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DOMINANCE AND PERSONALITY IN STUMPTAILED MACAQUES

Submitted for the degree of Ph.D.
March 1982

Graduation June 1982

For my parents

'How hard it is to keep from being King when

it's in you and in the situation'

Robert Frost

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it's in you and in the situation'

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CONTENTS

ACKNOWLEDGEMENTS

I am grateful to the Science Research Council for providing the grant for this research, and to Arnold Chamove, my supervisor for all his help, support and patience over the last 3 years.

This research would not have been possible without lots of people who helped me in many ways; Graham Cameron for teaching me what a computer was, Ranald MacDonald for statistical advice, the departmental technicians, especially John Russell who provided the drawings and Bob Lavery for photographic assistance.

I am also grateful to the staff of the Computer Unit, especially the programme advisors for their help with SPSS and BMDP and the operators for their co-operation in the printing of this thesis.

Thanks also to Jim Anderson for providing kindred spirit and Bill McGrew for providing references and encouragement.

I would like to thank Robin Campbell, for putting up with me over the last few months, for writing the computer programme used in Chapters 7 and 8 and for lending a sympathetic ear without yawning too much.

Finally, to all my monkeys, wherever they are now, in fond remembrance.

ABSTRACT

The concept of dominance has received considerable attention in studies of non-human primates. There are many diverse opinions regarding the function and evolution of dominance, due in part to the lack of consensus as to how to define and measure dominance. Some researchers believe that dominance is a universal principle of primate social organisation, which influences all aspects of social relationships, while others consider that dominance has been overrated as a general governing principle in social behaviour.

The study of personality in primates is less well documented, although the few studies which do exist have found a considerable degree of similarity between dimensions of human personality and those of primates. Recently, the study of human personality has explored the effects of the situation on the behaviour of an individual, and the complex relationship between personality and situational variables. This study considers the applicability to primate studies of human personality concepts and evaluates the extent to which the concepts of personality and dominance can increase our understanding of the behaviour of primates.

The effects of changes in dominance rank were examined by an experimental manipulation, designed to give experience in up to 5 dominance positions to each of 13 animals. Preliminary observations had indicated that there were individual differences in behaviour between animals of

differing dominance rank, and the manipulation phase was carried out with the object of discovering whether these characteristic differences were a function of the differences in dominance rank or in personality. The results of the manipulation indicated that changes in dominance rank affected fear and aggression levels, while some behaviours remained stable over changing dominance position, suggesting stable personality dimensions. However, most of the behaviour of an individual was found to be a function of the interaction between dominance and personality.

Thus the concept of dominance is useful in explaining some aspects of the behaviour of an animal and some aspects of his interaction with other animals. There was also evidence that the animals themselves differentiated other animals according to rank, in terms of how much grooming and visual monitoring they directed to animals of differing rank, suggesting that dominance rank is not only useful to human observers.

Studies of primate personality can help to indentify those aspects of an animal's behaviour which are independent of his dominance rank. It is proposed that dominance be defined in terms of how much limitation an animal has placed on his behaviour, but that just how aggressive a dominant animal is, or how fearful a subordinate animal is will be a function of his personality. The shotgun approach used by many researchers in trying to relate all aspects of social behaviour to dominance is misguided, since it ignores individual differences in the animals, and weakens the usefulness of the concept of dominance.

The personality of an individual animal was found to be an important variable both in determining his behaviour and aspects of the social structure of the group. Both trait/state and situational specificity theories of personality were investigated but rejected in favour of an interactionist theory, although it was concluded that while behaviour is a function of the interaction of personality and the situation we are limited in accounting for why and how such interaction occurs in the behaviour of primates.

In summary, the social behaviour of an animal is largely a function of the interaction between personality and dominance rank. Further studies of the social behaviour of primates would do well to investigate why animals compete for dominance, the complex interaction between dominance and personality and the effects of the personality of the animals within a group on the social structure of that group.

LIST OF TABLES

Table

Table

Table

Table

LIST OF FIGURES

Figure

Figure

LIST OF APPENDICES

Appendix

Chapter 1. THE CONCEPT OF DOMINANCE

Dominance is one of the most frequently investigated concepts in the behavioural sciences. An unfortunate result of the abundance of research on the topic is that rather than clarifying any of the issues involved in the concept, one is faced with an overwhelming number of studies which present a confusing and sometimes contradictory picture. Hinde & Datta (1981), commenting on a paper by Bernstein (1981), aptly reflect the feelings of many when the subject is raised '...we were not the only commentators who groaned at the sight of another article on the overused, often misused, overdiscussed but nevertheless often useful concept of dominance' (p. 442). In this section I will review the literature on dominance which encompasses several aspects; definition, measurement, function, species differences, group composition differences, sex and rearing condition differences, the particular characteristics associated with dominance/subordinance, and the usefulness of the concept.

1.1 Definition of dominance

The concept of social dominance was introduced by Schjelderup-Ebbe (1922, 1935) as a term to aid in the description of the social organization of domestic fowl. His finding of a unidirectional 'pecking order' in which one bird consistently pecked another gave rise to the now widely applied term 'dominance', which has since been applied to almost all vertebrates (review by Crawford, 1939), and, notes Syme (1974), has now been generalised to incorporate fish, amphibia and some invertebrates.

Schjelderup-Ebbe's original work, entirely observational in nature, described the dominance order solely in terms of overt aggression, which he held to be the outward manifestation of an underlying social organization governing all social behaviour in the fowl. This view of dominance as an aggressive order has undergone little change, although authors have attempted to relate dominance to other social behaviours and find other means of measuring the phenomena. Van Kreveld (1970) regards overt aggression as the primary index of dominance, defining dominance as 'a priority of access to an approach (meaning positive) situation or away from an avoidance situation that one animal has over another' (p. 146). Maslow (1936a) believes that dominance relationships pervade all behaviour, (a view shared by Jay, 1965) which is implicit in his definition of dominance; 'we shall define the dominant animal as the one whose behaviour patterns (sexual, feeding, aggressive, social) are carried out without deference to the behaviour patterns of his associates. The subordinate animal is one whose behaviour patterns (sexual, feeding, aggressive, social) are suggested, modified, limited or inhibited by the behaviour patterns of its more dominant associates' (Maslow, 1936a, p. 263).

This notion of the pervasiveness of dominance has not gone without criticism (Crook, 1970; Winter & Ploog, 1967). In addition, frequent misinterpretation of the notion of 'limitation of behaviour' has resulted in some confusion and debate as to how to measure dominance. A dominant animal may act without deference to the behaviour patterns of more subordinate individuals, but it does not follow that he will be more aggressive, eat more, copulate more frequently etc. The definition only implies that other animals will not limit the expression of these behaviours in a more dominant animal.

1.2 Measurement of dominance

(a) Aggression

The original aggressive peck-order measurements of dominance focused on aggression and the notion of limitation of behaviour by the dominant animal on that of the subordinate (Zuckerman, 1932; