For both sexes, there appears a general pattern of more dominant animals being rated as less sociable.

It seems likely that estimates of personality are influenced by more subtle appreciation of the quality and dynamics of each individual's social relationships. Although absolute differences between focals on distribution of affiliation were small, there was variation both between and within the sexes. For males, those animals who distributed their affiliation less evenly seemed to have more intense relationships. Patterns of affiliative diversity and intensity did not relate clearly to personality ratings for the five males; instead, the effects of age and status relationships between the males can perhaps most clearly explain patterns of affiliation. However, given the small sample size, there are suggestive relationships between some aspects of personality and quality of affiliation. For example, the highest scorer on Sociability (Nicky), while not spending a particularly high proportion of time in proximity, shows by far the highest number of reciprocal relationships, and has the highest diversity of affiliation among the males. Nicky also has the largest number of intense relationships among the males (compared, for instance, to Boris and Dylan, who are low scorers on Sociability).

For females, the effects of kin relationships appear to most clearly explain the quality of affiliation. All the focal females have at least one strong relationship within the group, but there are also some differences in affiliation which relate to the personality ratings. Cleo, the highest ranking female, is the highest scoring female on Sociability and shows the greatest diversity of affiliation among the females. Cleo also has more intense non-kin ties than the other females. The two females who score low on Sociability (Wanda and Florin) have fewer strong bonds within the group than the other females.

It is clear from the data presented here that personality ratings cannot be considered outside of sex-specific affiliation patterns. It is possible that these patterns are present as norms against which raters judge animals, or alternately, that they are simply not taken into account. For instance, Boris and Dylan are considered to be the least sociable of the males, yet both show different patterns of affiliation. Boris has few, intense relationships, whereas Dylan distributes his affiliation more widely but has few strong associates. These patterns would be expected given the relative age and status of each. An important question is whether raters are attributing internal, trait-like qualities to the animals (e.g. both males are considered to have an 'unsociable' temperament that simply expresses itself in different ways). It may be that raters' estimations of females are more likely to be expressive of perceived aspects of the individuals' temperament, since status has less of an impact on social relationships. In males, estimations of sociability and dominance seem more dependent on status-specific social patterning.

The animals rated as least sociable were also rated as most dominant and most curious: Boris, Dylan, Florin and Wanda. The nature of the Curiosity factor may be elucidated a little further by consideration of the social responsiveness of these animals. The highest loading items on this factor related to three areas: items reflecting active, physical exploration of the environment; items reflecting characteristics such as resourcefulness and persistence, and items such as *intelligent, adaptable,* and *deceitful,* which loaded more highly on other factors, but loaded moderately on the Curiosity factor. These latter items are more indicative of the Machiavellian factor, identified in Study 1. One aspect of Curiosity, then, might relate to a type of social vigilance or awareness, perhaps the kind of awareness necessary to compete for status.

In the light of this discussion, it is interesting that the females Florin and Wanda actually score more highly on Dominance than Cleo, who is widely considered to be the dominant female in the group. However, the Dominance factor seems to distinguish animals who are motivated to dominate others from those who are not, rather than more formal dominance roles. Thus it is Dylan and not Boris who is the highest scorer on Dominance. This is not surprising in the light of Dylan's frequent and persistent attempts to challenge the other males. Some of the highest loading items on the Dominance factor relate to overt signs of dominance; e.g. *displays, causes aggression,* as well as items relating to negative social style: e.g. *moody, unpredictable, impatient, deceitful.* These characteristics may be more typical of younger animals striving for dominance status, rather than older animals with established dominance roles. Thus Florin and Wanda score as high, or higher, than Cleo on items such as *causes aggression, motivated to dominate* and *persistent.*

6.8.4 Personality differences in relationship measures: Grooming and Play

High levels of grooming and play might be expected to be characteristic of more sociable animals, but the correlations between these measures and Sociability scores indicated that this was only the case for females. The most sociable males, Nicky and Wilson, groom for less of the total time observed, and have fewer grooming partners than the other males, while the most sociable females Cleo, Mandy and Kankan groom for longer, and have more grooming relationships than the other females (see sociograms Figs. 6.7 and 6.8). In order to understand this difference between the sexes, it is necessary to consider the effects of age and relative dominance. Although Boris grooms relatively rarely with other males except Wilson, he is a popular grooming partner for the females, and he receives more grooming from the females than he distributes. Dylan grooms more with the other males than Boris, but it is Dylan who is more responsible for these grooming relationships. Dylan receives more grooming than he gives from the females, although his female grooming partners tend to be younger and less dominant animals than Boris's grooming partners. As the next youngest male to Dylan (and a moderate scorer on Sociability) Friday also has a large number of grooming relationships. Like Dylan, Friday grooms a lot with the younger females, but also spends some time grooming with older females such as Cleo, Heidi and Kate. For these males, the distribution of their grooming may be related more to the cultivation and maintenance of dominance positions. While Boris is the current alpha, Dylan frequently challenges him, and often successfully intimidates Friday. It is interesting that it is also Dylan who spends the most time in play. These play bouts may also be attempts to cultivate relationships with females, by interacting with their infants; a common strategy for young males attempting to establish alliances with important others (e.g. de Waal, 1982). There is actually a positive relationship between Dominance and Curiosity scores and the time spent grooming and playing for males, but a negative relationship for females. It seems likely, then, that these activities are more influenced by status considerations for males than for females. This is to be expected; if grooming is indicative of sex-specific reproductive strategies then the frequency, duration and directionality of grooming is more likely to be status-linked for males than for females (Muroyama and Sugiyama, 1994; but see Baker and Smuts, 1994).

For both males and females, more anxious animals spend less time grooming. This pattern seems unusual if the function of grooming is to reduce tension (e.g. Seyfarth, 1976, 1977). However, there are important differences between the sexes in the relationship between anxiety and grooming. More anxious males give and receive less grooming, and initiate fewer grooming bouts. More anxious females give more grooming and initiate more grooming bouts, but receive less grooming. This pattern for females suggests that more anxious females do groom to reduce tension (and research suggests that grooming may reduce physiological tension; e.g. Goosen, 1987). The two females with the highest Anxiety scores, Mandy and Kankan are also the lowest scoring individuals on Dominance. The pattern for males may indicate that more anxious animals have fewer successful grooming relationships. While it is difficult to draw general conclusions from such a small sample, an examination of Nicky's grooming relationships is interesting. Nicky scores much more highly than the other males on Anxiety and is the lowest scorer on Dominance. Of all the males, Nicky has the fewest grooming partners, although he receives more grooming from those partners than he gives. Nicky is also the male least involved in status disputes; perhaps his grooming preferences are less linked to the dynamics of dominance relationships, compared to the other males.

6.8.5 Identity of the personality factors

Some of the differences in association, grooming and play behaviour do appear to be related to age and sex-specific patterns of behaviour, even though the sample for this study was small. Thus frequency, duration and distribution of proximity, grooming and play seem to be suggestive of sex-specific social strategies, and the differences between these measures suggest that they capture different aspects of chimpanzee social life.

Some of the frequency and duration measures of the social behaviours seemed to relate strongly to personality factor scores, indicating that the ratings do reflect important behavioural differences between the focal individuals. A more detailed examination of relationship characteristics such as the distribution and directionality of these social interactions helped to clarify the possible nature of each of the personality factors.

While there were differences between males and females in the number and distribution of proximity partners, those males and females with higher Sociability scores did have stronger associations in the group than low scorers. When grooming patterns were examined, high sociability was a good indication of grooming levels for females. For males, Sociability scores also distinguished amount of grooming, with highly Sociable males grooming less.

There was an important relationship between Sociability and Dominance scores; those animals scoring highly on Dominance were rated as less Sociable. Males and females rated as more dominant had fewer proximity partners, but were as likely as the less dominant individuals to have some strong associations. Thus, each of the focals had important association partners, and often these association patterns were indicative of age and sex-specific differences. For instance, the females with offspring associated with their infants for a large proportion of time. Animals rated highly on Dominance were also rated highly on Curiosity, and it was suggested above that the Curiosity factor may better be considered as indicative of social vigilance, or social awareness. While these two factors were linked for both males and females, they were predictive of different patterns of behaviour: males scoring highly on these factors spent more time grooming and playing, with the opposite pattern apparent for females. If Dominance and Curiosity scores are indicative of striving for status, then this appears to be expressed differently for males and females.

The Anxiety factor was strongly related to measures of grooming and proximity, but differently for males and females. Males who were rated as more anxious spent more time in proximity to others, but groomed less. More anxious females spent less time in proximity but groomed others more. The focals rated as most anxious were Nicky, Mandy and Kankan. While rated as being highly sociable, Nicky has fewer intense grooming relationships than the other males, and (along with Boris) distributed his grooming less evenly. Mandy and Kankan both have strong grooming relationships with other females; in Mandy's case however her closest partner is her daughter Zeezee).

It is likely that social anxiety may be manifest through more subtle measures than those utilised here. It seems clear that proximity and grooming cannot necessarily be assumed to be 'sociable' behaviours, since personality ratings may relate differently to each measure. The fact that trait-behaviour relationships differ so much between males and females may assist, rather than hinder, the interpretation of such relationships. Thus for anxious females, grooming may serve as tension reduction, or alternately be a way of increasing social bonds within the group. For males, anxiety may function to inhibit formation of social bonds through grooming. Alternately, since grooming relationships are shaped by status considerations in males (Simpson, 1973) more anxious males may simply be less able to manage social relationships.

The next chapter examines agonistic relationships in order to further clarify the relationship of personality ratings to behaviour.

CHAPTER SEVEN

Personality differences and agonistic relationships

7.1 Introduction

Perhaps more than any other aspect of social structure, dominance behaviour highlights the complex dialectic between characteristics of the individual and the supra-individual aspects of relationships. Because of the numerous internal and external influences on dominance behaviour, simple correlations between specific measures of dominance rank and individual characteristics may be unlikely. However, quantifiable measures of rank may be predicted more easily from characteristics of relationships. For instance, Simpson's (1973) measures of male chimpanzee dominance rank related closely to the direction of agonistic and grooming behaviour for particular dyads, but this pattern was much less clear when compared across dyads (Hinde, 1978). Thus, the level at which predictions are made concerning behavioural correlations is important.

While an individual's dominance is expressed within certain age and sex-specific constraints, individual differences in motivation, intelligence, and interaction histories should also influence dominance behaviour. Adaptive individual differences, perhaps maintained by frequency-dependent selection, would be expected to result in a number of alternative behavioural strategies (Budaev, 1999). Variation in the expression of alternative dominance strategies, such as coalitions, may therefore reflect both more and less flexible phenotypic traits (de Waal, 1978, 1984, 1989a; van Hooff and van Schaik, 1992).

While frequency-dependent selection may result in variation in temperament (resulting in differences in such characteristics as shyness-boldness, for instance) (Budaev, 1999), variability in dominance-related behaviour may be seen as a result of inherited social goals which lead to the adoption of particular behavioural strategies (e.g. de Waal, 1993b) or social tactics (Buss, 1991). Therefore personality differences in the domain of dominance behaviour may best be conceptualised as differences in the management of social relationships, via the adoption of a specific dominance strategy (or a number of strategies). Such variation would be expected in a species with a slow rate of maturation, and hence extended opportunity for social experience, together with a large number of flexible behavioural potentials (de Waal, 1993b).

In both chimpanzees and humans, the nature of social goals and dominance strategies shows sex-specific variation (de Waal, 1984, 1993b; Buss, 1991). At their most basic level, male strategies act to ensure optimal access to fertile females, while female strategies serve to maintain a secure social environment in which to raise offspring (de Waal, 1993b). The intragroup environment in which these goals are pursued has important consequences for the nature of the social strategies employed by each sex. Intragroup competition for females, and intergroup competition for resources and females, favoured the formation of a formalised male hierarchy, while relatively little female intragroup competition resulted in nonhierarchical dominance relationships among females (de Waal, 1978, 1984, 1993b).

In same-sex relationships, both the content and quality of relationships are structured by the nature of dominance strategies. Thus male social bonds are characterised by opportunistic and fluid alliances, while female bonds tend to be more stable and more kin-based (Baker and Smuts, 1994). Similarly, male-female bonds may be conceptualised as opportunities for both sexes to invest in potentially profitable partners: for males, bonds with females increase mating access in an environment of female choice; for females, dominant male associates may be powerful protectors or allies (van Hooff and van Schaik, 1992).

If social relationships are the outcome of the interaction between individual strategies (e.g. van Hooff and van Schaik, 1992) then intraspecific variation in dominance behaviour is more a function of the relationship than of the individual (c.f. Stevenson-Hinde, 1985; Stevenson-Hinde and Hinde, 1986; Hinde, 1992), and must be understood within this context. The aim of the present study was to examine agonistic relationships at a number of levels. The number and direction of pant-grunts was examined and compared to personality ratings. Rate of displaying was calculated for the five males. In addition, conflict episodes from the focal data and the video sequences were analysed to compare the relative role of each animal in conflict situations. These measures are considered within the context of each animal's network of relationships.

7.2 Personality differences and measures of formal dominance

Earlier research suggests that a reliable context-free indicator of dominance relationships in chimpanzees is the directionality of submissive pant-grunts (de Waal, 1977). When the dominance relationships in a group are unstable, pant-grunts, as a measure of formal dominance, may be withheld (de Waal, 1982).

Table 7.1 shows the frequency and distribution of pant-grunts recorded during the focal animal observations and the video observations.

General observations suggest that, of the adult males, Boris and Wilson are most dominant, although the adolescent Dylan constantly challenges Boris, and is openly aggressive to Friday. The female hierarchy is more complex; observations suggested that Cleo, Florin, and Heidi are most dominant, while Mandy, Farthing and Rosie are the least dominant of the adult females.

The distribution of pant-grunts supports these impressions. Of the 243 total pant-grunts recorded, Boris received about half. Dylan received the second largest amount, followed by Wilson. Nicky and Friday received a small number each. It is interesting that the only observed male-male pant-grunt was directed towards Dylan by Friday, suggesting that Dylan's concerted attacks on Friday have reversed the dominance order between them. The relative lack of observed pant-grunts among the males suggests that the male hierarchy is indeed in a state of flux. While Dylan appears to have little support from the other males in his attacks on Boris, there appears to be no clear male support for Boris either. The current dynamics of the male relationships are discussed in more detail below.

Only five pant-grunts were directed by females towards other females, and these occurred to Cleo and Florin, two of the highest ranking females. Mandy, Heidi, Farthing and Rosie gave the highest number of pant-grunts.

Table 7.1 Frequency and distribution of pantgrunts

	Pant-grunted to							
Pant-grunts	Boris	Wilson	Nicky	Friday	Dylan	Cleo	Florin	**Totals**
Boris								
Wilson								
Nicky								
Friday					1			**1**
Dylan								
Cleo	3			1				**4**
Florin	10	9						**19**
Mandy	19	1	2	1	17	2		**42**
KanKan				1	1			**2**
Wanda	6	3	1		7			**17**
Meg	5							**5**
Kate	3							**3**
Heidi	11	9		2	1			**23**
Ha'penny	9	3			6			**18**
Farthing	15	4	2		1			**22**
Rosie	7	1			16			**24**
Sarah	10	2			6		1	**19**
Sally	11	2	1		3		1	**18**
Kaylie	4	3			2			**9**
Layla	6					1		**7**
Alice	5	1			4			**10**
Totals	**124**	**38**	**6**	**5**	**65**	**3**	**2**	**243**

Frequency of pant-grunts was correlated with the factor scores for the whole group[2]. Number of pant-grunts received correlated most highly with Dominance scores for males (.80) and moderately with Sociability scores (-.60). Correlations were low for Anxiety (.10) and Curiosity (.20). None of these correlations were significant at the corrected alpha level. For females,

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[2] Spearman's *rho* was used for all correlations in this chapter. The criterion level of alpha was 0.0002, following Bonferroni correction.

number of pant-grunts given was correlated most strongly with Dominance scores (-.50, significant at p = .04) but there was little correlation with Sociability (-.01), Anxiety (.13) and Curiosity scores (.01). In general though, it seems that males who received the largest number of pant-grunts were rated as more dominant, anxious and curious, and less sociable. Females who gave the most pant-grunts were rated as less dominant and more anxious.

There was a moderate correlation between age and number of pant-grunts received for males (r_s = .40, n.s.), suggesting that older males receive more pant-grunts. However, number of pant-grunts given by females was not related to age. The basic measure of rank obtained by scores on the item *dominates other members of the group* was related highly to pant-grunts received for males (.97, p = .002; n.s. at corrected alpha level) but moderately for number of pant-grunts given for females (-.32). Similarly, scores on the item *motivated to dominate* were used as a simple guide to perceived differences in motivation to become dominant, and again this was positively correlated with pant-grunts received for males (.71) and negatively related to pant-grunts given by females (-.33).

Male rate of nondirected bluff displaying was also highly correlated with personality factor scores. Dylan performed 68 displays, almost 42% of the total 161 bluff displays recorded. Boris and Wilson performed 39 and 36 displays respectively; Friday 8 and Nicky only 5. The only female observed to display was Kate, who performed five nondirected bluff displays. Male rate of displaying was perfectly correlated with Dominance scores (1.00) and also highly correlated with Sociability (-.90, p = .02; n.s. at corrected alpha level) and Curiosity scores (.70). A low correlation was found between rate of displaying and Anxiety scores (-.10). Rate of displaying also correlated very highly with frequency of pant-grunts received (.80, p = .08; n.s. at corrected alpha level).

The relationships between the factor scores and the above measures suggest that, for males and females, it is scores on the Dominance factor that most clearly differentiate individuals in terms of basic behavioural estimates of rank.

7.3 Sex, age and personality differences in agonistic interactions

Details of agonistic episodes were recorded during the focal observations, and were videotaped during specific daily periods. The intensity of agonistic episodes was rated on a three point scale, to distinguish between mild agonistic behaviour (e.g. directed bluff displays, brief chases, mild threats), moderate agonistic behaviour (e.g. sustained chases, charges, brief hits and slaps) and high-intensity agonistic behaviour (e.g. physical assaults, displays culminating in sustained attacks). The categorisation of each agonistic episode incorporated the behaviour of the target of the agonism; particularly when conflict episodes must be recorded quickly, the type and intensity of vocal and other reactions are important clues to the way the target has interpreted the behaviour.

7.3.1 Analysis of conflict episodes

All of the conflicts involving one or more of the focal animals were analysed. Conflict episodes were classified as distinct if they were separated by pauses of not less than two minutes. Each conflict episode was split into dyads for the purpose of analysis. Dyads were categorised as 'pure' if there were only two animals involved in the interaction, and as 'impure' if a third animal became involved. Interactions between agonistic dyads were categorised according to the definitions used by de Waal and van Hooff (1981):

Multiple initiation

An animal initiates agonistic behaviour towards more than one target, either concurrently or in quick succession.

Redirection

The target of agonistic behaviour attacks a third individual within 30 seconds.

Side-directed communication

An individual involved in an agonistic dyad shows behaviour towards another individual who is not involved in the conflict, e.g. an appeal for assistance.

Agonistic intervention

A third individual shows agonistic behaviour towards one or both members of an agonistic dyad. The intervener may be impartial, or may show support for one of the dyad.

Semi-agonistic intervention

The intervener in an agonistic dyad bluffs toward or chases one or both members of the dyad, but does not attack either.

Non-agonistic intervention

The intervener may interrupt the conflict by moving between or toward the interactants, by showing submissive behaviour, or by consoling one of the interactants.

Attendance

One, or several, animals may approach the vicinity of the conflict to watch, but they do not become involved in the conflict.

Table 7.2 shows the frequency of observed conflict episodes of various types. Most of the agonistic interactions consisted of isolated dyads, i.e. dyadic interactions that were not part of larger conflict episodes. There was a small number of triadic episodes, but only 15 polyads; seven of these involving four animals, six involving five animals, one polyad of six animals and one of nine animals.

Table 7.2 Frequency and type of conflict episodes

Pure dyads	166
Impure dyads	70
Triads	27
Polyads	15
Total agonistic interactions	278

7.3.2 Initiation of agonistic episodes

The number of times each focal individual initiated a dyadic or triadic confrontation was calculated, together with the intensity of each confrontation and the context in which it occurred. Table 7.3 displays the frequency and proportion (out of the total agonistic interactions in which the focal was involved) of agonistic interactions in which the animal was the initiator or receiver of aggression, and the number of times the animal was involved in side-directed communication (i.e. intervened in the conflicts of others, or was the subject of an appeal by other agonistic interactants).

Table 7.3 Frequency and percentage of agonistic episodes for focal animals

	Initiated		**Received**		**Side-directed**		
	Frequency	**%**	**Frequency**	**%**	**Frequency**	**%**	**Totals**
Boris	43	49.4	28	32.1	16	18.3	87
Wilson	42	60.8	11	15.9	16	23.1	69
Nicky	13	28.8	6	13.3	26	57.7	45
Friday	6	14.6	28	68.2	7	17.0	41
Dylan	111	86.7	10	7.8	7	5.4	128
Cleo	14	31.8	17	38.6	13	29.5	44
Florin	5	25	10	50	5	25	20
Mandy	7	19.4	20	55.5	9	25	36
KanKan	5	33.3	5	33.3	5	33.3	15
Wanda	11	52.3	8	38	2	9.5	21
Totals	**257**		**143**		**106**		**506**

Dylan initiates the largest number of agonistic interactions, followed by Boris; both males are the highest scorers on Dominance. The large score here for Dylan reflects the changing nature of the dominance relationship between these two males. Both Friday and Dylan receive a large amount of agonism directed towards them. Nicky is involved in the largest number of side-directed interactions. Thus there are clear differences in the nature of the agonistic relationships for the five males.

Wanda initiates the highest number of agonistic conflicts, followed by

Kankan and Cleo. Wanda's pattern of agonistic behaviour is interesting; despite being the youngest focal female she initiates almost as many agonistic interactions as Cleo, and indeed Wanda and Cleo are the highest scorers on Dominance. Mandy receives the most agonism, and she is the highest scorer on Anxiety. The females initiate less agonistic interactions (*U* = 4.0, p = .07; n.s. at corrected alpha level) than males, and are involved in less side-directed interactions than males (*U* = 4.0, p = .07; n.s. at corrected alpha level).

Frequency of initiations is strongly correlated with Sociability (-.70) and Dominance scores (.90, p = .03; n.s. at corrected alpha level) for males, and moderately correlated with Anxiety (.30) and Curiosity (.40) scores. Frequency of agonistic interactions received was highly correlated with Anxiety (-.97, p = .004; n.s. at corrected alpha level) and moderately correlated with Sociability (-.35), Dominance (-.52), Curiosity (.35) and Age (.35). The strongest relationships here suggest that scores on the Dominance factor are most closely related to agonism initiated, while scores on the Anxiety factor are closely related to agonism received. Frequency of side-directed communication was highly correlated with Curiosity (-.94, p = .01; n.s. at corrected alpha level) and Sociability (.73), and moderately correlated with Dominance (-.53), Anxiety (.52) and Age (.63), suggesting that males who are more involved in side-directed communication are rated as highly sociable. The relationship between side-directed communication and Curiosity scores may be influenced by age. The youngest male Dylan scores highest on the Curiosity factor, but, as expected, does not show as much side-directed communication as the adult males. This suggests that his high Dominance score is a reflection of his high level of agonistic challenges, rather than a reflection of more subtle aspects of dominance (such as the tendency to intervene in conflicts of others).

For females, initiation of agonistic interactions is highly correlated with Anxiety (-.66; n.s. at corrected alpha level) and moderately correlated with Sociability (.35), Dominance (.20), Curiosity (-.10) and Age (.35). Frequency of agonistic interactions received was highly correlated with Age (.80, n.s. at corrected level) and Sociability (.60; n.s. at corrected alpha level) and moderately correlated with Dominance (-.40), Anxiety (.10) and

Curiosity (.20). The size of the correlation between frequency of agonistic interactions received and Anxiety is much larger for males than for females; however, this difference was not significant at the corrected level of p = 0.0005 (but significant at an uncorrected level of p = 0.01).

Frequency of side-directed communication for females was highly and significantly correlated with Sociability (.97; p = 0.004, n.s. at the corrected level) and Age (.97; p = 0.004, n.s. at the corrected level) and moderately correlated with Dominance (-.61; n.s. at corrected alpha level), Anxiety (-.05) and Curiosity (-.41). Frequency of side-directed communication, therefore, appears to be strongly related to Sociability scores for females. Two of the strongest relationships in the female data suggest an important effect of age; with older females receiving more agonistic interactions, and being more involved in side-directed communication.

Tables 7.4 and 7.5 show the total number of initiations for males and females, and the proportion of initiations of each level of conflict intensity. The proportion of interactions composed of bluff dyads is also shown; a bluff dyad is defined as a non-vocal bluff display directed at a particular individual or individuals, sometimes culminating in an attack.

The adolescent Wanda was the only female who was observed to direct bluff attacks; she displayed twice against other adolescent females. Wanda is also the female with the highest score on the Dominance factor.

Dylan initiated the greatest number of agonistic conflicts; more than twice the amount initiated by Boris and Wilson. This pattern clearly indicates the extent to which Dylan utilises agonism to further his dominance status. Less than half of Dylan's large number of agonistic initiations were bluff dyads, suggesting that, unlike Boris and Wilson, his conflict interactions are more about furthering status, rather than simply maintaining it.

About half of the total conflicts initiated by the males were of the lowest intensity. Boris and Wilson show similar patterns of distribution over the three levels of intensity; both initiated more Level 1 intensity conflicts than Level 2, and more Level 2 conflicts than Level 3. This pattern is the same for Friday. Nicky initiates slightly more Level 2 and 3 conflicts than Level 1. Dylan initiates almost equal amounts of Level 1 and Level 2 conflicts, which may reflect his status as a challenger to Boris' alpha position.

The percentage of initiations that were composed of directed bluff displays was almost the same for both Boris and Wilson: almost two thirds of their total initiations. The proportion of bluff dyads for Dylan and Nicky is lower, and Friday did not initiate any bluff dyads.

Table 7.4 Relative frequency of agonistic initiations for focal males

	Level of conflict intensity				
	1 %	2 %	3 %	**Total number of initiations**	**% of bluff dyads**
Boris	58.1	27.9	13.9	43	**67.4**
Wilson	57.1	30.9	11.9	42	**66.6**
Nicky	23.0	38.4	38.4	13	**38.4**
Friday	66.6	33.3	0.00	6	**0.00**
Dylan	46.8	42.3	10.8	111	**42.3**
Total number of initiations	**108**	**79**	**28**	**215**	

Table 7.5 Relative frequency of agonistic initiations for focal females

	Level of conflict intensity			
	1	2	3	**Total number of initiations**
Cleo	50.0	14.2	35.7	**14**
Florin	40.0	40.0	20.0	**5**
Mandy	71.4	14.2	14.2	**7**
KanKan	80.0	20.0	0.00	**5**
Wanda	63.6	18.1	18.1	**11**
Total number of initiations	**25**	**8**	**9**	**42**

As expected, the frequency of agonistic initiations of all levels of intensity was lower for females ($U = 4.0$, $p = .07$; n.s. at corrected alpha level).

Cleo initiated the greatest number of conflicts, followed by Wanda. These females also initiated more Level 3 intensity conflicts than the other females; Cleo initiated more Level 3 than Level 2 conflicts, and Wanda initiated the same number of Level 2 and Level 3 conflicts. Most of the conflicts initiated by the females were Level 1 intensity, and the proportion of total conflicts that were Level 1 conflicts was about the same for males and females (50.2% and 59.5% respectively). Males initiated slightly more Level 2 conflicts than females (36.7% and 19.0% respectively), but females initiated slightly more Level 3 conflicts than males (21.4% and 13.0% respectively).

To summarise, the males who initiate the most agonistic confrontations score highly on Dominance, Curiosity and Anxiety and low on Sociability. Females initiating the most confrontations score low on Anxiety. There is a small tendency for older females, but not males, to initiate more agonism, although the high rate of agonism shown by the young male Dylan skews the male data somewhat.

Those males who receive most agonism are rated as less anxious and sociable, and more dominant and curious. Females receiving the most agonism are rated as more sociable and less dominant. For both males and females, animals rated as more sociable and less dominant are involved in more side-directed communications.

7.4 Distribution of agonistic interactions

Tables 7.6 and 7.7 show the frequency and distribution of dyadic agonistic initiations for all males and females (excluding infants).

The distribution of agonistic interactions among the males clearly shows the status struggle between Dylan and Boris. Dylan directs an almost equal amount of agonism towards Boris and Friday. While Dylan appears to be dominant to Friday, the status relationship between him and Boris is not so clear. While Boris appears to remain the most dominant male, he is the subject of occasional attacks by Wilson and Nicky.

Boris directs most agonism towards Cleo, one of the most dominant females, and one of his closest associates. Many of these initiations occurred within the context of agonistic polyadic interactions, and frequently when Dylan had challenged Boris. Boris' attacks on Cleo may be attempts to ensure her continued allegiance.

Table 7.6 Distribution of agonistic initiations for focal males

	Initiator					
	BS	WN	NK	FD	DY	Totals
Receiver						
Boris		3	3		20	**26**
Wilson	5				6	**11**
Nicky		2			5	**7**
Friday	2	2	1		23	**28**
Dylan	4	1	1	1		**7**
Cleo	11	4			3	**18**
Florin	3	2			3	**8**
Mandy		1		1		**2**
Kankan		1			6	**7**
Wanda	2	2		1	1	**6**
Meg	1					**1**
Kate	3	2	2		2	**9**
Halfpenny	4		2		4	**10**
Farthing		8			1	**9**
Heidi		1			5	**6**
Rosie	1	2		1	23	**27**
Sarah		3			2	**5**
Sally	1	3		2	3	**9**
Kaylie	3	2			3	**8**
Layla		3	2		2	**7**
Alice	5	2	2		3	**12**
Totals	**45**	**44**	**13**	**6**	**115**	**223**

Wilson distributes his agonistic initiations fairly evenly amongst the females. He directs most agonism towards Farthing, his closest proximity partner and the animal to whom he directed the most grooming. His agonism towards her was often in the context of his repeated attempts to mate her.

Friday and Nicky initiate very few agonistic interactions. While Nicky initiates five interactions against adult males (three of which are against Boris), Friday initiates only one towards the males. This is against Dylan and is in the context of a larger polyadic conflict. Together with Dylan, Nicky receives the lowest number of agonistic initiations. The young adult male Friday, however, receives aggression from all the males, and a large proportion of this is from Dylan.

In his agonistic initiations against the females, Dylan aggresses most against Rosie, Heidi, Kankan and Halfpenny. Rosie and Heidi are actually Boris' closest proximity and grooming partners, and some of Dylan's bluffs attacks on Boris occurred when Boris was associating with these females. Kankan is also one of Boris' close grooming partners and Rosie and Kankan were often the subject of high level physical aggression from Dylan.

The other female receiving most aggression from Dylan is Halfpenny. She is one of Dylan's strongest proximity and grooming partners, and it is Dylan who is responsible for this association. As with Boris' attacks on Cleo, Dylan's aggression against Halfpenny may be an attempt to win her support.

In general, females did not direct any agonistic initiations towards males; the only two recorded are by the dominant females Florin and Cleo, towards Boris and Friday respectively. Cleo and Wanda initiate the most agonism against other females; Cleo directs most of hers towards adolescents Kaylie, Layla, Alice and Sally. Wanda also directs initiations towards Kaylie, Alice and Sally, but also initiated two interactions against Mandy. Mandy, Kankan and Florin do not initiate many interactions; Kankan and Mandy direct all their interactions towards the adolescent females, while Florin directs most towards adult females, but one towards Boris.

Table 7.7 Distribution of agonistic initiations for focal females

	Initiated																
	CL	FL	MD	KN	WD	MG	KT	HD	HP	FG	RS	SR	SL	KY	LY	AL	Tot
Rec'd																	
BS		1															1
WN																	0
NK																	0
FD	1																1
DY																1	1
CL							1										1
FL						1	1										2
MD					2			1		1			1		4	4	13
KN																	0
WD															1		1
MG																	0
KT	1				1												2
HD		1															1
HP	1																1
FG		1															1
RS		1			1												2
SR																	0
SL	3				1												4
KY	3		1	1	3												8
LY	1		1														2
AL	3		1	1	3												8
Total	13	4	3	2	11	1	2	1	0	1	0	0	1	0	5	5	49

7.5 Side-directed communication

The extent to which individuals engage in side-directed communication may provide important information concerning differences in the way individuals manage their conflict interactions, as well as highlighting the dynamic nature of chimpanzee dominance relationships (Walker Leonard, 1979). Side-directed communication is important in the construction and maintenance of coalitions and alliances (de Waal, 1984), and the distribution of such coalitions has important effects on the quality of social bonds within the group. The categories of side-directed communication examined in this study consisted of appeals (where one individual solicits aid from another), re-directed aggression, agonistic, semi-agonistic and non-agonistic interventions, and non-agonistic support (e.g. consoling the victim of aggression).

7.5.1 Agonistic interventions and support choices

Instances where one individual intervened in an agonistic dyad were recorded. The identity of the intervener was noted, and which participant the intervention was in support of. Also noted was whether the intervention was in support of the initiator of the agonistic interaction, or the receiver, and whether the intervention supported the winner or loser of the conflict (following de Waal, van Hooff and Netto, 1976; Nishida and Hosaka, 1996).

Ninety-two agonistic interventions were recorded. The general patterns of interventions involving the focal animals will be discussed here (support choices of focal animals are shown in Appendix VIII). In addition, basic estimates of the intensity of social bonding (the 'familiarity index') were obtained by summing the percentage of point samples each focal spent in proximity (including grooming) with other members of the group (de Waal, 1984). The extent to which familiarity was associated with support choices was assessed by calculating the percentage of support choices that were in favour of the more familiar partner (e.g. if A has a higher familiarity index with B than with C, we might expect A to support B against C) (de Waal, 1978, 1984). All observed familiarity-dependent interventions for the focal animals are presented in table 7.8.

The data presented in table 7.8 are based upon very small frequencies of interventions and so must be treated with caution. However, it appears that, of the adult males, Boris and Nicky show the largest proportion of familiarity-linked interventions (over 50%). However, Wilson and Dylan show a low proportion of familiarity-linked interventions (only one intervention was observed for Friday). De Waal (1984) has suggested that the support choices of more mature males may be less connected to their social bonds; that is, they may be more opportunistic, and that this disparity may be greater during periods of dominance instability. However, the pattern of interventions shown here does not support this, although it is possible that the frequency of interventions is too small to draw many general conclusions.

Table 7.8 Familiarity-dependence of focal animal support choices

	No. of familiarity-linked interventions	Total no. of interventions	Percentage of familiarity-linked interventions
Boris	4	5	80
Wilson	3	10	30
Nicky	7	12	58.3
Friday	0	1	0
Dylan	1	4	25
Cleo	1	4	25
Florin	0	2	0
Mandy	5	6	83.3
KanKan	3	3	100
Wanda	1	1	100

Males intervened more than females in agonistic interactions, although this difference was not significant. Nicky initiated the largest number of (agonistic and non-agonistic) interventions (16) out of all the focal animals. Four of these were impartial interventions. The majority of his directed interventions were in support of females, although he supported Boris once against Dylan, and Dylan three times against Friday. Nicky seemed to be a loser-supporter, and he generally supported the receiver in each agonistic dyad. The only exception was his support of Dylan, which occurred in the context of a lengthy conflict which Dylan had initiated against Friday. The outcome of this context was curious; it occurred outside in full visibility of the rest of the group, and it was a clear, unprovoked attack on Friday. Friday appealed for help to the other males, whereupon Boris, Nicky, Wilson and Cleo attacked Friday. The only support Friday received was from the old female Meg, who chased Dylan.

Wilson was recorded as initiating 12 interventions, two of which were impartial. Most of these interventions involved females and were loser-supports. Wilson supported Boris once against Cleo; on this occasion Boris was the initiator of aggression, and Cleo the loser.

Boris supported others only six times. One of these was an impartial support, and the rest were loser-supports in favour of females (with the exception of the Friday — Dylan conflict discussed above).

Friday and Dylan showed the lowest frequency of interventions. Dylan supported Mandy twice against other females, and he supported Cleo twice, once against Friday and once against Sally. Interestingly, on both of these occasions Cleo was the initiator of the conflict, and the winner. Friday intervened only three times: two of these were impartial interventions in conflicts between Florin and Rosie, and Boris and Florin. The other intervention also involved Florin, but Friday supported Kate in an attack on Florin.

Although the sample size is small, these patterns support previous work on the identity of support choices in chimpanzees. In particular, the present data suggest that more dominant males are likely to intervene most, and are likely to be loser-supporters (c.f. de Waal, 1978; de Waal and van Hooff, 1981). The tendency of dominant males to assume a 'control' role (i.e. support losers) is an important part of male dominance strategies (de Waal, 1978, 1984). The tendency to support the loser in a conflict may help male status efforts in two ways: by forming potentially profitable alliances in order to rise in status, and by maintaining status by breaking up conflicts and supporting weaker individuals (who may be future allies) (de Waal, 1984). The present data suggest that the oldest males Boris, Wilson and Nicky were consistent loser-supporters. The number of recorded interventions for Friday and Dylan is low, but Friday showed no loser-supports, and Dylan supported Cleo (a winner, and a high-ranking female) on two occasions. While winner-supports may act to maintain the existing dominance hierarchy (e.g. de Waal, 1978, 1984), there may be occasions when supporting a winner is the most strategic option to choose, if the winner is a more useful ally. On the two occasions that Dylan supported the dominant female Cleo, it was against Sally, an adolescent female, and against Friday, who appears to be lower-ranking to Dylan.

Of the focal females, Mandy intervened the most. Of her six interventions, three were in favour of her infant Zeezee. She supported Sarah against Heidi once, and supported Friday against Dylan, both loser-supports. On one occasion Mandy supported Alice against Sarah, a winner-support.

Cleo intervened in 5 conflicts. One of these was impartial, and two were in favour of Zeezee, whom Cleo 'allo-mothers'. Cleo supported Sally against Dylan once (a loser-support) and Nicky against Friday once (a winner-support).

Florin and Kankan intervened in only three conflicts. Florin gave impartial support in a conflict between her daughter Alice and her sister Halfpenny. On the other occasions, Florin supported Kaylie against Layla and Sally against Halfpenny, both of these were winner-supports.

Kankan was observed to support her mother Kate against Dylan once, and Meg against Sarah, both loser-supports. She also supported Farthing against Mandy, but the initiator and the outcome of this conflict was unclear.

Wanda was only observed to intervene once; this was to support her mother Heidi against an attack by Florin.

As expected, the frequency of intervening was smaller for females than for males. Although the sample size is small, the pattern of intervention choices found suggests that, unlike males, female support choices are more kin-related (c.f. de Waal, 1978, 1984).

7.5.2 Non-agonistic support

Sixteen instances of non-agonistic support were noted; details are given in Appendix IX. A quarter of these supports were by Nicky, and consisted of consolation of a loser in a conflict.

Nicky was also the focus of specific appeals by individuals involved in agonistic conflict. Of 23 clear solicitations for aid, seven were directed to Nicky. Slightly more were directed to Boris (8), only two to Wilson and one to Friday. Five appeals were made to females; one to Alice, one to Kate and three to Cleo. Thus older males and females were more likely to be the subject of appeals.

7.6 Agonistic strategies

In order to fully understand the patterns of agonism and agonistic intervention in the group a brief description of some of the more complex dynamics of the agonistic relationships is necessary.

7.6.1 Separating interventions

De Waal (1982) described the process whereby an adult male will charge toward two or more associating individuals, who will then separate. Twelve clear separating interventions were observed, eleven of which were performed by Dylan. Seven of these were directed towards Boris and Rosie. Rosie is one of Boris' closest proximity and grooming partners. Four separating interventions were directed towards Boris and Nicky, when these pair were in proximity or grooming. Nicky's role in the Boris — Dylan conflict may be crucial; Nicky appears unwilling to support either Boris or Dylan fully. In the largest polyadic conflict observed in the group, where Dylan attacked Boris, Boris repeatedly appealed to Nicky, with full fear-grins and screams. Nicky repeatedly avoided Boris, although he eventually displayed briefly towards Dylan. It seems clear that the roles of Nicky and Wilson may be important in the outcome of Dylan's status challenge, and the latter's pattern of separating interventions seems to support this.

Dylan performed only one separating intervention towards Friday, and that was when the male was grooming with Cleo. A further seven possible separating interventions were also noted. The classification of these was not as clear, but it seemed likely that their function was to separate associating animals. Three of these were by Dylan: one separated Boris from Rosie and Heidi, who were grooming Boris at the time. One was directed by Boris towards Wilson and Cleo. Three were directed by Wilson; one towards Boris and Kaylie, one towards Nicky and Florin, and one towards Boris and Heidi.

7.6.2 Strategies of 'intimidation'

Dylan's attempts to dominate Boris involved one particular type of agonistic behaviour which is worth mentioning here. During the last 2-3 years, twelve-year old Dylan has successfully managed to dominate the youngest adult male, Friday. Up until this time, Friday appeared to be the main challenger to Boris's position. In a relatively short span of time, however, he has become the least dominant male, even though he is almost twice the age of Dylan. In his agonistic confrontations with Friday, Dylan often uses a particular type of intimidation. He will approach Friday, sit or stand face-to-face with him and begin to playfully wrestle, or 'finger-wrestle' very gently. Often both males display a play-face. Gradually, sometimes over several minutes, Dylan's wrestling becomes gradually rougher and more aggressive, and he no longer displays a play-face. At this point the pair will often move around the enclosure, still playfully wrestling, but with Friday retreating backwards. Eventually, Dylan either hits or pushes Friday too hard, and Friday screams and often flees, with Dylan pursuing and sometimes attacking further. During these episodes, other individuals will sometimes intervene and appear to try to distract Dylan. For example, Wilson sometimes approaches the pair and playfully grabs at Dylan's foot. Occasionally this results in Dylan ceasing the behaviour and leaving Friday.

While a large number of Dylan's agonistic interactions were directed at Friday (20%) an equal number were directed at Rosie. Dylan used a similar type of 'intimidation strategy' towards Rosie. He would approach and initiate a bout of finger-wrestling. Both animals would display play-faces. Again Dylan would gradually become rougher, usually fairly quickly, and would attack Rosie. Often, his play-wrestling would become soft thumps, quite gentle at first, and delivered with a play-face. The thumps would become harder until Rosie would show a fear-grin and eventually yelp or scream. Dylan would sometimes initiate this when Rosie was in proximity to Boris. This 'pummelling' of less dominant females, usually directed at Rosie and Kankan, would often occur just before or after a bluff display by Dylan, but it was not part of the display. Goodall (1986) has suggested that attacks incurred by female targets of bluff displays, in the context of group excitement, may be interpreted as less severe than attacks occurring in other contexts; i.e. they are taken less 'seriously' by the victims. However, Dylan's agonism against Friday, Rosie and Kankan often appeared pre-meditated and often occurred in the absence of group excitement. The effect of these sustained attacks was that Rosie very often showed a fear-grin, and squealed when Dylan approached her, or passed by close to her. It was also apparent that when Dylan was close, Boris would consistently avoid Rosie. Rosie made a large number of approaches to Boris, and often invited grooming from him, or attempted to groom him repeatedly. Dylan's separating interventions thus appeared to result in Boris' avoidance of Rosie, but his attacks on Rosie had the opposite effect, as she would frequently approach or appeal to Boris during them (although Boris rarely intervened on her behalf).

Dylan's use of play to initiate his agonistic interventions is interesting. It seems unlikely that his behaviour was simply an ambiguous response to an existing playful situation, as he did not show a similar escalation of aggression in play with other partners. In addition, his approach was rarely playful, he did not exhibit a play-walk or display the usual gestures of invitation. He would approach his targets silently and quickly, and immediately establish contact and begin wrestling. That these contacts were responded to, at least initially, with play-faces and panting by the targets indicates that they actually were interpreted as play to begin with. One interpretation is that Dylan was attempting to test the limits to which he could aggress, certainly this seems likely with Friday. Indeed, sometimes these wrestling bouts would not become aggressive and both males would separate peaceably. It is tempting to assume that Dylan used the context of play to explore the limits of his power over others.

7.7 Discussion

The agonistic interactions observed within the group appear to relate to some extent to the personality ratings, as well as to indicate a certain amount of instability in the male hierarchy. At the most basic level, the extent and direction of pant-grunting is closely related to Dominance scores for both males and females, as well as strongly related to Anxiety scores for females (i.e. more anxious females pant-grunt more). The other simple measure of dominance recorded, rate of male bluff displays, also appeared to relate strongly to Dominance scores for males.

There were clear differences between the focal animals in the amount of agonistic interactions initiated and received, and in the distribution of those interactions. However, only a small number of agonistic interactions were recorded for some focals and, given the small sample size and the complexity of agonistic behaviour, it is perhaps unwise to draw general conclusions regarding the correlations between the factor scores and these measures.

However, there are interesting relationships between each chimpanzee's personality profile and the general nature of their agonistic interactions. For example, despite being the youngest male Dylan scores the highest on the Dominance factor. While the frequency of pant-grunting suggests that Boris is the dominant male, it is in fact Dylan who initiates the largest number of agonistic interactions. At a further level of analysis, the direction of Dylan's agonistic initiations is also significant: he targets other adult males frequently (particularly the most and least dominant males) and he targets specified females, notably Boris's close associates. It is clear that Dylan is becoming a serious threat to Boris' alpha position, and the Dominance scores reflect this. It is interesting to note in this context that Dylan is in fact the second highest scorer (after Boris) on the personality trait item *motivated to dominate*. Individual differences in dominance 'style' have been linked before to differences in motivation (e.g. Riss and Goodall, 1977) but the extent to which motivation can be said to be an individual characteristic is unclear. While such descriptions may be simply summaries of the dominance strategy/strategies used by an individual, it is likely that they also implicitly involve some estimation of more long-lasting personal qualities.

The females rated as most dominant, Wanda, Florin and Cleo also show interesting patterns of agonistic behaviour. Florin and Cleo are the only 2 females (out of the whole group) to be pant-grunted to. Wanda is the only female observed to direct bluff displays towards other individuals. Wanda and Florin also receive a relatively small amount of aggression directed towards them. Cleo receives a larger amount of aggression, but most of this (nearly 60%) is from Boris. As discussed above, these attacks may be attempts on the part of Boris to secure Cleo's support, and so may not be comparable to other agonistic interactions. Cleo and Wanda initiate the most agonistic interactions among all the females, and Cleo and Florin are the only two females observed to direct agonism towards a male.

The female rated as most anxious, and least dominant, is Mandy. Mandy receives the largest amount of aggression of all the focal females, and pant-grunts the most. General observations suggest that Mandy is a very nervous animal. She appears to be particularly sensitive to the possible threat of attack; many of Mandy's conflicts result from her reactions to the close proximity of boisterous infants and juveniles. Mandy often threatens a younger animal who has moved too close to her, and monitors nearby play sessions carefully. Often she appears to 'over-react' to seemingly accidental contact by a playful juvenile. In addition, however, Mandy is often a target for teasing by the young adolescents Kaylie, Layla and Alice, and by Kankan's juvenile daughter Whitney. On these occasions, Mandy reacts to even mild teasing with annoyance and often aggression. By comparison, the difference between Mandy and Cleo's behaviour in these situations is striking; Cleo is extremely relaxed around younger animals, and frequently enters into interactions with playful juveniles and infants.

The role of Nicky is also worth mentioning in more detail here. Nicky is the highest scorer on Sociability and the lowest on Dominance, while scoring highly on Anxiety. Nicky receives the fewest pant-grunts out of all the males, and initiates the lowest number of agonistic interactions. The caretakers maintain the opinion that Nicky, although the largest male in the group, is a 'coward'. However, despite Nicky's low Dominance ratings, he actually receives the smallest amount of agonism from other individuals. It seems that, far from being submissive, Nicky has an important 'control' role in the group. De Waal (1994) described the tendency of some chimpanzees, often the most dominant individuals, to frequently intervene in the agonistic interactions of others. Nicky intervenes in more conflicts than any other animal and most of these interventions support losers. Nicky is obviously perceived by others to be an effective ally, as he often receives solicitations for aid from others. In addition, Nicky's role in the Dylan — Boris relationship indicates that both males value, and seek, Nicky's support but, generally speaking, Nicky avoids involvement in male agonistic interactions. Previous researchers have noted Nicky's 'lack of motivation to dominate' (e.g. Murray, 1995) and this impression seems to be supported by his low

Dominance and high Anxiety score, and by the measures obtained in this study. However, such a judgement may (as discussed above) be an attempt to conceptualise differences in dominance strategies in terms of more personal characteristics and traits.

To summarise, some of the measures of agonistic behaviour examined here relate clearly to the personality factor scores, while others necessitate more detailed analysis of dominance relationships. The current conflict between Boris and Dylan makes it more difficult to simplify the personality-behaviour relationships, but also serves the purpose of highlighting the importance of the relationship context for understanding personality differences. Both the personality ratings and informal conversations with the caretakers suggest that subjective personality impressions actually mirror quite subtle differences between the animals very well, but these distinctions may relate to more subtle behaviour that is difficult to easily quantify. For instance, the nervous demeanour of Mandy was highly apparent during observations, but is not necessarily strongly expressed in every behaviour pattern recorded here. However, it seems clear that more detailed analysis of agonistic interactions, e.g. the examination of side-directed communication and support choices, may enable more complete evaluations of the utility of personality ratings. In addition, such an analysis may help to tease out the more stable aspects of each individual's personality from more temporary situational contexts like dominance take-overs.

The present findings highlight the importance of a number of issues in the search for trait-behaviour correlations in the realm of dominance relationships. In chimpanzees, the relative status of an individual within the group affects many other aspects of their relationships (Simpson, 1973). The centrality of dominance to chimpanzee social life is clearly reflected in the factor structure found in the present study; while Dominance was the second factor generated, it shares almost as much variance with the first extracted factor of Sociability (see section 3.3.4). Behaviourally, dominance has been successfully measured in a number of ways and this multitude of different behaviours provides a fertile field within which to search for trait-behaviour interactions. However, what is clear is that individual differences in dominance can *only* be considered as a function of social relationships. That is, they are expressed through specific sex-linked behavioural strategies, within the context of intra-specific competition. While status relationships may limit the flexibility of the behaviour that can be expressed, such relationships also provide important information about how effectively individuals 'negotiate' their social relationships (Hinde, 1976; de Waal, 1996).

With dominance behaviour in particular, the nature of the trait-behaviour relationship must come under close scrutiny, as it throws into question the exact causal nature of the observed variation. That some chimpanzees manage their social relationships better than others is clear, but the precise inherited and environmental factors that determine such differences are less apparent. However, given the dynamic and complex nature of chimpanzee social organisation and dominance relationships, it is likely that some aspects of social skill (such as the ability to successfully utilise coalitions and alliances) may be linked to inherent differences in social intelligence (e.g. de Waal, 1982) and motivation (Riss and Goodall, 1977), or to the ability to tolerate social stress (e.g. Suomi, 1991). The nature, and the extent, to which these individual characteristics are expressed, however, seems to depend very heavily upon the social goals inherent to each sex (e.g. de Waal, 1984).

The present findings suggest that, as Hinde (e.g. 1976, 1978, 1995) has indicated, a relationship approach to the study of personality differences has much to offer the study of primate personality. While more basic measures of rank appear to relate well to personality ratings (e.g. the correlation between pant-grunting and Dominance ratings), such ratings may not always predict more dynamic and complex aspects of dominance (e.g. the formation of coalitions). This may be significant for our understanding of the differences between human and chimpanzee dominance factors. In humans, it may be possible to link differences in dominance more clearly to aspects of the individual (e.g. Ellis, 1992), while in chimpanzees dominance may be better conceptualised as an function of relationship (c.f. Stevenson-Hinde, 1985).

CHAPTER EIGHT

General discussion and future work

8.1 Introduction

Although humans have long been attributing personality to animals, the empirical study of such attributions, and their possible relationships to behaviour, is much more recent. Despite this, the field of animal personality touches upon many of the most long-standing and challenging questions about behaviour. In many ways, these questions reflect central issues in human personality psychology. At the same time, recent trends within personality psychology itself show increasing awareness of the utility of evolutionary approaches in building eclectic explanations of the structure and function of personality. As Gosling (2001) notes, part of the value of research on animal personality lies in the assumption of at least some continuity between species in the structure and development of personality differences.

Recent reviews of animal personality work (Clarke and Boinski, 1995; Gosling, 2001) demonstrate a wide variety of sub-issues within the literature; to some extent, however, the type of species under investigation clearly determines the theoretical issues addressed. For example, most studies of personality trait ratings have been conducted on mammals, with the vast majority of these on primates, while more basic measures of temperament (e.g. reactivity) have been conducted on non-mammals (c.f. Gosling, 2001). While this might suggest cross-species differences in personality structure, it also suggests a difference in the way that humans relate to various species. Thus the study of animal personality not only provides an opportunity to examine issues relating to the genetic and environmental bases of personality, to the reliability and validity of trait ratings, and to the relationship of ratings to behaviour, but also provides a window on the psychological processes of attribution and the nature of the human-animal relationship.

This chapter discusses the implications of the present work with regard to questions about the structure and function of animal personality, considered within the context of animal-human relationships.

8.2 The structure of primate personality

Although the wide range of rating methods used make it difficult to compare personality dimensions across studies, there does appear to be some similarity in the personality structures identified in primate studies, including the present study. To facilitate comparison, studies on personality in apes and monkeys can be considered within three broad groups: those studies utilising a rating scale derived from Stevenson-Hinde and Zunz (1978), those studies using items relating to the human Five Factor model of personality, and all other studies. Of this latter group, the studies using correlational or factor analysis are most useful for the present purpose, as they present an opportunity for comparison with other findings. The few studies based upon Plutchik and Kellerman's (1974) Emotions Profile Index, for example, are difficult to compare with other work as they did not produce broad personality factors or dimensions (e.g. Buirski *et al.*, 1978; Martau *et al.*, 1985; Buirski and Plutchik, 1991; Carlstead, Mellen and Kleiman, 1999).

Stevenson-Hinde and Zunz (1978) and Stevenson-Hinde *et al.* (1980a) identified three personality dimensions in rhesus macaques: confident — fearful, active/excitable — slow and sociable — solitary. A number of later researchers have identified the same or similar dimensions in macaques using scales based wholly or partially on the Stevenson-Hinde and Zunz (1978) instrument (Caine *et al.*, 1983 for pig-tailed monkeys; Bolig *et al.*, 1992 for rhesus macaques; and Figueredo *et al.*, 1995 for stumptail macaques). Mondragon-Ceballos, Santillan-Doherty and Chiappa (1991) identified the sociable and confident factors but also a dominance factor (but no active/excitable factor) in stumptail macaques. Only one study using this instrument identified four factors instead of the original three: Capitanio (1999) identified factors of sociability, confidence and excitability in rhesus macaques, together with an additional factor of equability.

Only two studies of Great Ape personality used ratings based on the Stevenson-Hinde and Zunz (1978) items. Murray's (1995) ratings of captive gorillas, chimpanzees and bonobos produced dimensions of confident, sociable and excitable (Murray, 1995, 1998). However, in their ratings of captive gorillas, Gold and Maple (1994) found four factors, rather than three: extraverted, dominant, fearful and understanding.

Despite some disparity between the studies based upon Stevenson-Hinde and Zunz' items, factors of sociability and confidence were common to all the species studied, and most also found an active/excitable dimension. It is interesting to note here that a sociability factor was also found in three studies on monkeys using different rating scales (Chamove *et al.*, 1972 on rhesus macaques; Raleigh, McGuire and Brammer, 1989 and McGuire *et al.*, 1994 on vervets). In addition, both of the vervet studies also identified an 'opportunistic' or 'devious' dimension, not present in the Stevenson-Hinde and Zunz (1978) factor structure (in the study by Chamove *et al.* (1972) a 'hostile' factor also appeared).

More recently, some researchers have argued for a 'common language' in personality description across species and have urged the use of the human five factor model (FFM) in rating animals (e.g. Gosling and John, 1999; Gosling, 2001). There seems to be increasing consensus in human personality work as to the existence of the five basic factors of Extraversion, Agreeableness, Neuroticism, Openness to Experience and Conscientiousness (Costa and McCrae, 1992; but see Zuckerman, 1992 for an alternative view). To date, the FFM has only been used twice in studies of animal personality, both studies have rated captive chimpanzees. This instrument yielded factors resembling the human five factors in King and Figueredo's (1997) study, with the addition of a dominance factor. Lilienfeld *et al.* (1999) generated 37 personality items, partially on the basis of items used in a number of previous studies, to measure the Big Five traits along with a measure of psychopathy in chimpanzees. Psychopathy items correlated positively with chimpanzee Extraversion scores, and negatively with Agreeableness scores (Lilienfeld *et al.*, 1999). This pattern reflects that found in the human literature, suggesting that both the psychopathy items and the Big Five items are useful measures of chimpanzee personality.

Using the FFM as a common instrument for rating nonhumans has the advantage of enabling cross-species comparisons of personality structure, including that between humans and nonhumans. Personality factors similar to Extraversion, Neuroticism and Agreeableness appear to be common across many different species, including non-primates (Gosling and John, 1999; Gosling, 2001), while the factor of Conscientiousness may be restricted to chimpanzees (Gosling and John, 1999). One difference between the personality structure of humans and nonhumans is the relative importance of a separate factor of dominance or aggression. Dominance appears part of the Extraversion factor in humans, but achieves greater prominence in the factor structure of the other primates, as well as in species such as the dog and the hyena (Gosling and John, 1999).

While cross-species comparisons of personality structure constitute important clues as to the function of such differences, such comparisons need to account for species-specific personality differences, as well as cross-species commonalities. This means that any potential common rating instrument must also possess the flexibility to incorporate additional species-specific items if the full range of a species' personality is to be measured (Gosling, 2001).

A key aim of the present study was the utilisation of a constructivist technique of item generation to underpin the construction of a common rating scale for chimpanzees. One assumption of the constructivist approach is that personality descriptions reflect the rich relationships between raters and ratees, as well as constituting generally reliable judgements about subjects' patterns of behaviour (Kelly, 1955). The adoption of such an approach encourages the sampling of the full range of rater descriptions, increasing the liklihood that all important aspects of chimpanzee character would be included. An examination of rater descriptions in the present study revealed generally good agreement between raters on what constitutes the most important dimensions of chimpanzee personality; subsequent work using the same methodology in pigs has shown similar close agreement between personality constructs generated separately by different raters (Grajfoner, 1999; Wemelsfelder, Hunter, Mendl and Lawrence, 2000).

The present study is the first to examine the factor structure of chimpanzee personality using items generated wholly by the raters, rather than based upon an existing rating instrument. The generation of four factors, Sociability, Dominance, Anxiety and Curiosity, provide additional evidence of the ubiquity of these dimensions in primates (and perhaps in non-primates too). Moreover, the present data suggest that such dimensions, as in humans, are not easily defined but reflect complex patterns of characteristics. For example, the Sociability factor identified in this study subsumes items relating to quality, as well as quantity, of social interactions, and also reflects skill in dominance interactions (see 3.3.4).

A separate dominance factor has been identified previously in ratings of apes using both the FFM items (King and Figueredo, 1997) and the Stevenson-Hinde and Zunz (1978) items (Gold and Maple, 1994), and was also a feature of the present factor structure. The existence of this as a separate factor in nonhuman (but not human) primates provides a fruitful area in which to pursue questions regarding the nature and function of species-specific personality factors, as well as questions regarding the rater-ratee relationship. If observer ratings can reliably capture intra-species differences in personality, this tells us as much about humans as a rating instrument as it does about the animals being rated.

8.3 The adaptive nature of traits

Key questions regarding the explanation of personality factor structures in humans and animals have hinged upon the nature of the trait concept. At one extreme personality traits may be seen as anthropomorphic descriptions of animal behaviour, at the other they may be seen as possessing explanatory power and relating closely to behavioural patterns. To the extent that trait ratings relate closely to behaviour they are seen to be valid.

Several primate studies have found relationships between ratings on broad traits and behaviours, and these are generally in the predicted directions. For instance, ratings on a sociability factor have been linked to number of close associates for rhesus macaques (Stevenson-Hinde *et al.*, 1980a); to the amount of time spent in social interaction for vervets (McGuire *et al.*, 1994); and to the frequency of grooming initiation in chimpanzees (Murray, 1995).

One of the aims of the present study was to provide a rich sample of behaviour (collected over a relatively long period of time) to compare with trait ratings. Current personality theory suggests that, if there are clear relationships between ratings and behaviour, these will only be evident by considering a wide range of behaviours within the context of several different relationships (Stevenson-Hinde and Hinde, 1986). In addition, there is good evidence to suggest that factors such as the overall quality of a subject's relationships may be more important indicators than *content* of behaviour (Hinde, 1995; see also Reynolds, 1991).

The findings of the present study suggest that, while some basic frequency measures strongly relate to trait ratings, the addition of more detailed information about the type and quality of affiliative and agonistic associations clarify the interpretation of the personality factors. Moreover, this study found clear sex differences in both the magnitude and direction of relationships between factor scores and behaviour. For example, those chimpanzees scoring highly on Sociability spent more time in proximity to others and had stronger affiliative associations. However, while more sociable females spent more time grooming, more sociable males spent *less* time grooming. Similarly, the pattern of relationships between Anxiety scores and behaviour suggested that highly anxious males spend more time in proximity to others, while highly anxious females spend less time in proximity.[3]

Such findings illustrate the difficulty of ad hoc predictions of trait-behaviour relationships. While such predictions are desirable in order to achieve adequate discriminant validity (Gosling, 2001), they necessitate the kind of detail that characterises human personality theory, but is presently lacking in animal personality models. Although some (e.g. King and Figueredo, 1997) have assumed that trait-behaviour relationships will be simpler to determine in nonhumans, the present findings suggest otherwise. What appear to be conceptually similar behaviours seem to relate to trait ratings in different ways, suggesting that in fact they may be functionally dissimilar (Bates, 1986). In addition, the disparity between trait-behaviour relationships in males and females indicates that traits may have different selective advantages in males and females.

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[3] While many of these correlations were not significant at the stringent level of alpha applied, the fact that these effect sizes were often substantial indicates that even in small samples of animals broad, perhaps sex-specific, patterns of variation can be ascertained.

Any explanation of trait-behaviour relationships (in humans and nonhumans) is necessarily shaped by the conceptualisation of the trait concept itself. While there are many problems with the notion of traits as causal mechanisms, not least the inherent assumption within this view of simple trait-behaviour correspondences (Barratt, 1984), most theories of personality are dependent upon it. Within evolutionary psychology, for instance, personality differences are assumed to be the expression of internal psychological mechanisms interacting with (and activated by) environmental factors (e.g. Buss, 1984, 1991). Such mechanisms are numerous and domain-specific, and assumed to underlie alternative goal-directed behavioural strategies. Thus consistency in behaviour "must be sought at the level of basic psychological mechanisms and the events that reliably activate them not.....at the level of manifest behaviour" (Buss, 1991, pp. 478-479). Such hypothetical 'internal psychological mechanisms' are essentially no different to the traditional notion of inherent traits, except that in more recent accounts, they are specifically linked to behavioural strategies. However, conceptualising personality as the differential realisation of adaptive behavioural strategies may make it possible to make more complete predictions of how individuals may be expected to differ, and may facilitate explanation of personality differences both within and between species.

Animal personality studies can help in determining the selective advantages of particular personality characteristics. This process may be both more difficult in humans (due to the complexity of culture) and run the risk of being too simplistic (Bateson, 2000; Herrnstein Smith, 2000). However, the assumption that traits fulfill an adaptive function necessitates evidence that the expression of personality through particular strategies does serve to increase an individual's fitness. One possibility is that global personality traits represent the results of a species' attempts to solve particular adaptive problems (Buss, 1992, 1996). For example, the prevalence of five personality factors that seem to explain a great deal of variation within humans may indicate the most common adaptive problems experienced during hominid evolution (Buss, 1991; King *et al.*, 2000). In this view, the factors of Agreeableness, Extraversion, Openness, Conscientiousness and Neuroticism are not arbitrary ways of categorising individual variation, but may indicate key aspects of human experience, particularly in the social domain. For instance, the importance of the factors Extraversion and Agreeableness as the first two factors to emerge in factor models suggests that an important characteristic of the 'adaptive landscape' in which humans evolved was the variation among individuals both to cooperate with and to aggress against each other (Buss, 1991, 1992, 1996; King *et al.*, 2000).

In studies of nonhumans, Extraversion and Agreeableness also appear to be among the most important personality traits to emerge (Gosling and John, 1999). Convergent evolution may explain similarities in factor structures among different (unrelated) species. However, the prevalence of some cross-species traits appears to depend more upon homology; for instance, the prevalence of a separate dominance factor seems more specific to social mammals, and (nonhuman) primates in particular. The fact that a separate dominance factor is not a characteristic of human personality, but appears in factor analyses of chimpanzees (present study) and gorillas (Gold and Maple, 1994) suggests important differences between the species in the adaptational importance of personality characteristics relating to the striving for, and the achievement of, dominance status. In humans, personality differences in dominance appear to reflect differences in scores on Extraversion and Agreeableness (more extraverted and less agreeable individuals are considered to be more dominant). The present findings indicate that more sociable animals are not necessarily more dominant. While more dominant individuals do have some strong associations within the group, they have fewer proximity partners than less sociable animals. Such cross-species differences may be useful in elucidating the nature of the relationship between personality ratings and behaviours, but they also highlight the species-specific constraints on behavioural expression that lead to differences between, for example, the exact nature of sociability in humans and in chimpanzees.

Recent studies investigating the heritability of personality traits provide important insights into the nature of some of the main personality traits. Although heritability for the major five factors (FFM) varies, there seems a growing consensus that, in humans, most of the variation in personality between individuals results from genetic differences, together with nonshared environment effects (Bouchard, 1994; Weiss, King and Figueredo, 2000). Weiss *et al.* (2000) found a similar pattern for chimpanzees, with a dominance trait in particular showing high heritability, while between zoo differences (i.e. shared environmental effects) were minimal (Weiss *et al.*, 2000). Such findings provide further support for the possible relevance of the FFM in explaining both human and chimpanzee personality.

The present findings indicate the importance of taking into account sex-specific social strategies when interpreting individual differences in chimpanzees. If predictions regarding trait-behaviour relationships are to be useful, they must be based around the expected intra-sexual variation in behaviour that a species is expected to show. Such variation may be more limited for some species than for others, but may also show sex-specific limitations. For instance, in those species where males compete for access to females, individual variation in dominance strategies would be expected to be greater for males. In one sense, this could be viewed as placing more constraint upon the total variation possible for males; alternatively, it might suggest that personality structure is simply different for the sexes, and reflects sex-specific social roles. Future work with much larger samples might fruitfully examine the factor structure of male and female chimpanzees separately.

8.4 Do animals have a 'concept' of personality?

The importance of social life in shaping primate personality, behaviour and cognition (e.g. Dunbar, 1993; Whiten, 2000) suggests that the ability to reliably differentiate conspecifics according to basic personality differences might be adaptive (Buss, 1991; Buss and Greiling, 1999; King *et al.*, 2000). For example, the ability to distinguish more anxious from less anxious potential mates would be useful, as the latter would be more able to effectively cope with environmental stressors (King *et al.*, 2000).

One problem with applying this argument to personality attribution of nonhumans is the difficulty of studying cognition and awareness in animals (e.g. Nagel, 1974). While it is clear that humans use broad concepts of personality to structure and filter behavioural impressions of others, it is not clear whether nonhumans use similar such concepts. Thus while animals may be able to distinguish between relatives and nonrelatives, allies and nonallies in choosing association partners, problems are encountered when such behaviour is assumed to indicate the ability to form personality concepts (e.g. King *et al.*, 2000).

This difficulty is familiar to those who have sought to investigate complex mental abilities like theory of mind in nonhumans (e.g. Premack and Woodruff, 1978; Premack, 1988). While primates in particular may show a capacity for at least some aspects of abstract thought (see Tomasello and Call, 1997 for a review), such abilities have often been seen as quantitatively, if not qualitatively, different from the human ability to conceptualise (Heyes, 1998). That is, a chimpanzee may reliably distinguish between reciprocators and nonreciprocators in its choice of grooming partner, but that does not imply that it is using a concept of 'dependability' to do this.

To an extent, such a distinction raises difficult questions about the extent to which behaviour and mental concepts are isomorphic. To the extent that our chimpanzee can use past information about the dependability of its conspecifics to influence current behaviour, then surely it is behaving 'as if' it possessed a concept of dependability. Yet it is clear that the concepts that humans possess function as more than loose mental organising principles that shape behaviour. They are also characterised by a level of abstractness that the chimpanzee presumably does not possess; helped by language, humans are able to mentally manipulate such abstract concepts like no other species.

On one extreme, we might assume that while nonhumans do use information about behavioural consistency in their social interactions, personality distinctions represent an added layer of abstractness that only human subjects use to distinguish between animals. Alternatively, if we assume that animals like chimpanzees possess a theory of personality, we may be left with Nagel wondering exactly how to gain access to the chimpanzee concept of personality. However, we should at least assume some kind of continuity between personality attribution in humans and nonhumans, particularly among species that are closely related to humans, like the chimpanzee. Given mental continuity between such species, similarities in mental schemas, emotional experience and basic categorisation seem likely. Recent approaches in cognitive science suggest that abstract conceptualisation in humans is built upon, and structured by, basic bodily schemas shaped by perceptual and motor mechanisms (Lakoff, 1987; Johnson, 1987; Lakoff and Johnson, 1999). To the extent that related species share some basic aspects of bodily experience, these approaches may provide an important tool to help us gain a window into their mental experience.

Although it may be likely that, for the same adaptive reasons, humans and chimpanzees perceive similar basic individual differences in others, the process of personality attribution in humans is a constructive one, a process of engagement of a rater with a subject (Kelly, 1955; Hinde, 1995). The fact that trait ratings seem to correspond most closely with *aggregations* of functionally related behaviours, rather than with simple measures, displays some of the extent to which personality attributions reflect ways that humans conceptually organise individual differences and similarities. This is further illustrated by the tendency for personality attribution to be difficult, or impossible, in circumstances where a subject's behaviour appears disorganised or changes very rapidly (see Martau *et al.*, 1985; Bolig *et al.*, 1992).

Although the details of what happens to personality attribution in such situations have been little studied in the animal personality literature, they clearly show that personality attribution is itself a function of the relationship between rater and ratee. It is interesting to conjecture whether the same is true for nonhumans. The type of physical attitude an animal has towards another is clearly determined by their relationship: a subordinate chimpanzee crouches upon the bluff-approach of a dominant. The same context-dependence may also characterise *mental* attitude. As in human attribution, circumstances where personality attribution breaks down may provide important clues to the attribution process. The tendency of one animal to seemingly 'overreact' (i.e. give a more extreme fearful response than others) to a given stimulus (e.g. an approaching animal of higher status) tells us as much about the personality of the first animal as it does about the second. Thus, while some animals may be more successful 'personality psychologists' than others (perhaps those animals scoring highly on 'machiavellian' type traits) it is likely that, in the other great apes at least, personality discriminations are both structured and constrained by relationship parameters.

8.5 Personality attributions and the animal-human relationship

While constructivist approaches to personality place emphasis upon the rater-ratee relationship, often this relationship is seen as something that potentially distorts or otherwise confounds the assumed objectivity of ratings. An alternative view is to assume that ratings, while capturing some real differences between individuals, also reflect to some degree the nature of the relationship between the rater and the human/animal being rated. This is a potential problem for the possible development of a common set of cross-species personality traits (based upon the FFM) that has been urged by some (e.g. Gosling and John, 1999; Gosling, 2001). However, if a common set of rating traits were to be developed, such a set would need to be sufficiently flexible to embrace species-specific traits (King *et al.*, 2000). Such a common set of traits, to be truly applicable to as many species as possible, would perhaps include a set of central or 'core' traits that may be relevant to, for instance, many social mammals (e.g. terms such as 'sociable', 'fearful' etc.). Additional traits would then need to be added to ensure that ratings captured the full range of behaviour of a particular species. For example, Dutton and Andersson (in prep.) used the FFM trait terms generated by Gosling and John (1999) together with additional terms specific to snake behaviour to rate the personality of captive Royal Pythons (*Python regius*).

A concern to capture all aspects of chimpanzee behaviour motivated the adoption of a constructivist technique for generating personality trait terms in the present study. Despite this, the factor structure produced showed good resemblance to those found in other studies of primate personality (see 8.1 above), and bore some resemblance to the FFM model. In addition, reliability between raters was generally moderate (though not always significantly so) but varied substantially between zoos, and between items. This pattern fits in well with findings from other studies. Reliabilities for ratings of nonhumans are generally as high as those for ratings of humans, but do seem to vary across species (more active species are generally easier to rate) and across traits (Gosling, 2001). In addition, factors such as the experience of raters seem to be an important influence on ratings. Such variation suggests important ways in which the experience of raters interacts with ratings produced.

The present findings suggest that some traits were indeed easier to judge than others. Across zoos, those traits relating to sociability and dominance showed higher agreement between raters, while traits relating to complex mental capacities (such as deceptiveness) were more difficult to judge. This pattern is reflected in other animal personality studies (see Gosling, 2001) and in human studies (John and Robins, 1993; Gosling, 2001). It seems to be the case that some traits are simply more visible than others, and thus easier to perceive. This raises the issue of the extent to which ratings of captive animals are able to capture the full range of behaviour, particularly if captive environments are not rich (de Waal, 1994; Wemelsfelder, 1997a). Where animals are kept in semi-natural settings (such as those in the present study), the problem may not be a limitation in the full range of exhibited behaviour, but rather a problem in the visibility of more subtle behaviours. To some extent, this is less of a problem if experienced raters are used who are able to observe the animal in many different settings. The degree of acquaintance of raters does seem to affect ratings of both humans (Funder and Colvin, 1988; Funder, Kolar and Blackman, 1995) and animals (Martau *et al.*, 1985), though no significant differences between more and less experienced raters were found in the present study. Perhaps because of the difficulty of obtaining large numbers of raters of many differing levels of experience to rate large samples of animals, there has been little work focusing specifically upon the effects of experience on ratings of nonhumans (Gosling, 2001). However, with increased awareness of the complexities of rater-ratee relationships, this may be an area that receives more attention in the future. Current work by Grajfoner, for instance, focuses upon exploring the effects of rater experience on ratings of horses (Grajfoner, personal communication).

If degree of familiarity with a subject is an important influence upon ratings, this suggests two things. Firstly, constructivist approaches to animal personality may be of considerable value in allowing raters to express the full extent of their knowledge of familiar animals, particularly in situations where personality description is utilised for welfare purposes (e.g. Wemelsfelder *et al.*, 2000; Wemelsfelder, Hunter, Mendl and Lawrence, in press). Secondly, this implies that personality ratings capture very subtle attributions that reflect the attitude of a rater to a particular animal. This may happen in two senses: both the actual type of relationship (e.g. is the animal being rated a pet, a working animal, a laboratory subject etc.) and the level of intimacy of the relationship (e.g. does the rater respond in a emotionally positive or negative way to the animal) may affect ratings. Closer relationships may not just lead to more positive personality ascriptions, but may in fact lead to the attribution of a greater *range* of characteristics. This may apply more to those human-animal relationships that are characterised by close contact, such as pet-owner relationships, rather than the kind of relationships explored in many animal personality studies (e.g. where caretakers or observers rate animals). However, even in the latter type of relationships, there is a tendency for animals who behave 'out of character' or who are hard to decipher (e.g. individuals that appear to be less expressive) to be considered in more negative terms (Rajecki, Rasmussen, Sanders, Modlin and Holder, 1999). Moreover, some species are commonly considered to be more socially responsive than others (Driscoll, 1995; Bowers and Burghardt, 1992), highlighting the difficulty of considering personality attributions independent of the human-animal relationship.

The question thus arises as to exactly what personality ratings of animals capture. I would argue that, far from being anthropomorphic, they appear to function precisely in the way that personality ratings of humans do. They appear to reflect actual behavioural differences between individuals (and between species) and they show inter-observer and temporal consistency. Just like ratings of humans, however, personality ratings of animals provide rich information about the dynamics of the relationship between human raters and their subjects. Thus trait ratings, because they are based on multiple sources of information, may be seen as an extra dimension of the human-animal relationship that complement behavioural ratings, but that also allow the rater to verbally explore perceived similarities and differences within and between animals (Bates, 1986). As such, trait ratings may capture some of the most important aspects of personality, such as the quality of an individual's social relationships (Hinde, 1995), as well as the assumed psychological continuity underlying disparate acts of behaviour.

8.6 Management and welfare implications

The human predilection for differentiating animals in terms of their motives, behaviours and intentions (all of which are implicated in the use of personality trait terms) suggests that the study of subjective well-being in other species might be a simple enterprise. Instead, the judgement of more subtle aspects of well-being (as opposed, for instance, to simple measures such as appetite) is a complex task, hindered in part by the difficulty of reconciling more objective accounts of behaviour with inferences about an animal's subjective mental life (see Wemelsfelder, 1997b, 1997c, 1999).

Some authors, however, are optimistic about the utility of animal personality work in addressing questions about well-being in humans (e.g. Suomi and Novak, 1991). For instance King (1999) found that observers could reliably rate chimpanzees on a measure of subjective well-being, or 'happiness', and that such ratings corresponded with high levels of extraversion and low levels of neuroticism in these subjects (essentially the same pattern as that found in humans (King, 1999)). Similarly, Lilienfeld *et al.* (1999) have suggested that chimpanzees may differ along a dimension of psychopathy that is similar to human psychopathy. Individuals scoring highly on their measure showed greater agonism, greater amounts of sexual behaviour, and displayed more teasing, tantrums and 'daring behaviour':

> These findings are consistent with descriptions of human psychopaths as aggressive, sexually promiscuous, sensation seeking, interpersonally provocative, and short-tempered.....(p. 371).

Such patterns are suggestive but their interpretation is problematic, especially with less central traits like psychopathy. While it may be reasonable to assume that those traits which in humans tend to correlate to psychological well-being (e.g. extraversion) may be important for animals too (Sackett, 1991), constructs like psychopathy may involve more subtle assumptions of what is 'normal' behaviour. Thus, trait terms such as 'provocative' or 'lazy' invite a particular moral stance when used to describe humans, making their application to nonhumans problematic. Similarly, higher-order traits like 'manipulative' or 'intelligent' may be readily used by humans to interpret an animal's behaviour, but are evidently slippery when operationalised into ratings or behaviour codings.

In the attribution of animal personality or well-being much of this difficulty may be avoided by attempting to ground attributions within species-specific parameters. For example, Buss (1991) has argued against the expectation of simple relationships between trait scores and behaviours on the grounds that the adaptiveness of specific behaviours may not be immediately apparent (i.e. adaptiveness of behaviour should be judged with reference to the species' original environment, rather than the current one). Thus, while there are obviously some common cross-species criteria that denote psychological suffering (e.g. stereotypy), the assumption of psychological continuity (and the judgement of psychological well-being) must be framed within a consideration of species-specific behaviour (Rosenblum, 1991).

Attempting to understand the full range of experience of other species is clearly essential to an understanding of welfare issues (e.g. Wemelsfelder, 1997c), and the study of animal personality can offer valuable insights. It is, however, debatable what the role of standardised personality instruments is within this enterprise. Some authors (e.g. Gold and Maple, 1994; King, 1999) view such instruments as central to the management of captive groups of animals. It would be useful, for instance, to know that a particular animal was characterised as 'withdrawn' or 'unsociable'. Such attributions may highlight problems in the dynamics of a captive social group and have consequent implications for the management of the group. It is debatable, however, whether such a tool would provide additional information for experienced caretakers of captive groups. On large rating instruments (which provide a more complete set of trait terms than smaller instruments) factor scores provide the best way of summarising variation between individuals. While researchers have found these useful to compare with behavioural ratings, caretakers may well consider them to be nothing more than simplistic profiles of their animals.

The ultimate place of personality attributions of animals within animal behaviour research may well prove to be context-dependent. Ratings of animal temperament or personality have been utilised at both ends of a spectrum of quantitative and qualitative research; from studies of the biological and genetic bases of temperament (e.g. Zuckerman, 1996; Lesch, Meyer, Glatz *et al.*, 1997) to accounts of pet-owner interactions (e.g. Shapiro, 1988). It is perhaps to the latter realm of human-animal relationships that more work needs to be addressed, in order to map out the subtleties of this relationship. Our sense of who we are as humans seems intricately tied to our sense of similarity to and difference from other species (Shepard, 1983; 1997, 1998; Serpell, 1996; Hindley, 1999). The boundaries that we draw between ourselves and other animals often determine the quality of the relationships we enjoy with them, whether we experience them as pets, laboratory subjects or zoo animals (Arluke and Sanders, 1996). Perhaps the most valuable application of animal personality work is to make us reassess those relationships.

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How difficult it is, though, to refrain from replacing the thing with its sign, to keep the object alive before us instead of killing it with a word.

Johann Wolfgang von Goethe, Theory of Colour
(in Naydler, 1996: 33).

CHIMPANZEE PERSONALITY RATING SCALE

Rater:

Chimpanzee:

Please read these instructions carefully

This questionnaire is intended to measure personality characteristics of chimpanzees. In the items below, you are asked to consider the personality of a particular chimpanzee. In each case, you are asked to think of the **usual** behaviour of the animal; you may have particular incidents in mind when you are considering the items but try not to be too influenced by any specific or unusual occurrences of the behaviour. You are asked to assess each personality characteristic in terms of its frequency. When you are considering each item, think if you can of the **relative frequency** with which the characteristic occurs; i.e. how frequently does the animal, **relative to other animals**, display the characteristic?

Try to respond fairly quickly to the items, rather than considering them for too long: your first 'gut' reaction is probably the most appropriate. Answering will involve ticking a box on the scale to the right of each item. Please tick only **one** box.

Please do not discuss your responses to the items with any of the other respondents; it is likely that responses between individual raters will vary somewhat. It would be best if you completed the scale in private and at a time when you are unlikely to be interrupted.

I appreciate that that this is a time-consuming task to do, and you are welcome to space out the questionnaires over a couple of months. If you can complete all of the questionnaires within a few weeks this would be good; it is best to assess the personalities of all the animals within the same time scale since changes in social structure may affect personality.

Please return your scales in the SAEs provided. If you need extra scales/envelopes or have any questions please contact me at the address below.

Thank you very much for taking part in this research. It is greatly appreciated.

Diane Dutton
Psychology Department
Liverpool Hope University College
Hope Park
Liverpool
L16 9JD
0151 291 3077

*Each of these questions are answered by ticking **one** of the seven boxes on the scale in the panel to the right. Each answer may take the form of always, very frequently, frequently, occasionally, rarely, very rarely or never.*

			always	very frequently	frequently	occasionally	rarely	very rarely	never
1	He is persistent when attempting to achieve a goal	1	☐	☐	☐	☐	☐	☐	☐
2	He shows an adaptability to changing circumstances	2	☐	☐	☐	☐	☐	☐	☐
3	He is aggressive towards other group members for no apparent reason	3	☐	☐	☐	☐	☐	☐	☐
4	He associates regularly with a large number of other animals	4	☐	☐	☐	☐	☐	☐	☐
5	He is moody	5	☐	☐	☐	☐	☐	☐	☐
6	His behaviour is unpredictable	6	☐	☐	☐	☐	☐	☐	☐
7	He shows fear, e.g. by screaming, for no apparent reason	7	☐	☐	☐	☐	☐	☐	☐
8	He is popular with other group members	8	☐	☐	☐	☐	☐	☐	☐
9	He will attempt to reconcile others in aggressive situations	9	☐	☐	☐	☐	☐	☐	☐
10	He is anxious in social situations	10	☐	☐	☐	☐	☐	☐	☐
11	He can easily enlist the support of most of the other animals in the group	11	☐	☐	☐	☐	☐	☐	☐
12	He will intervene to stop conflict between other group members	12	☐	☐	☐	☐	☐	☐	☐
13	He is inquisitive about events happening around him	13	☐	☐	☐	☐	☐	☐	☐
14	Other members of the group look for reassurance from him before they do things	14	☐	☐	☐	☐	☐	☐	☐
15	He is bold and fearless in aggressive encounters with other animals	15	☐	☐	☐	☐	☐	☐	☐
16	He avoids aggressive situations	16	☐	☐	☐	☐	☐	☐	☐
17	He is successful at dominating other group members	17	☐	☐	☐	☐	☐	☐	☐
18	He is willing to investigate new objects or foodstuffs	18	☐	☐	☐	☐	☐	☐	☐
19	He submissively greets other members of the group	19	☐	☐	☐	☐	☐	☐	☐
20	He is impatient	20	☐	☐	☐	☐	☐	☐	☐

41 He is protective of other infants in the group

42 He shows stereotypic behaviours, e.g. rocking, pulling of own hair

43 During conflicts, he is supported by allies within the group

44 He withdraws from social contact with other animals

45 His behaviour is inflexible

46 In interactions with others, he is trusting

Thank you for completing this rating scale

	always	very frequently	frequently	occasionally	rarely	very rarely	never
41	☐	☐	☐	☐	☐	☐	☐
42	☐	☐	☐	☐	☐	☐	☐
43	☐	☐	☐	☐	☐	☐	☐
44	☐	☐	☐	☐	☐	☐	☐
45	☐	☐	☐	☐	☐	☐	☐
46	☐	☐	☐	☐	☐	☐	☐

Rater

After completing all of the scales you may like to fill in the section below. I would very much appreciate your thoughts on such aspects as the clarity of the scale, and how relevant you found the items. For instance, did you find it relatively easy to apply these personality concepts to your chimpanzees or did you struggle to answer the items? Was it easier to complete the scale for particular animals or particular items? If so, why do you think this was the case? etc. Please don't feel obliged to spend a great deal of time on these comments; but any suggestions you have on improving this scale will be useful.

Your comments and suggestions:

How long have you worked with the present group of chimpanzees? Years _____ Months _____

I am hoping that the results of this study will provide information about the sorts of personality dimensions that are used in describing the personality of captive chimpanzees, and that these dimensions may prove useful as a more formal means of comparing different animals. If you would like to receive information about the findings of this study, or would like to receive personality profiles of your animals based on the findings please indicate below:

Would you like to receive information about the findings of this study? Yes ☐ No ☐

Would you like to receive personality profiles for your animals? Yes ☐ No ☐

Thank you very much for taking part in this research.

Appendix II

Biographical details of chimpanzees

Table 1 Chester zoo chimpanzees

NAME	DATE OF BIRTH	PLACE OF BIRTH	ARRIVAL AT CHESTER	MOTHER	FATHER
Boris	1966	Wild	22.8.69	Unknown	Unknown
Wilson	22.2.68	Chester	22.2.68	Meg	Bolden
Nicky	21.1.69	Chester	21.1.69	Jane	Kongola
Friday	6.2.76	Chester	6.2.76	Jane	Bimbo
Dylan	9.4.87	Chester	9.4.87	Farthing	Friday
Meg	1947	Wild	1950	Unknown	Unknown
Gloria	1965	Wild	23.6.86 d. 5.8.96	Unknown	Unknown
Kate	23.12.70	Chester	23.12.70	Jane	Algie
Cleo	1971	Wild	23.7.81	Unknown	Unknown
Heidi	20.6.72	Chester	20.6.72	Judy	Bimbo?
Rosie	29.1.73	Chester	29.1.73	Jeanie#	Bolden
Halfpenny	20.5.75	Colwyn Bay	16.9.84	Penny	Joey
Farthing	19.9.75	Colwyn Bay	16.9.84	Mabel	Joey
Mandy	19.9.77	Chester	19.9.77	Meg	Bolden
Florin	21.6.80	Colwyn Bay	17.4.90	Penny	Joey
Kan Kan	14.11.83	Chester	14.11.83	Kate§	Bolden?
Sarah	16.10.86	Chester	16.10.86	Halfpenny	Boris
Wanda	24.9.87	Chester	24.9.87	Heidi	Bolden
Sally	4.6.88	Chester	4.6.88	Rosie	Boris?
Kaylie	24.9.90	Chester	24.9.90	Halfpenny	Boris
Layla	2.11.90	Chester	2.11.90	Farthing	Friday
Alice	6.11.91	Chester	6.11.91	Florin	Boris
Whitney	30.5.93	Chester	30.5.93	Kan Kan	Rory?
Zee Zee	15.2.94	Chester	15.2.94	Mandy	Wilson?
Lizzy	22.3.95	Chester	22.3.95	Rosie	Boris
Holly	12.12.95	Chester	12.12.95	Sarah	Friday
Kiki	10.2.96	Chester	10.2.96	Halfpenny	Boris
Chrissie	11.3.96	Chester	11.3.96	Florin	Boris/ Wilson

Table 4 Sedgewick zoo chimpanzees

NAME	DATE OF BIRTH	PLACE OF BIRTH	ARRIVAL AT SEDGEWICK	MOTHER	FATHER
Marbles	1.1.69	Wild	Unknown	Unknown	Unknown
Gomez	1.7.77	Sedgewick	1.7.77	Unknown	Unknown
Mwana	1.11.83	Sedgewick	1.11.83	Unknown	Unknown
Bahati	1.6.85	Sedgewick	1.7.85	Unknown	Unknown
Kisana	1.7.91	Sedgewick	1.7.91	Unknown	Unknown
Holly	1.1.68	Wild	Unknown	Unknown	Unknown
Audra	1.1.69	Wild	Unknown	Unknown	Unknown
Harriet	1.1.69	Wild	Unknown	Unknown	Unknown
Hazina	1.5.86	Sedgewick	1.5.86	Unknown	Unknown
Husasa	1.2.91	Sedgewick	1.2.91	Unknown	Unknown

Table 5 Twycross zoo chimpanzees

NAME	DATE OF BIRTH	PLACE OF BIRTH	ARRIVAL AT TWYCROSS	MOTHER	FATHER
Benji	12.1.82	London	15.9.83	Brenda	Bimbo
William	30.6.82	Twycross	30.6.82	Noddy	Bobby
Melody	1.1.57	Wild	1.12.85	Unknown	Unknown
Rose	30.5.76	Twycross	30.5.76	Tina	Oscar
Samantha	1.1.80	Wild	31.8.83	Unknown	Unknown
Holly	27.5.82	Twycross	27.5.82	Choppers	Bobby
Jolly	16.9.83	Colchester	2.5.84	Mandy	Rastus
Elly	29.4.90	Twycross	29.4.90	Samantha	Benjie

Table 6 Aalborg zoo chimpanzees

NAME	DATE OF BIRTH	PLACE OF BIRTH	ARRIVAL AT AALBORG	MOTHER	FATHER
Didrik	7.5.67	Wild	7.8.72	Unknown	Unknown
Martin	16.1.89	Aalborg	16.1.89	Dorthe	Didrik
Mickey	20.12.89	Aalborg	20.12.89	Unknown	Didrik
Marco	3.9.90	Aalborg	3.9.90	Jutta	Unknown
Dorthe	7.5.67	Wild	7.8.72	Unknown	Unknown
Jutta	1.6.74	Wild	13.3.80	Unknown	Unknown

Table 7 Krefelder zoo chimpanzees

NAME	DATE OF BIRTH	PLACE OF BIRTH	ARRIVAL AT KREFELDER	MOTHER	FATHER
Charly	1.1.73	Wild	9.9.76	Unknown	Unknown
Hubert	15.7.90	Krefelder	15.7.90	Gombe	Unknown
Balli	1.1.73	Wild	22.4.75	Unknown	Unknown
Flo	1.1.73	Wild	22.4.75	Unknown	Unknown
Gombe	1.1.73	Wild	22.4.75	Unknown	Unknown
Lara	13.1.82	Krefelder	27.5.82	Flo	Unknown
Fulani	28.9.87	Krefelder	28.9.87	Flo	Unknown
Menolly	27.12.84	Krefelder	27.12.84	Gombe	Unknown

Appendix III

Comparison of ratings for male and female raters

Table 1 Values of Mann-Whitney for questionnaire items

	U	p		*U*	p
Persistant	20.00	.73	Resourceful	22.00	.94
Adaptable	19.50	.68	Displays	9.00	.07
Unreasonably aggressive	19.00	.64	Dominance motivated	21.00	.84
Associates with others	20.00	.73	Easily frightened	21.00	.84
Moody	12.00	.16	Interacts with infants & juveniles	13.00	.20
Unpredictable	10.50	.10	Associates with dominants	16.00	.38
Unexplained fear	14.00	.25	Influential	15.50	.35
Popular	19.50	.68	Causes conflicts	2.00	.006
Reconciles	13.50	.23	Deceptive	19.50	.68
Anxious	5.00	.01	Aggressive	22.00	.94
Can enlist support	21.00	.84	Submissive	15.00	.31
Intervenes	22.00	.94	Active	14.00	.25
Inquisitive	21.00	.84	Nervous	16.50	.42
Reassures	9.00	.07	Intelligent	21.50	.89
Bold	17.00	.46	Difficulty forming friendships	22.00	.94
Avoids aggression	10.00	.09	Confident	22.00	.94
Dominant	22.00	.94	Playful	16.00	.38
Investigative	12.00	.16	Protective	11.00	.12
Submissively greets	17.00	.46	Stereotypic	21.50	.89
Impatient	21.00	.84	Supported by allies	14.00	.25
Interacts with others	17.50	.50	Withdrawn	20.00	.73
Socially aware	15.00	.31	Inflexible	12.50	.18
Impulsive	16.00	.38	Trusting	17.00	.46

Appendix V

Frequency distributions for the factor scores on Factors I — IV and Dominance rank

Fig. 1 Distribution of Factor I Sociability

Chi square = 1.18 (d.f. = 5), p = .94
K-S d = 0.06, p = n.s.

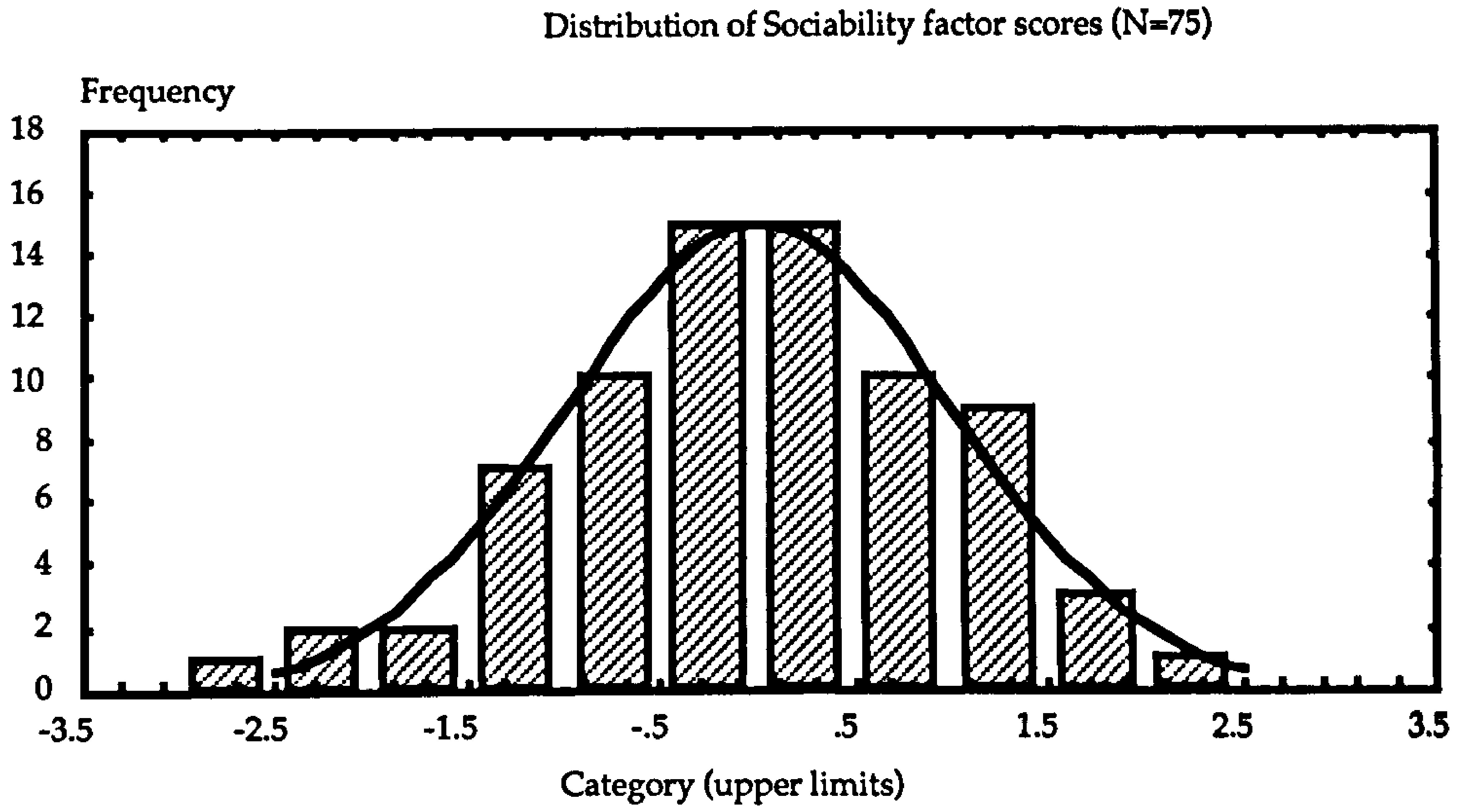


Fig. 2 Distribution of Factor II Dominance

Chi square = 12.395 (d.f. = 5), p = .029
K-S d = 0.12, p = n.s.

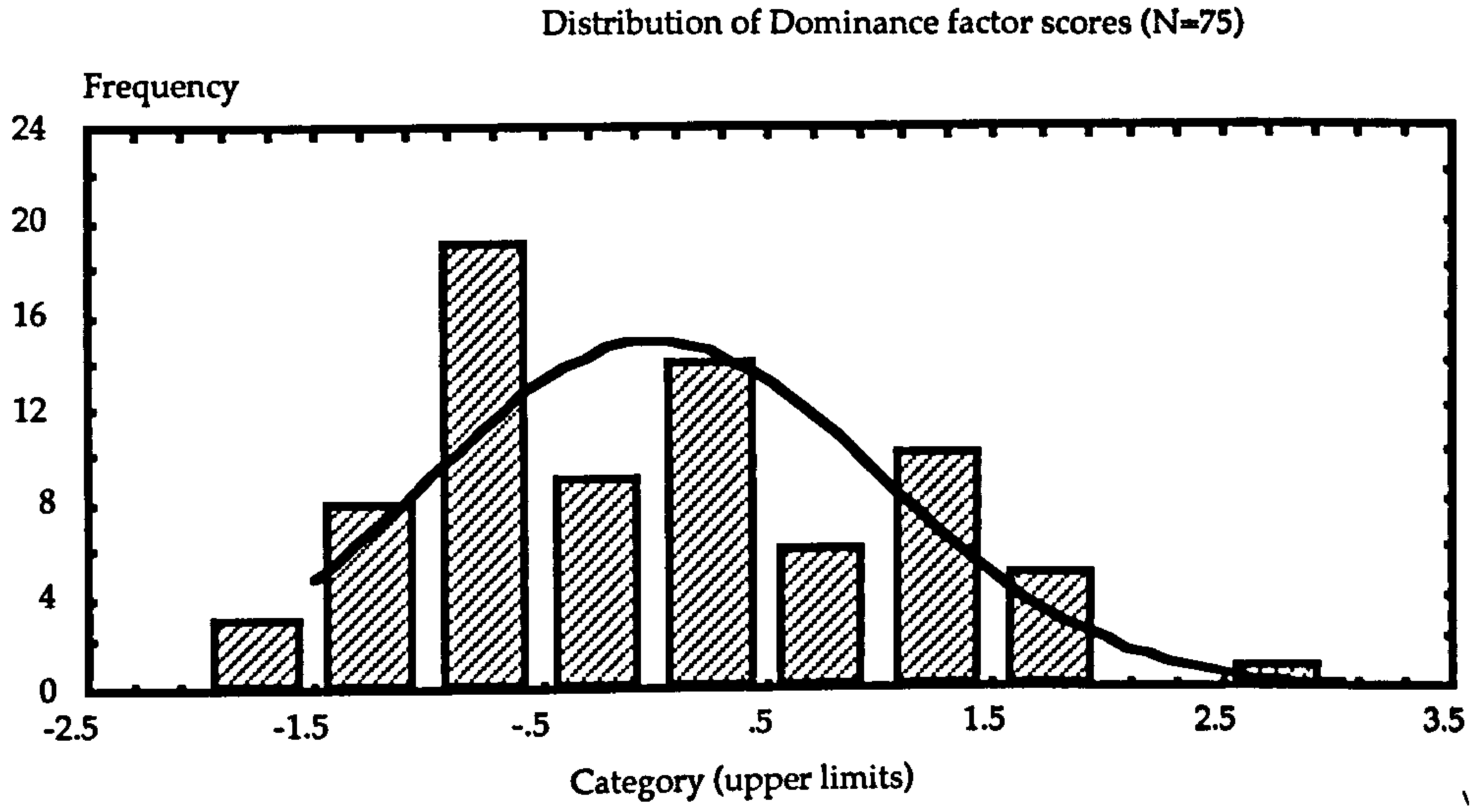


Fig. 3 Distribution of Factor III Anxiety

Chi square = 9.551 (d.f. = 5), p = .089
K-S d = 0.10, p = n.s.

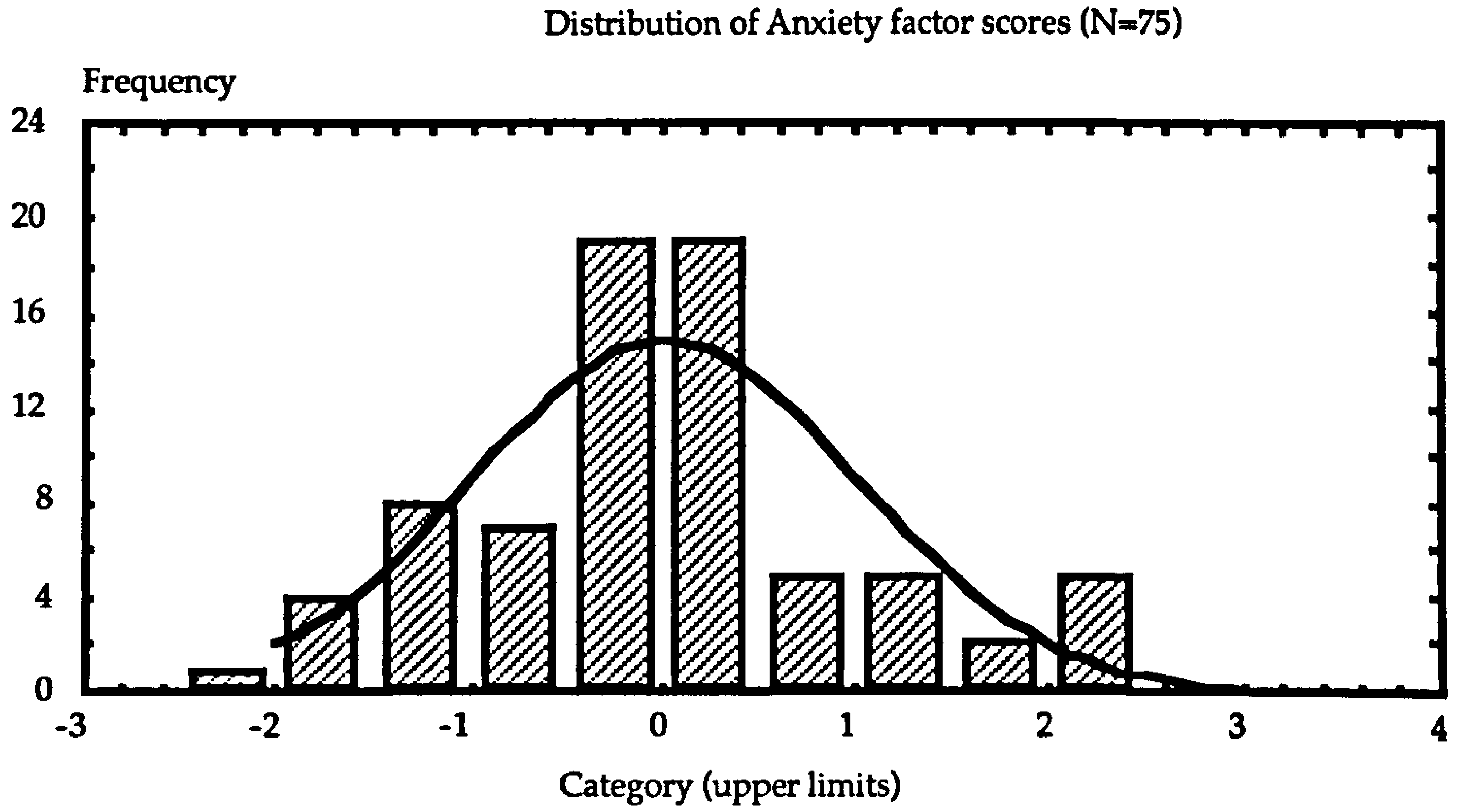


Fig. 4 Distribution of Factor IV Curiosity

Chi square = 1.876 (d.f. = 5), p = .866
K-S d = 0.04, p = n.s.

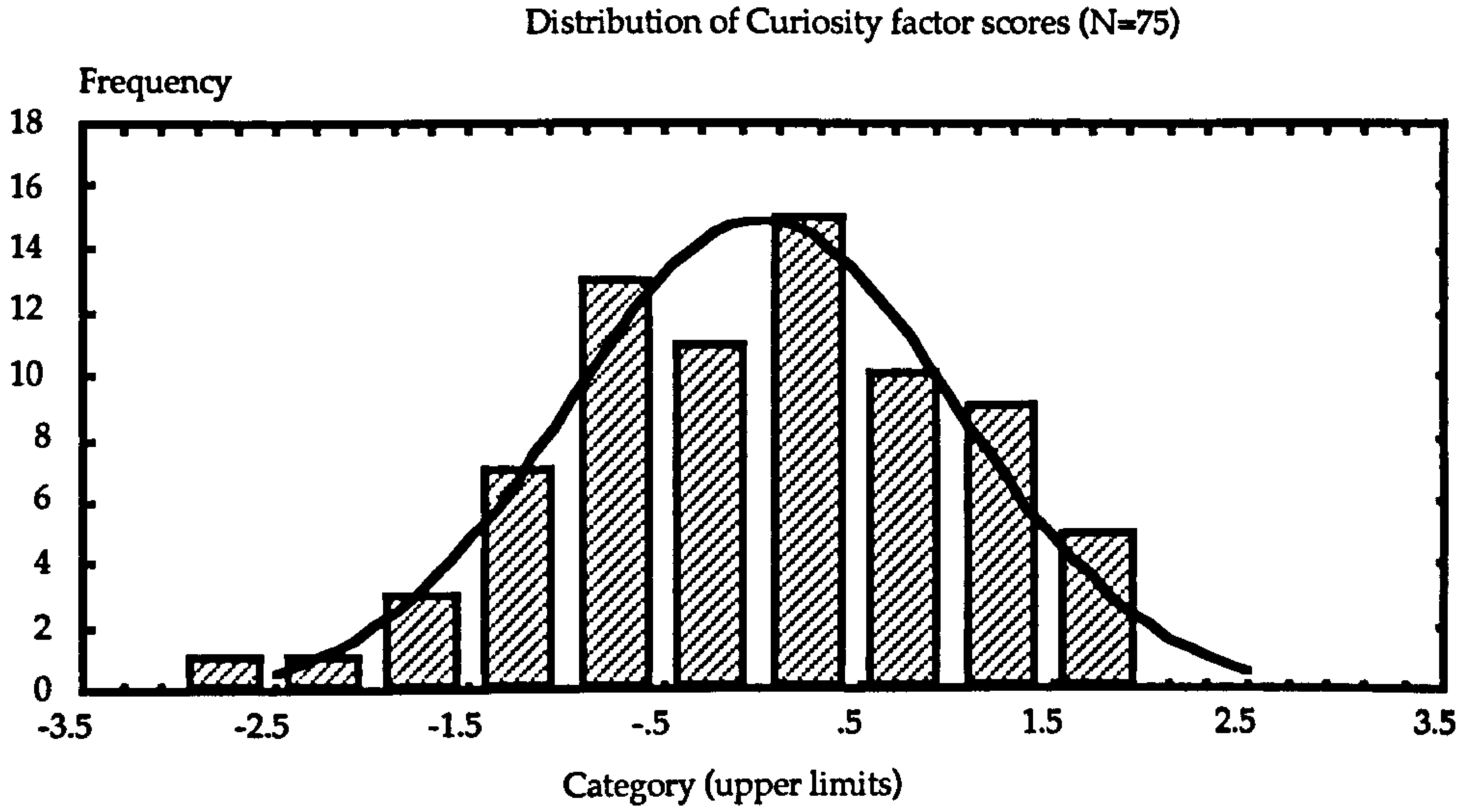
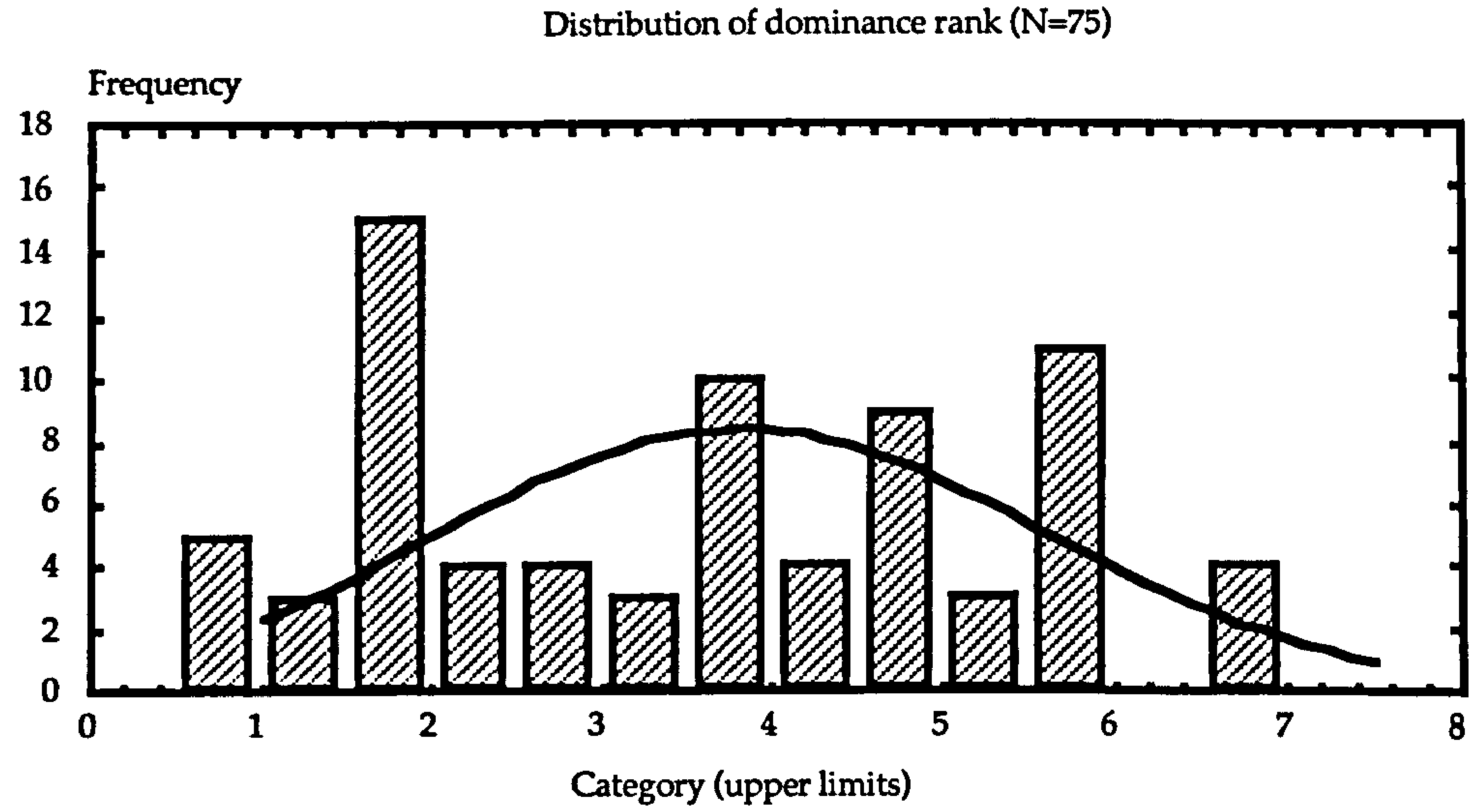


Fig. 5 Distribution of Dominance rank

Chi square = 17.319 (d.f. = 6), p = .008
K-S d = 0.15, p < .10



Appendix VI

Frequency distributions for the four personality factors by sex

Fig.1 Distribution of Sociability scores: Males

Chi Square = 1.10 (d.f. = 1), p = .29
K-S d = .09, p = n.s.

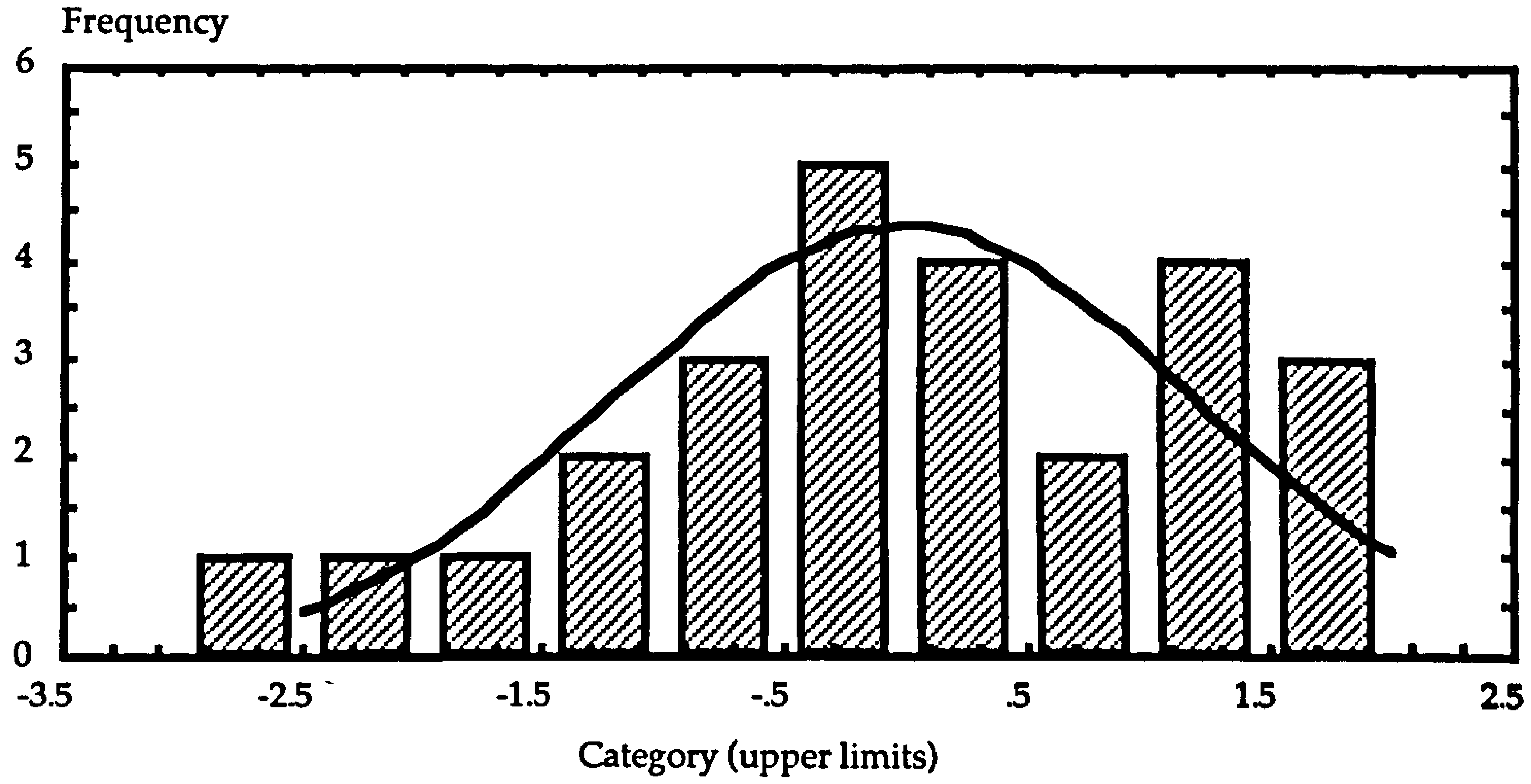


Fig.2 Distribution of Sociability scores: Females

Chi square = .20 (d.f. =3), p = .97
K-S d = .06, p = n.s.

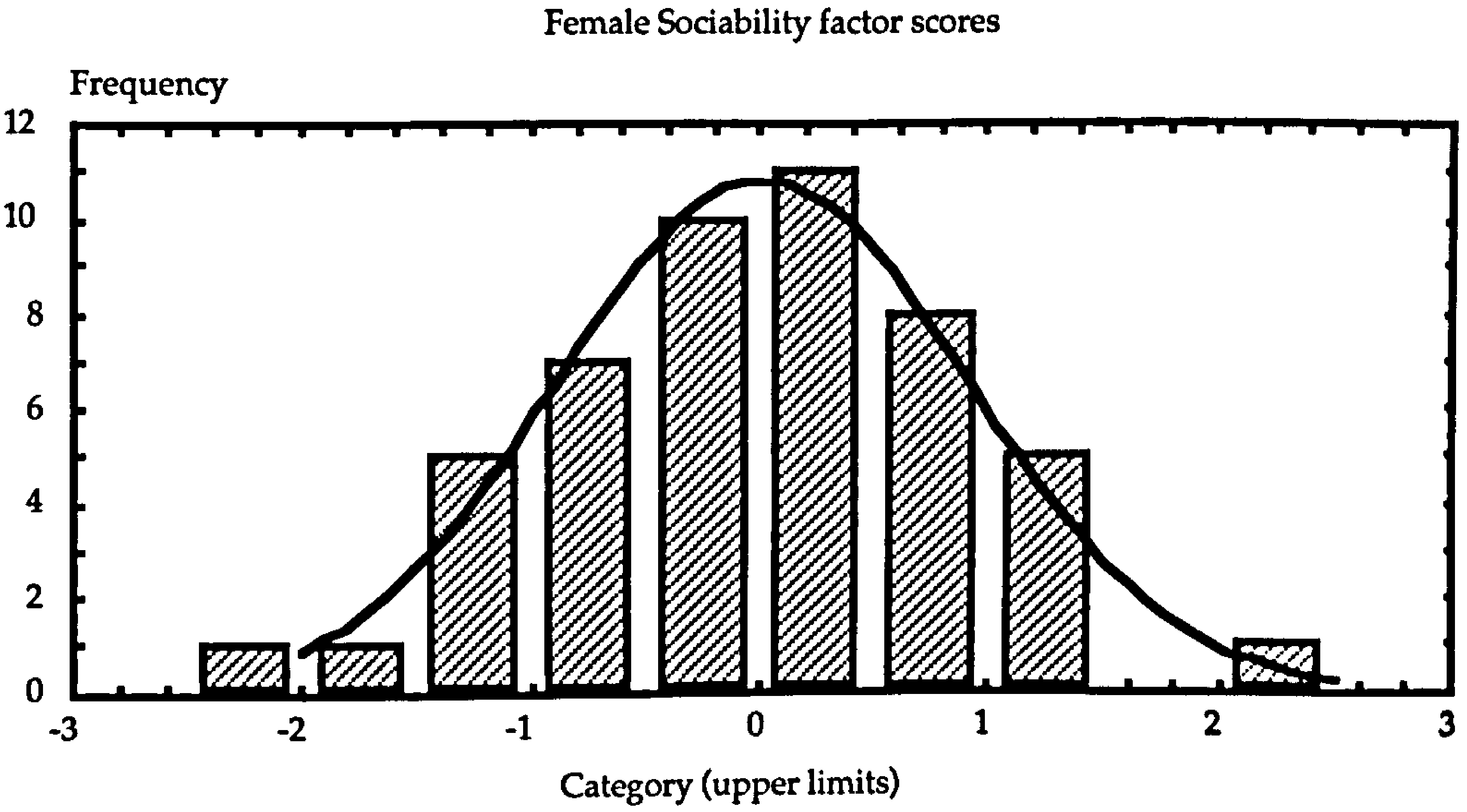


Fig. 3 Distribution of Dominance scores: Males

Chi square = 1.19 (d.f. = 1), p = .27
K-S d = .07, p = n.s.

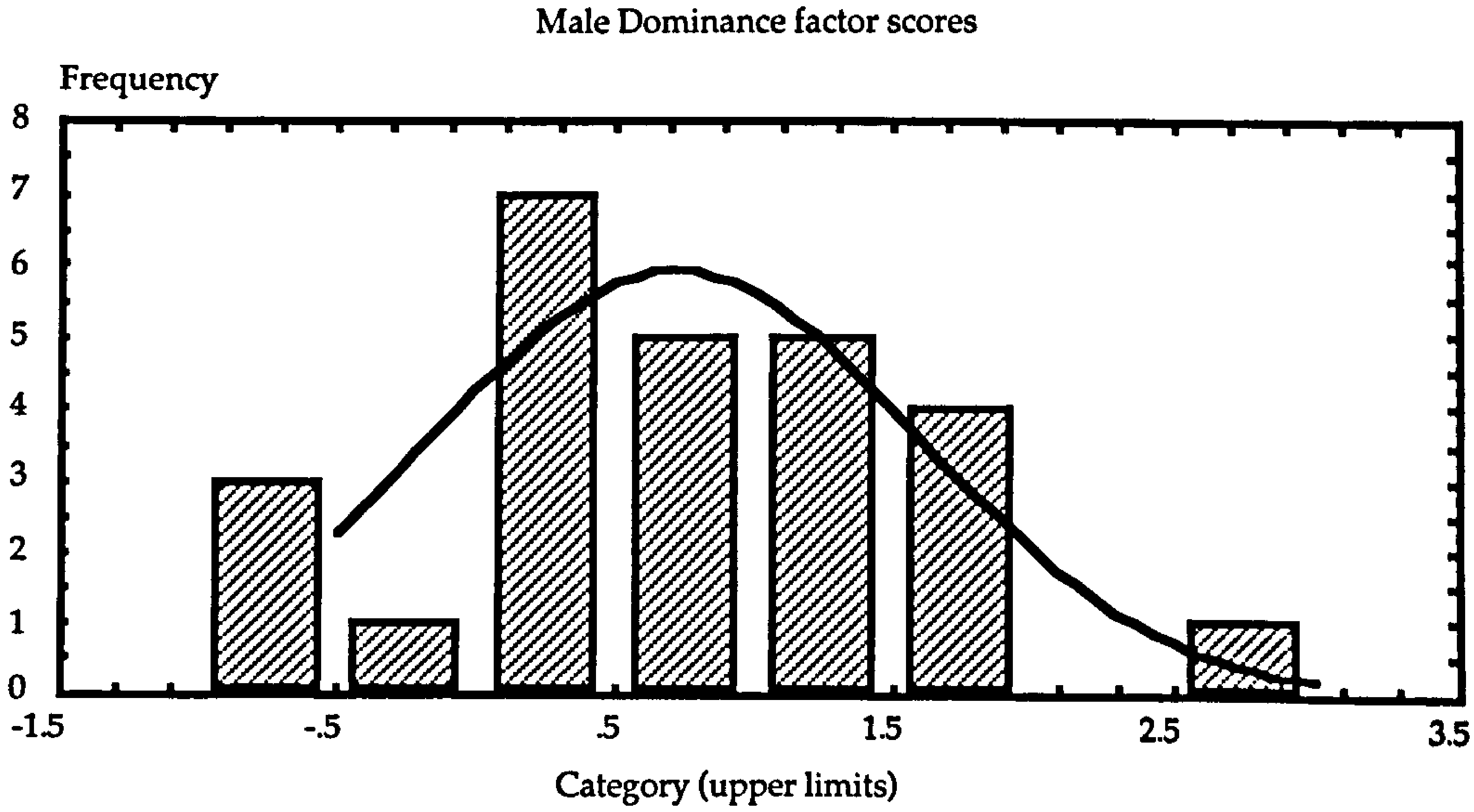


Fig. 4 Distribution of Dominance scores: Females

Chi square = 12.31 (d.f. = 4), p = .01
K-S d = .16, p = < .15

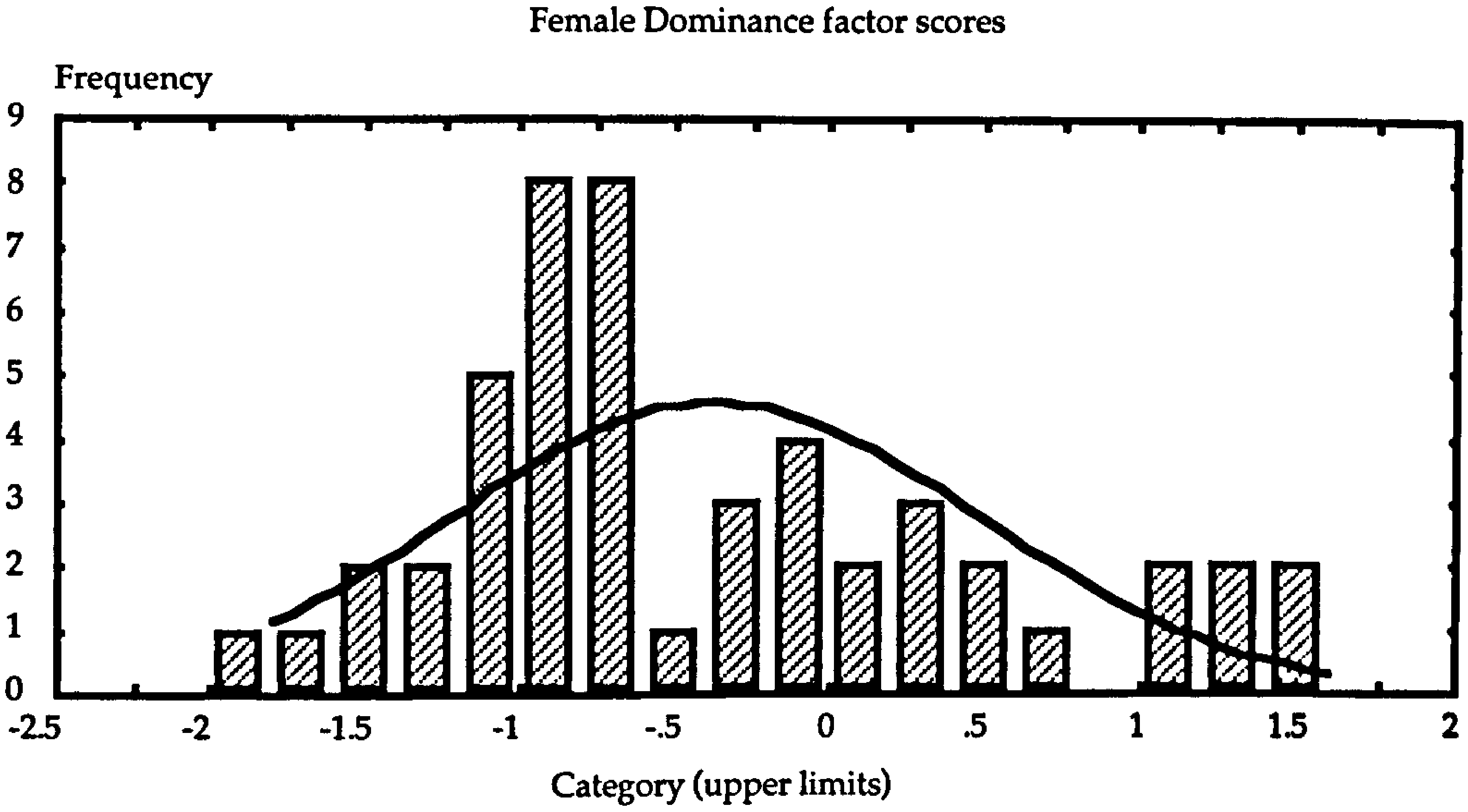


Fig.5 Distribution of Anxiety scores: Males

Chi square = no value (d.f. = 0), p = 1.00
K-S d = .15, p = n.s.

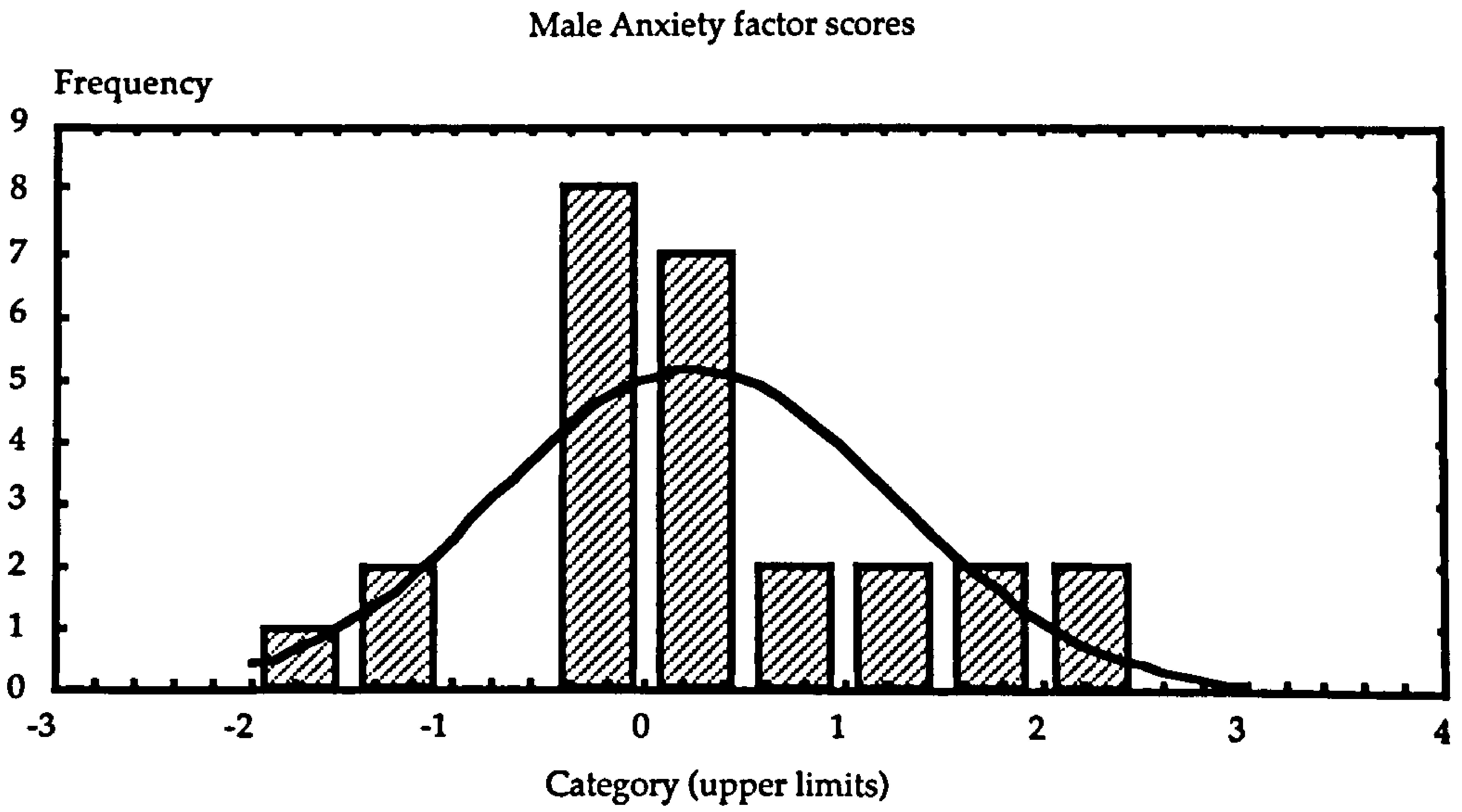


Fig. 6 Distribution of Anxiety scores: Females

Chi square = 3.31 (d.f. = 3), p = .34
K-S d = .09, p = n.s.

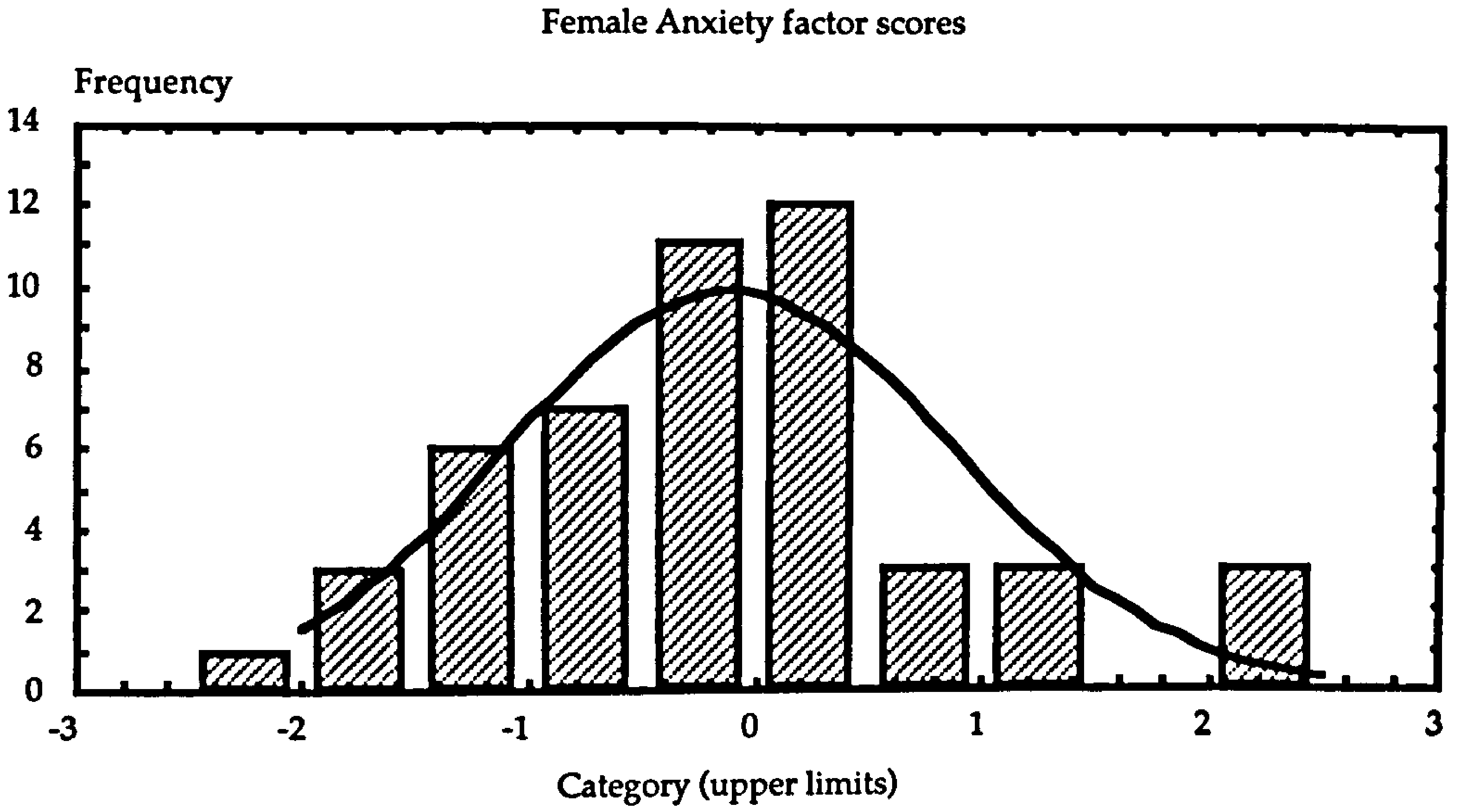


Fig. 7 Distribution of Curiosity scores: Males

Chi square = no value (d.f. = 0), p = 1.00
K-S d = .10, p = n.s.

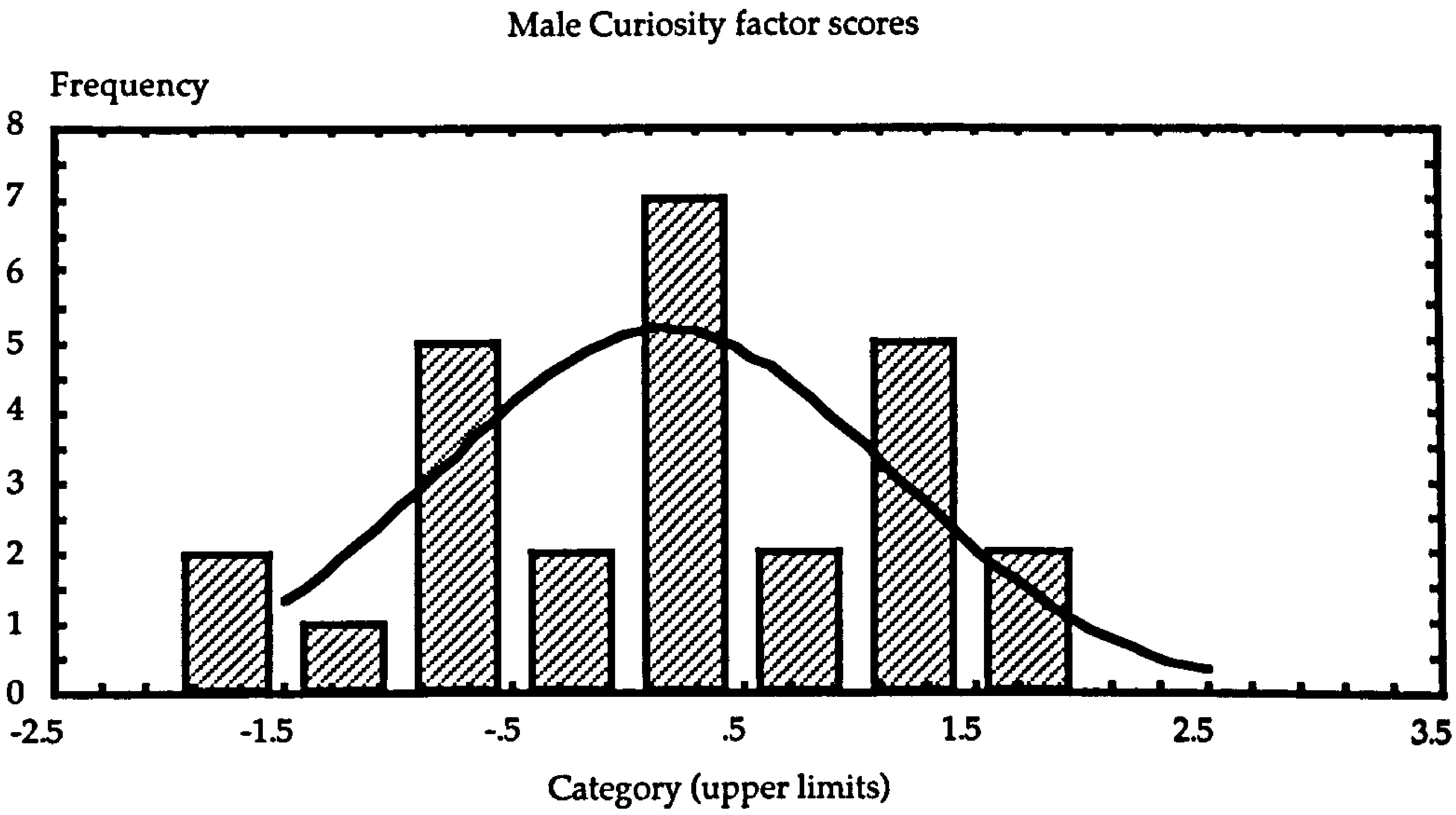
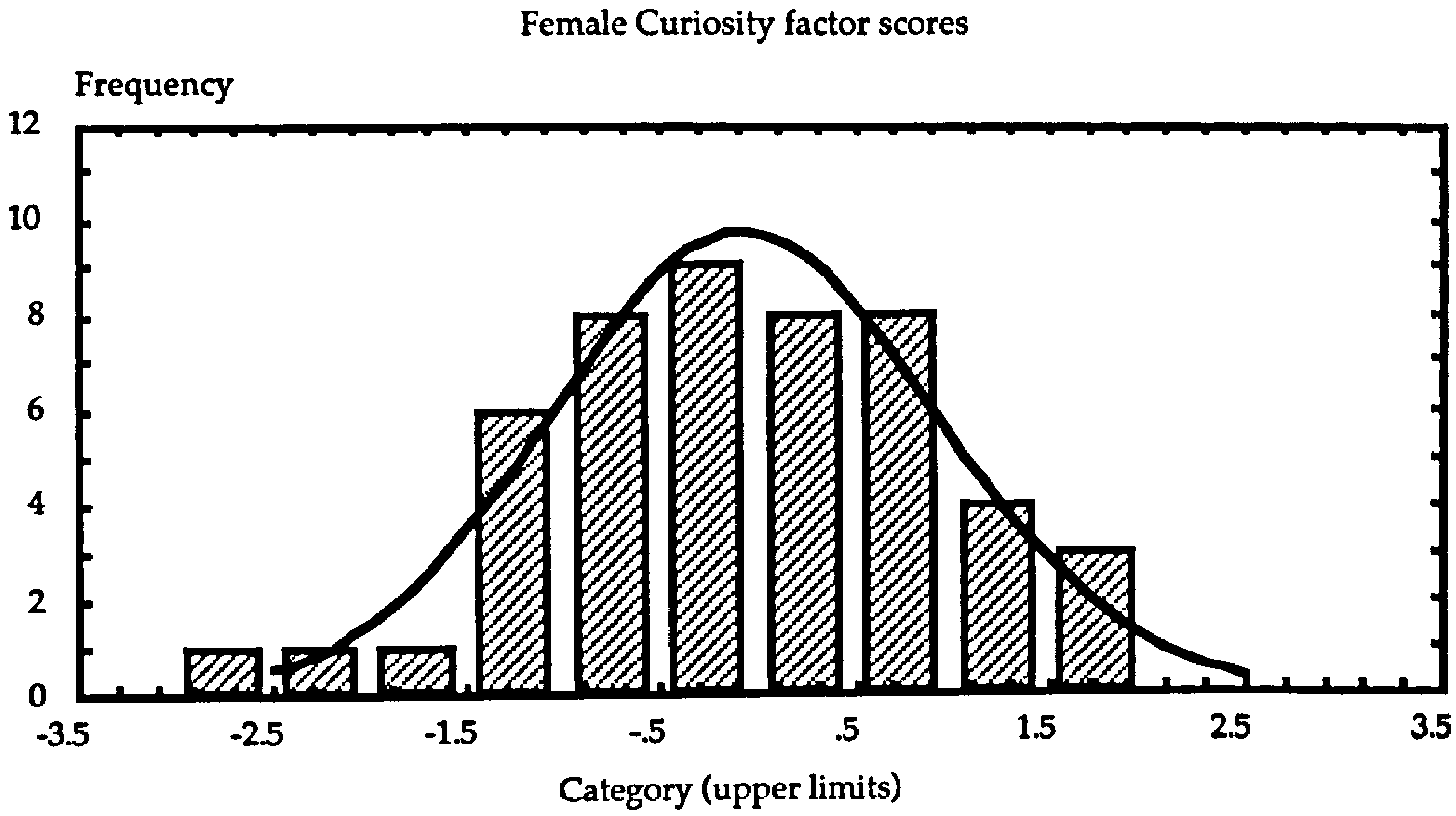

Male Curiosity factor scores

Fig. 8 Distribution of Curiosity scores: Females

Chi square = .36 (d.f. = 3), p = .94
K-S d = .05, p = n.s.


Female Curiosity factor scores

Appendix VII

Frequency distributions for Factors I — IV and age

Fig. 1 Distribution of Sociability scores: Infants and Juveniles

Chi square = no value (d.f. = 0), p = 1
K-S d = .22, p = n.s.

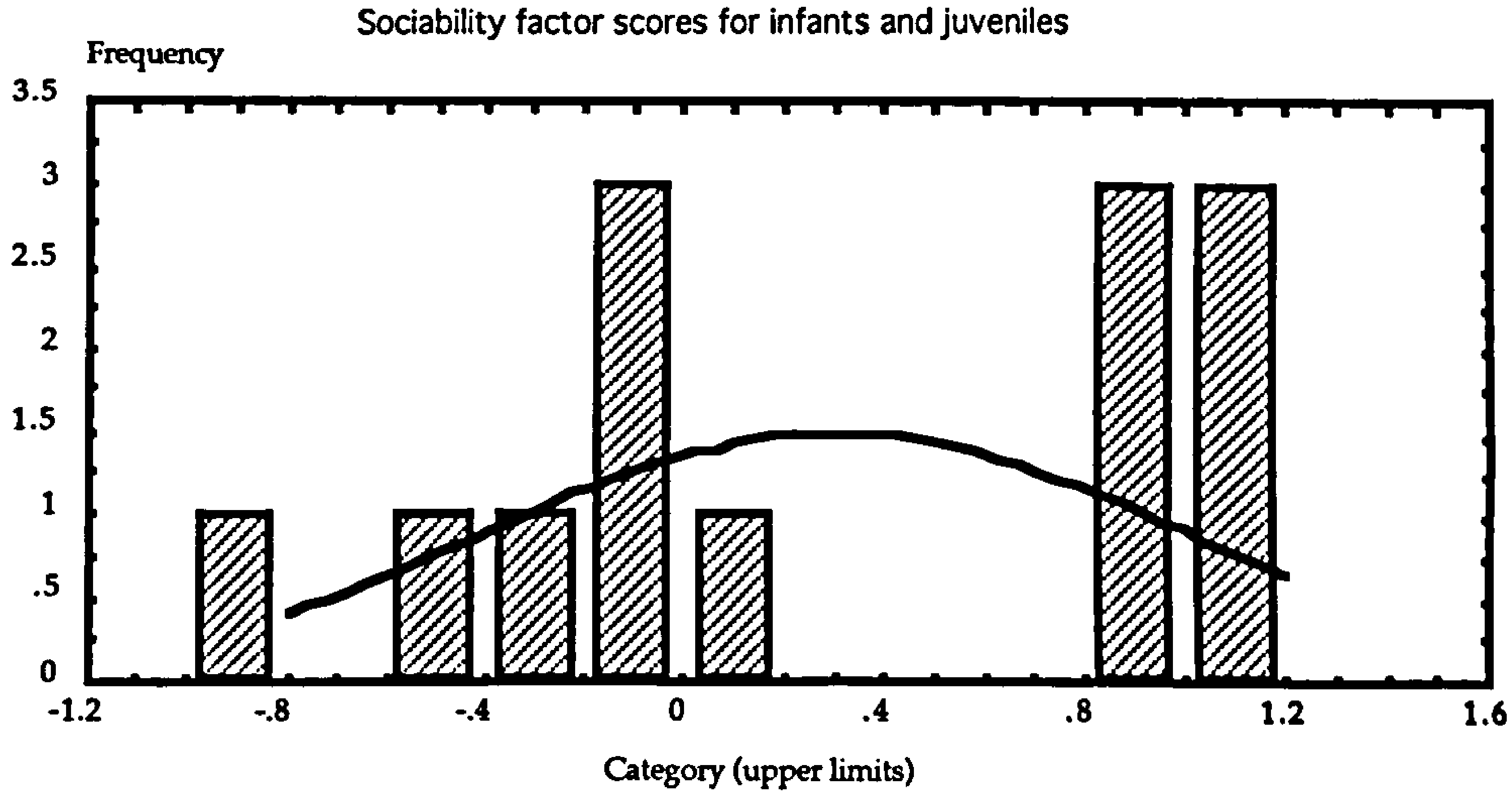


Fig. 2 Distribution of Sociability scores: Adolescents

Chi square = no value (d.f. = 0), p = 1
K-S d = .11, p = n.s.

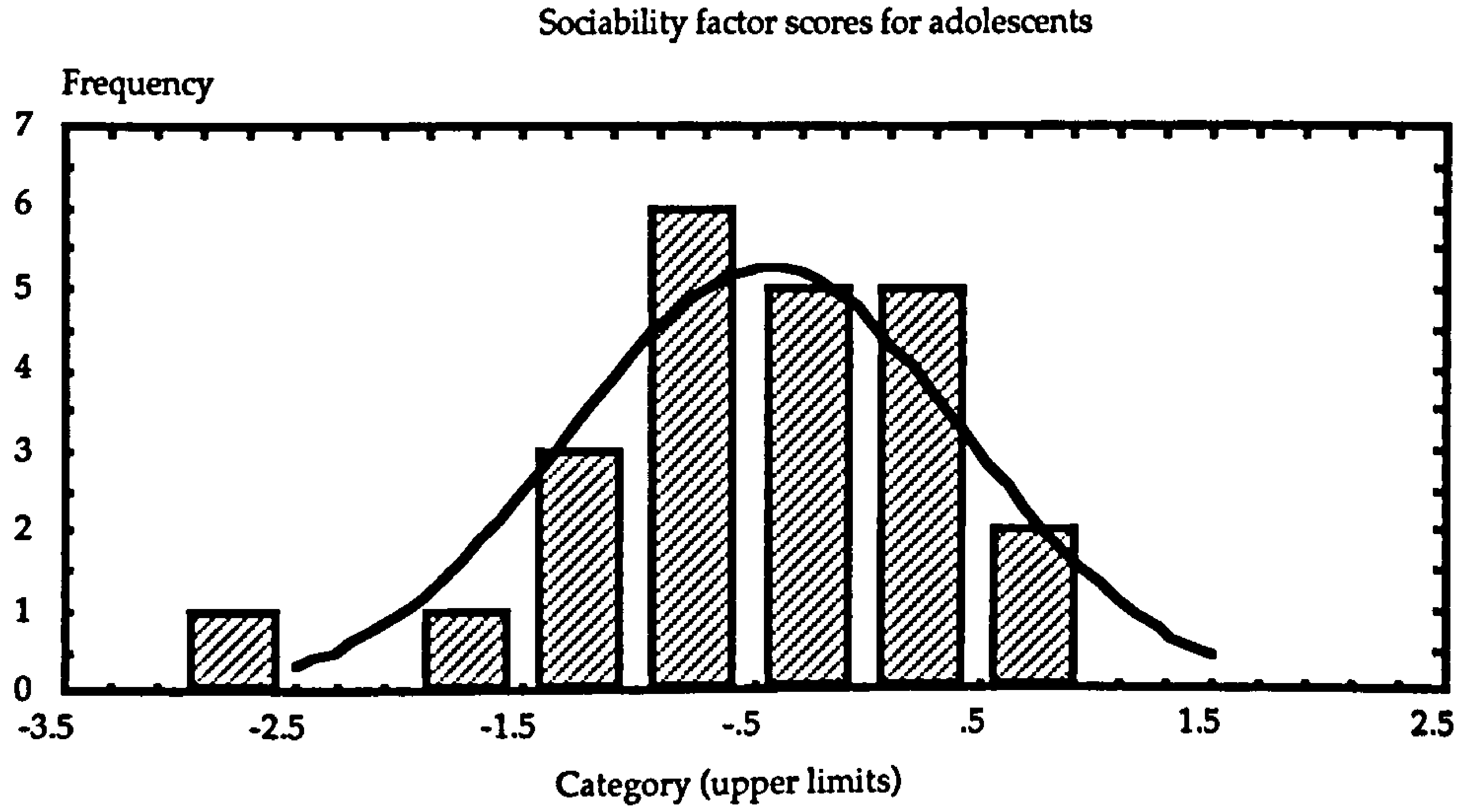


Fig.3 Distribution of Sociability scores: Adults

Chi square = 2.54 (d.f. = 3), p = .46
K-S d = .11, p = n.s.

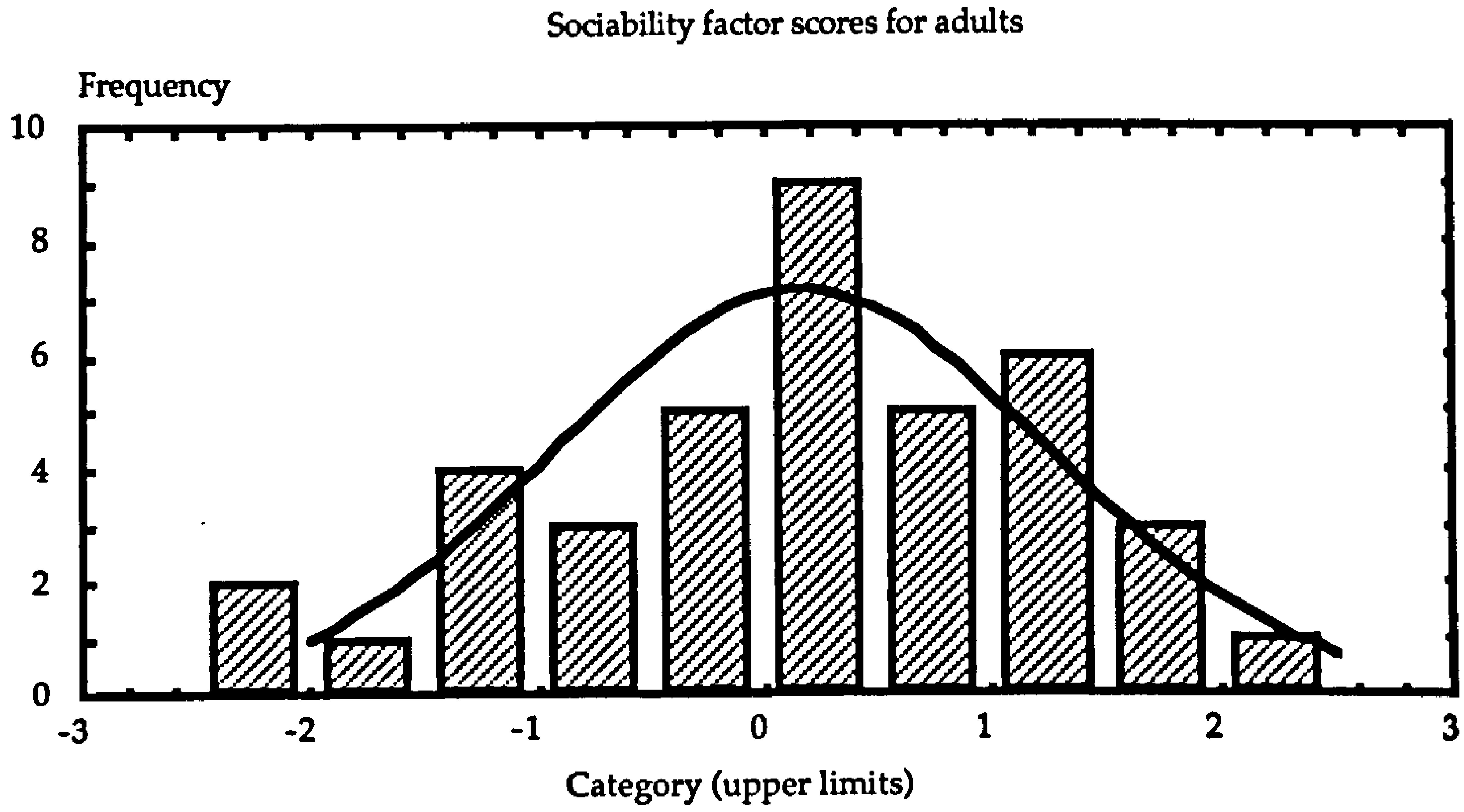


Fig. 4 Distribution of Dominance scores: Infants and Juveniles

Chi square = no value (d.f. = 0), p = 1
K-S d = .10, p = n.s.

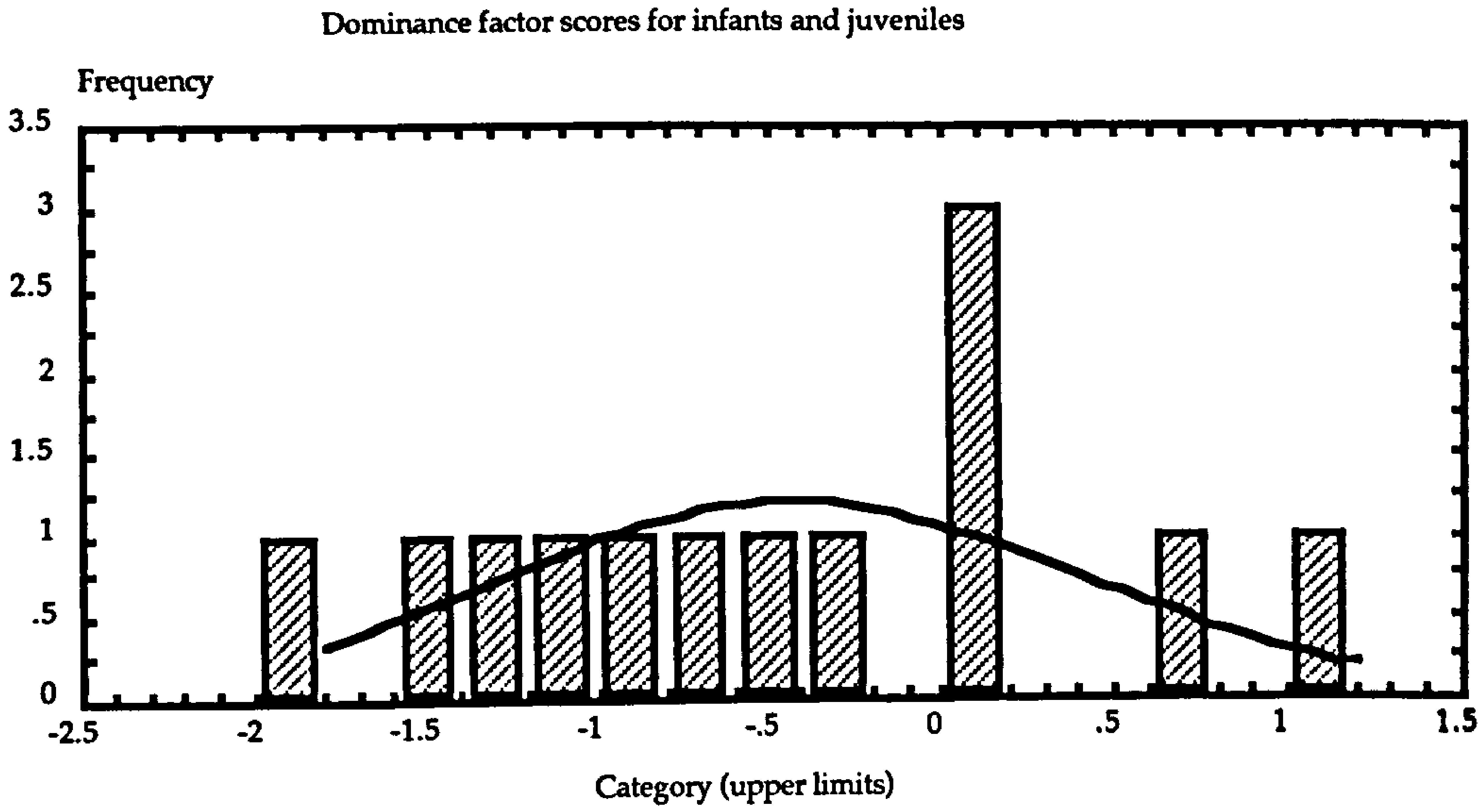


Fig. 5 Distribution of Dominance scores: Adolescents

Chi square = 4.51 (d.f. = 1), p = .03
K-S d = .19, p = n.s.

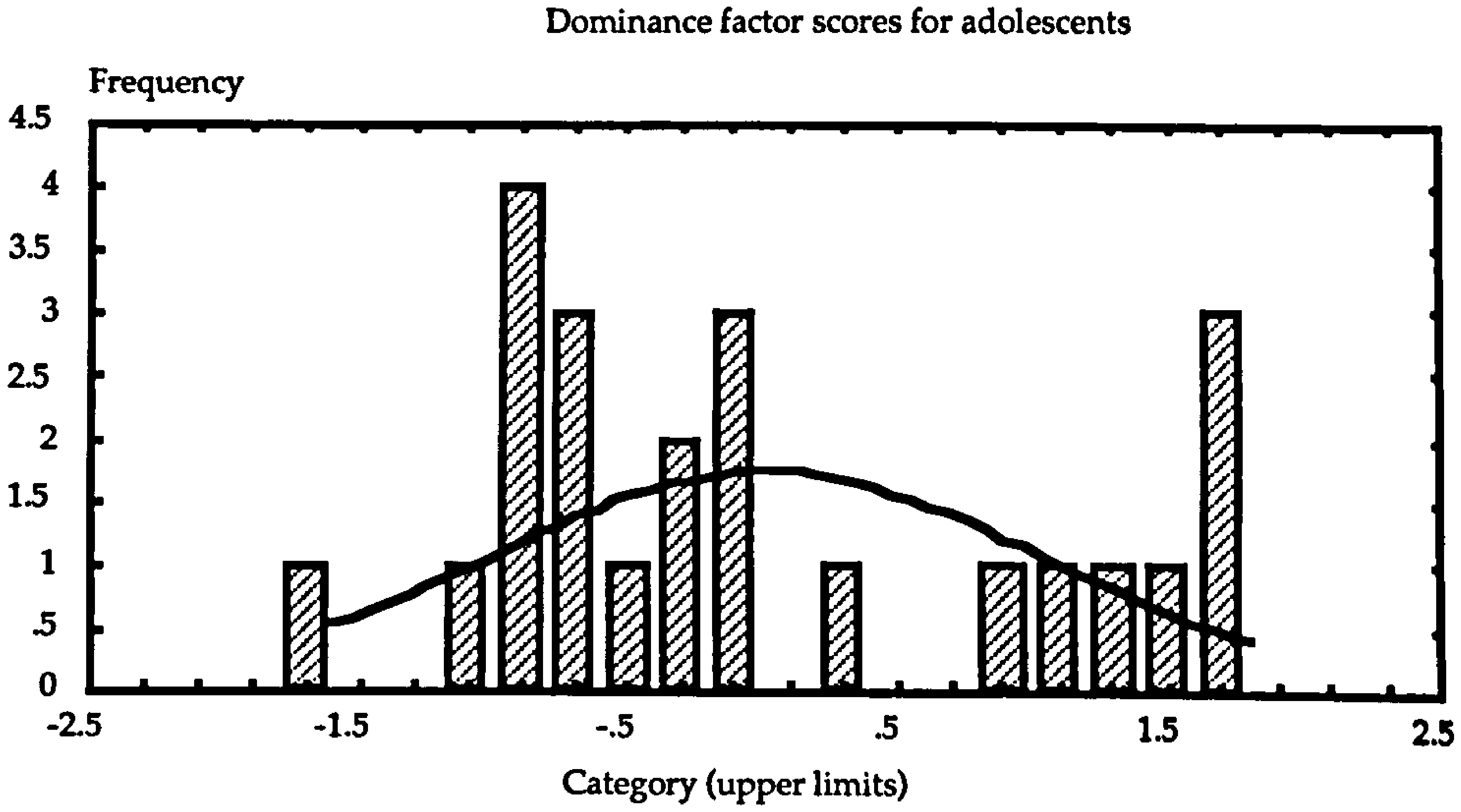


Fig. 6 Distribution of Dominance scores: Adults

Chi square = 7.06 (d.f. = 2), p = .02
K-S d = .13, p = n.s.

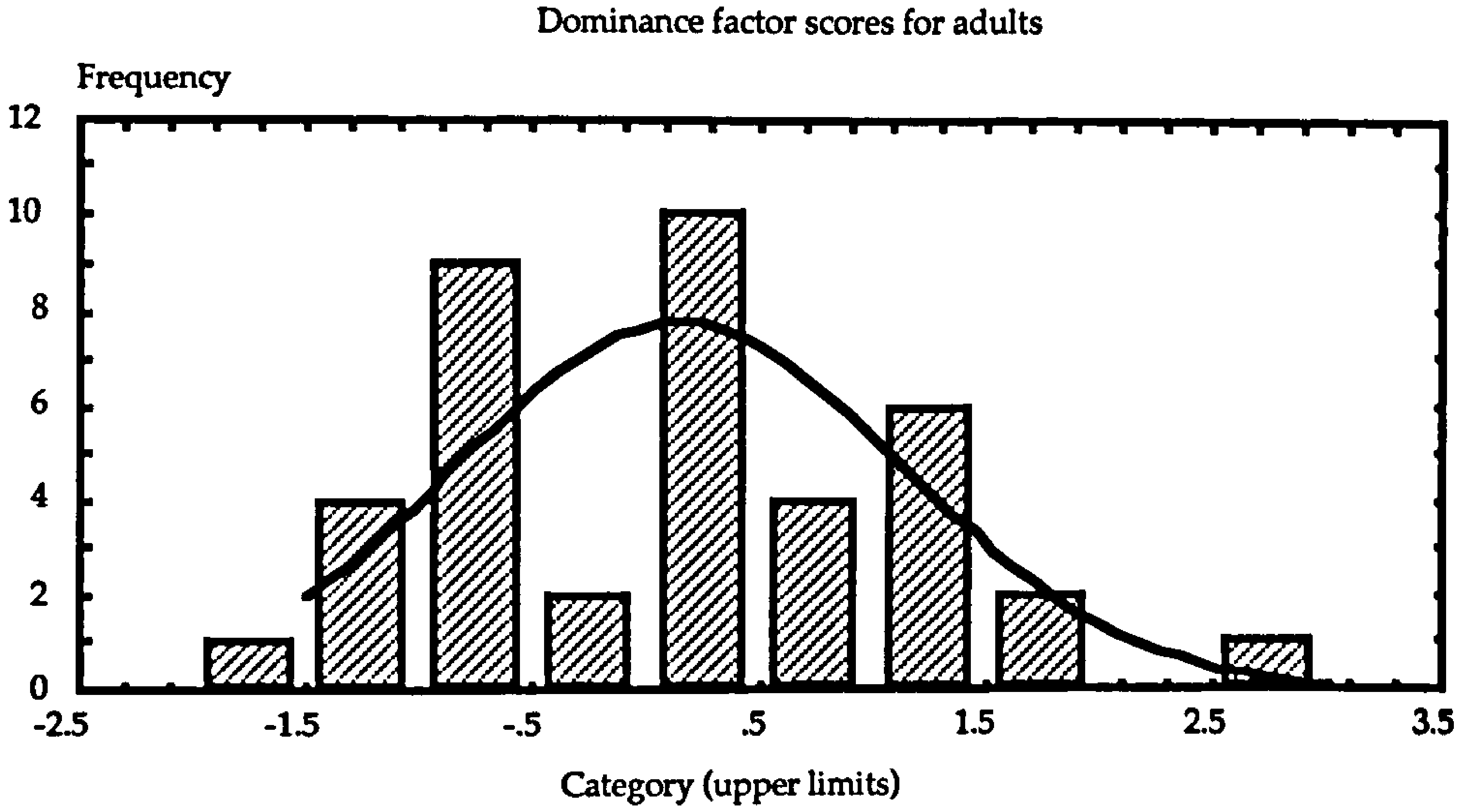


Fig. 7 Distribution of Anxiety scores: Infants and Juveniles

Chi square = no value (d.f. = 0), p = 1
K-S d = .21, p = n.s.

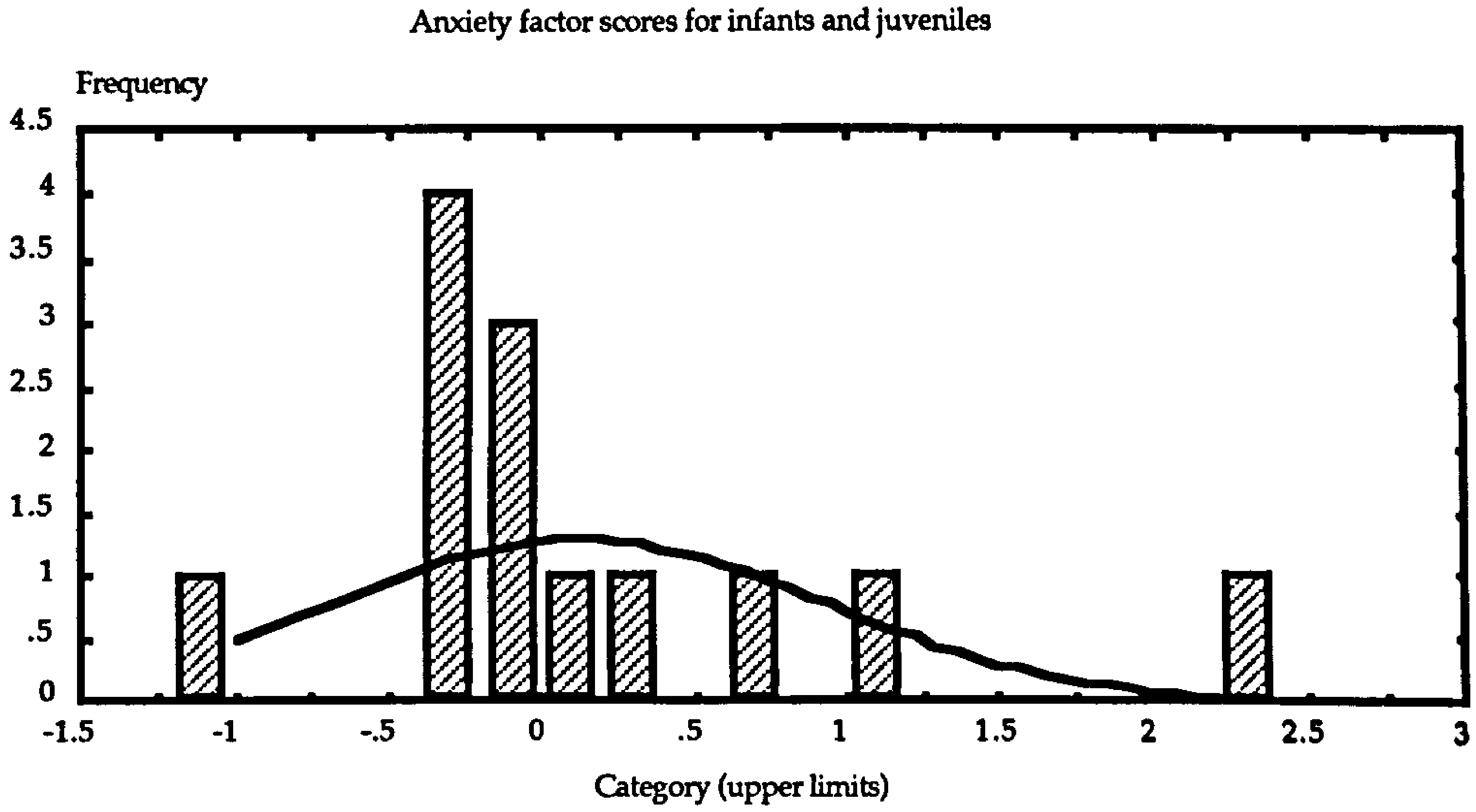


Fig. 8 Distribution of Anxiety scores: Adolescents

Chi square = no value (d.f. = 0), p = 1
K-S d = .17, p = n.s.

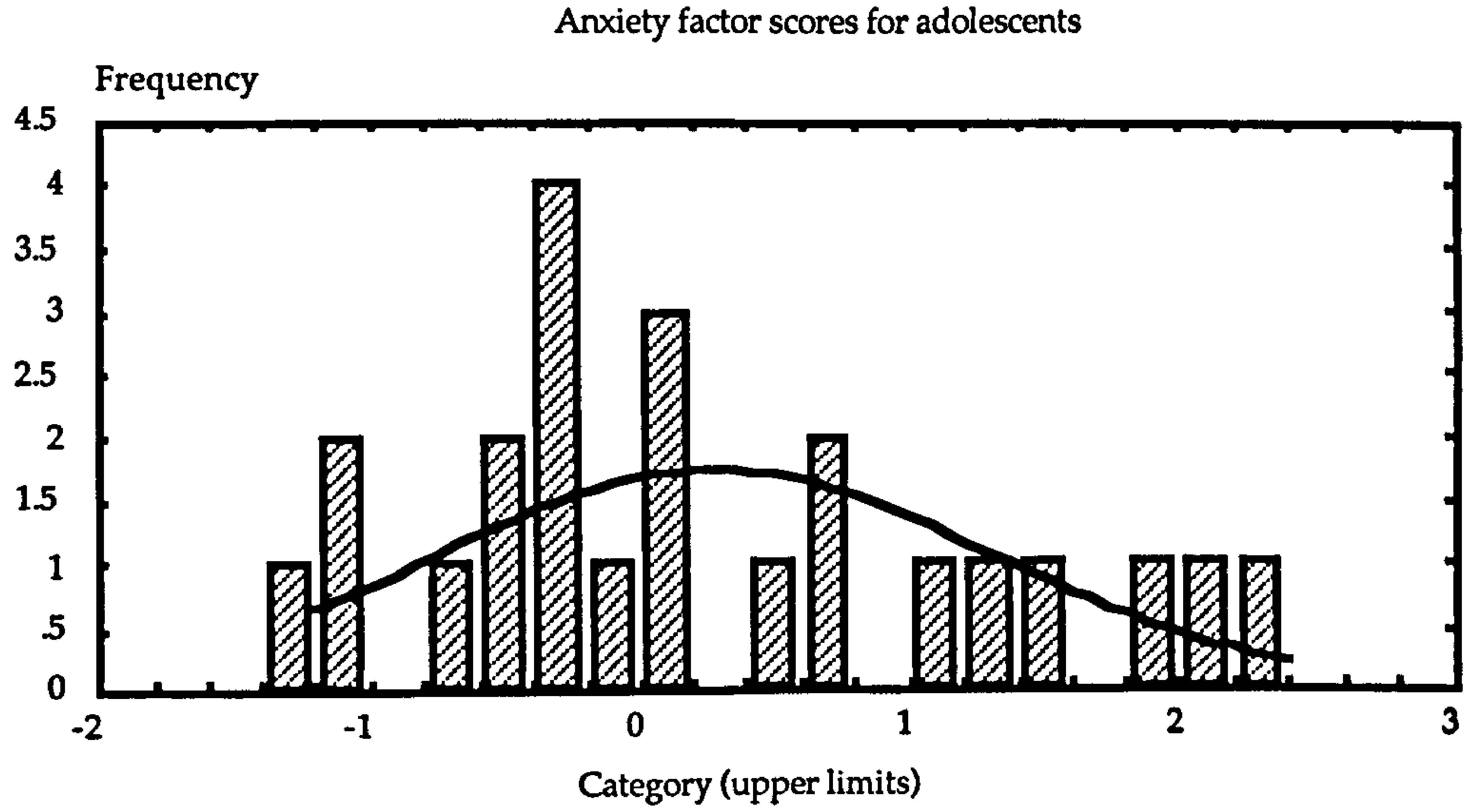


Fig. 9 Distribution of Anxiety scores: Adults

Chi square = 7.44 (d.f. = 2), p = .02
K-S d = .10, p = n.s.

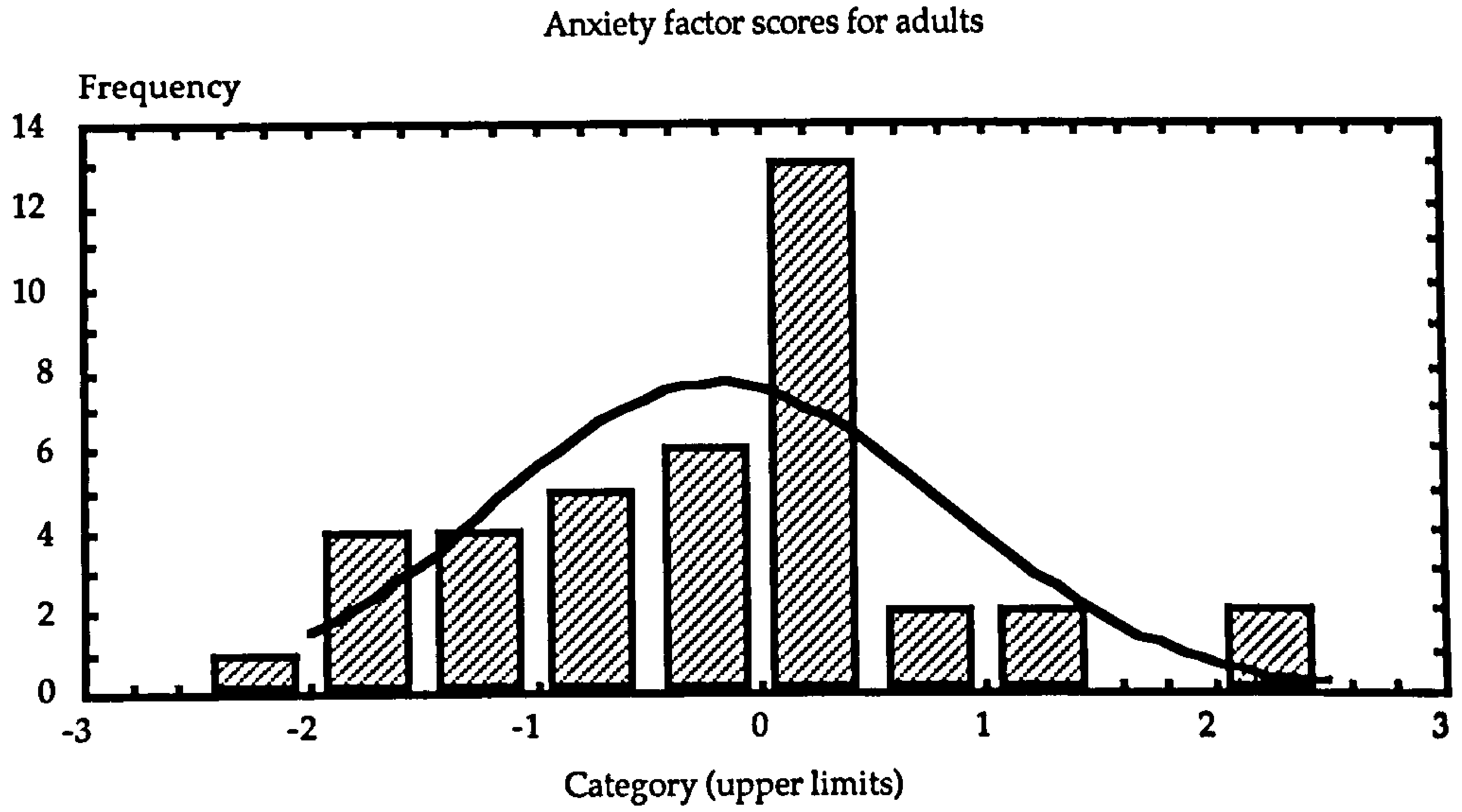

Anxiety factor scores for adults

Fig. 10 Distribution of Curiosity scores: Infants and Juveniles

Chi square = no value (d.f. = 0), p = 1
K-S d = .21, p = n.s.

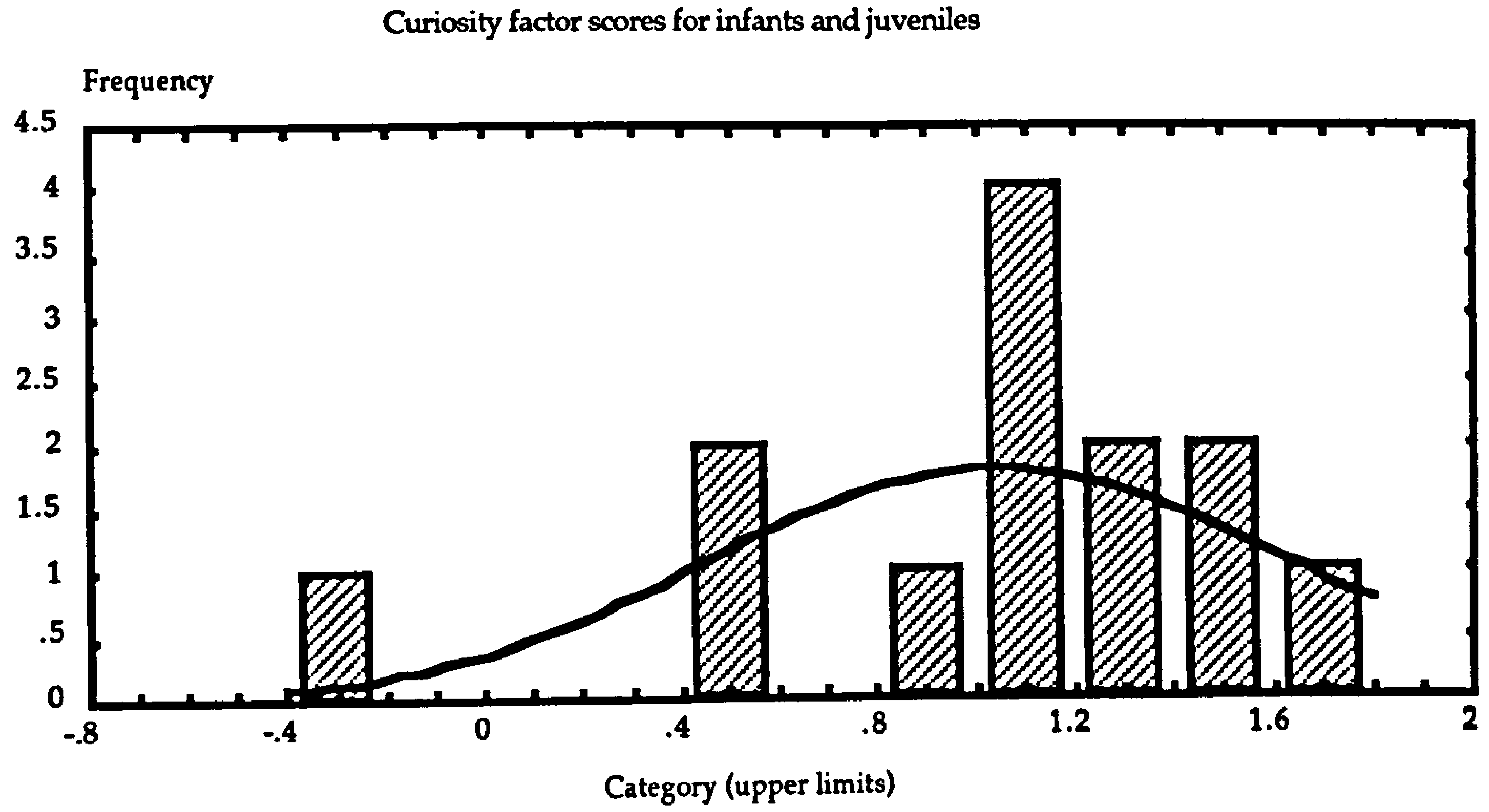

Curiosity factor scores for infants and juveniles

Fig. 11 Distribution of Curiosity scores: Adolescents

Chi square = .74 (d.f. = 1), p = .38
K-S d = .09, p = n.s.

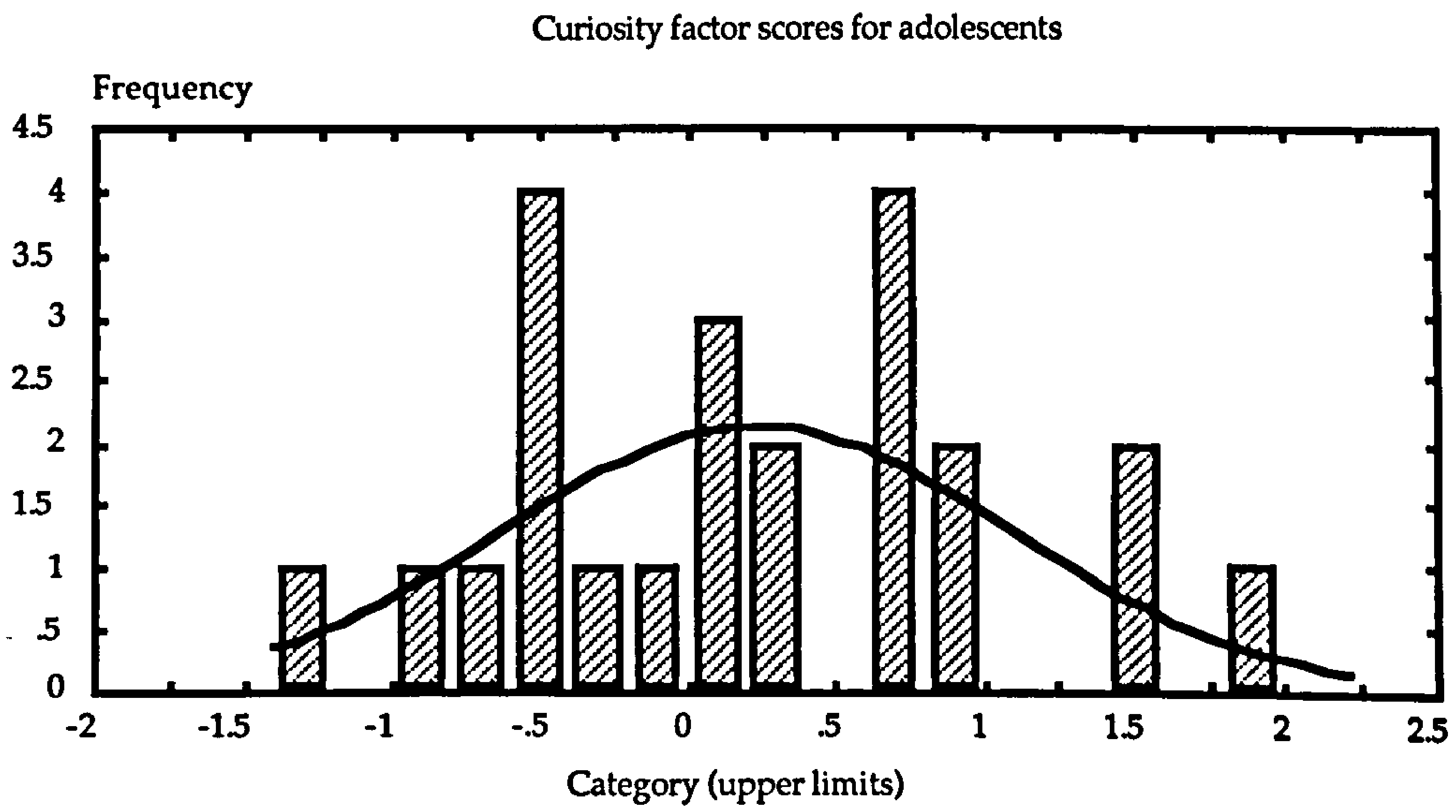
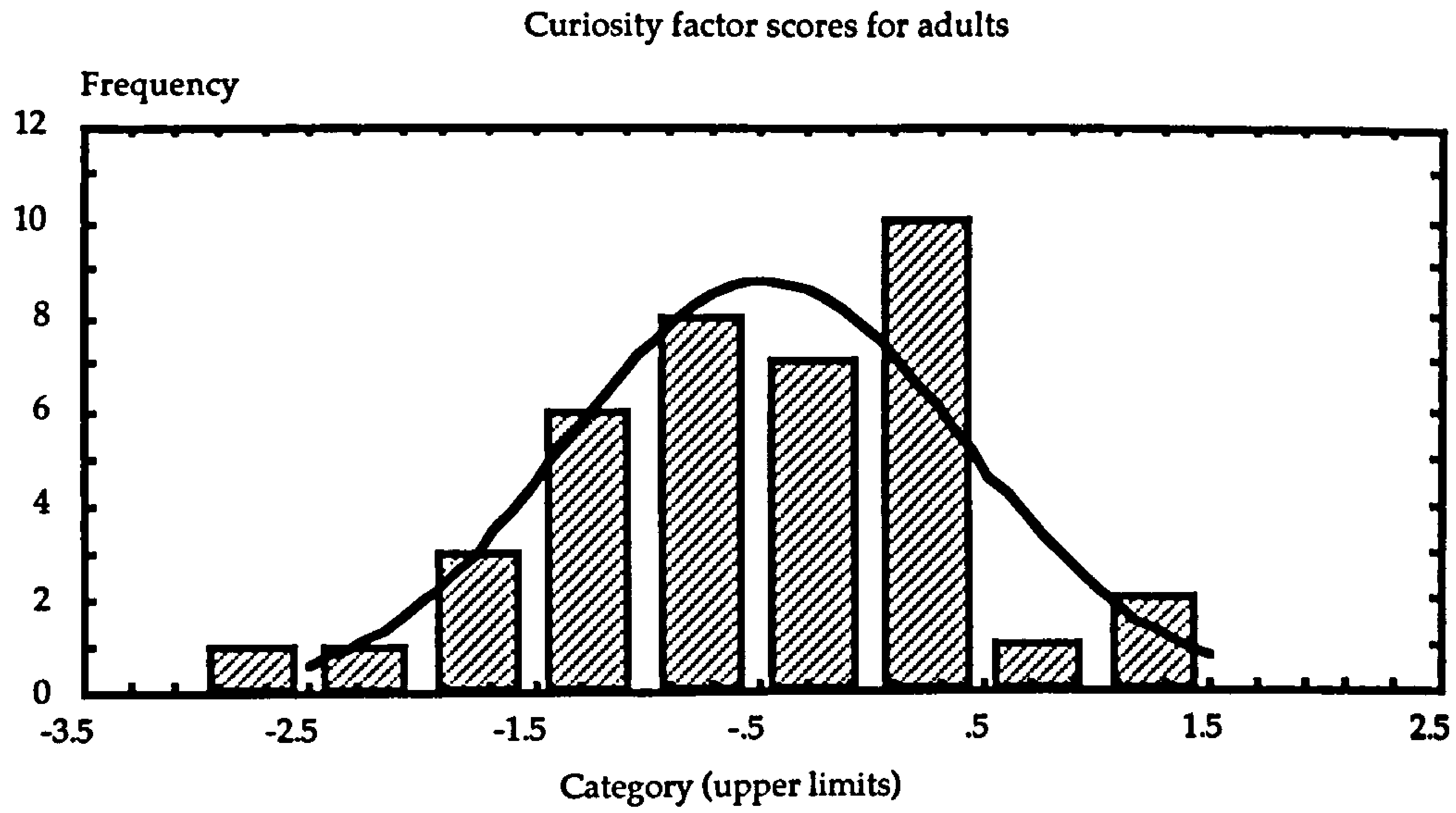


Fig. 12 Distribution of Curiosity scores: Adults

Chi square = 3.48 (d.f. = 2), p = .17
K-S d = .07, p = n.s.



Appendix VIII

Agonistic support choices of focal animals

Supporter	Pro	Contra	Impartial	AA/RA	WS/LS	Type
BS	HD	DY		RA	LS	I
BS			FL RS			I
BS	DY	FD		AA	WS	I
BS	RS	WD		RA	LS	I
BS	RS	DY		RA	LS	SI
BS	KN	DY		RA	LS	I
WN	LZ	MD		RA	LS	I
WN	CL	BS		RA	LS	I
WN	AL	SL		?	?	I
WN	RS	DY		RA	LS	SI
WN	BS	CL		AA	WS	I
WN	FL	KT		RA	LS	SI
WN	RS	FG		RA	LS	NI
WN			MD AL SR			NI
WN	RS	DY		RA	LS	NI
WN	MD	FG		RA	LS	SI
WN			FL RS			SI
WN	DY	FD		AA	WS	SI
NK	FL	KT		RA	LS	SI
NK			WD MD			NI
NK	FL	RS	?	?		I
NK	RS	DY		RA	LS	NI
NK	FG	LZ		RA	LS	SI
NK	KY	CL		RA	LS	NI
NK	RS	AL		RA	LS	I
NK	KN	DY		RA	LS	SI
NK	BS	DY		RA	LS	SI
NK			WN FL			I
NK			WT KY			I
NK			HL LZ			NI
NK	CL	WN		RA	LS	SI
NK	DY	FD		AA	WS	I
NK	DY	FD		AA	WS	SI
NK	DY	FD		AA	WS	SI
FD	KT	FL		AA	WS	SI
FD			FL RS			SI
FD			BS FL			SI
DY	CL	FD		AA	WS	SI
DY	MD	AL		RA	LS	SI
DY	MD	FG		?	?	SI
DY	CL	SL		AA	WS	SI
CL			HD MD			NI
CL	NK	FD		AA	WS	I
CL	ZZ	AL		AA	LS	NI
CL	SL	DY		RA	LS	I
CL	ZZ	BS		RA	LS	NI
FL			HP AL			NI
FL	KY	LY		AA	WS	I
FL	SL	HP		AA	WS	SI

MD	AL	SL		AA	WS	SI
MD	SL	HD		RA	LS	SI
MD	ZZ	KN		RA	LS	SI
MD	FD	DY		RA	LS	NI
MD	ZZ	AL		RA	LS	I
MD	ZZ	KN		RA	LS	I
KN	MG	SR		RA	LS	SI
KN	KT	DY		RA	LS	I
KN	FG	MD		?	?	I
WD	HD	FL		RA	LS	SI

AA/RA	Actor supporter/Reactor supporter
WS/LS	Winner supporter/Loser supporter
NI	Non-agonistic intervention
SI	Semi-agonistic intervention
I	Agonistic intervention

Appendix IX

Nonagonistic support choices for focal animals

Supporter	Pro	Contra	AA/RS	WS/LS
BS	KT	WN	RA	LS
BS	KT	FL	AA	WS
NK	RS	DY	RA	LS
NK	KY	CL	RA	LS
NK	SR	RS	?	?
NK	HD	FL	RA	LA
DY	LY	AL	AA	WS
FL	KN	KY	RA	LS
FL	CS	KT	?	?
MD	BS	WN	RA	LS
KN	MD	FG	?	?

AA/RA	Actor supporter/Reactor supporter
WS/LS	Winner supporter/Loser supporter

Appendix X

Session totals for inter-rater reliability of agonistic behaviour

Table 1 Frequencies of recorded low-level conflicts

Session	Rater 1	Rater 2
1	2	3
2	8	5
3	3	2
4	7	8
5	0	1
6	4	3
7	1	1
8	3	2
9	5	3
Totals	**33**	**28**

Table 2 Frequencies of recorded moderate-level conflicts

Session	Rater 1	Rater 2
1	1	0
2	4	6
3	3	3
4	1	0
5	3	1
6	1	2
7	5	4
8	2	2
9	5	6
Totals	**25**	**24**

Table 3 Frequencies of recorded high-level conflicts

Session	Rater 1	Rater 2
1	2	2
2	0	0
3	0	0
4	0	0
5	0	0
6	1	1
7	0	1
8	0	0
9	0	0
Totals	**3**	**4**

Table 4 Frequencies of recorded mild submissive responses

Session	Rater 1	Rater 2
1	1	0
2	2	2
3	6	5
4	3	2
5	0	0
6	9	7
7	5	4
8	10	8
9	6	4
Totals	**42**	**32**

Table 5 Frequencies of recorded moderate submissive responses

Session	Rater 1	Rater 2
1	0	0
2	0	0
3	0	0
4	0	0
5	0	0
6	1	1
7	0	0
8	0	0
9	0	0
Totals	**1**	**1**

Table 6 Frequencies of recorded highly submissive responses

Session	Rater 1	Rater 2
1	1	1
2	0	0
3	1	1
4	0	0
5	0	0
6	0	0
7	0	0
8	0	0
9	0	0
Totals	**2**	**2**

Table 7 Frequencies of recorded agonistic interventions

Session	Rater 1	Rater 2
1	2	2
2	1	0
3	1	1
4	1	1
5	0	0
6	2	1
7	0	0
8	0	0
9	0	0
Totals	**7**	**5**

Table 8 Frequencies of recorded side-directed communication

Session	Rater 1	Rater 2
1	0	0
2	1	1
3	0	0
4	0	0
5	1	0
6	0	0
7	0	0
8	0	0
9	0	0
Totals	**2**	**1**

Table 9 Frequencies of recorded semi-agonistic interventions

Session	Rater 1	Rater 2
1	0	0
2	2	1
3	1	1
4	1	1
5	1	0
6	2	1
7	2	2
8	0	0
9	1	1
Totals	**10**	**7**

Table 10 Frequencies of recorded non-agonistic interventions

Session	**Rater 1**	**Rater 2**
1	1	0
2	0	0
3	2	2
4	0	0
5	2	1
6	0	0
7	2	1
8	2	2
9	3	2
Totals	**12**	**8**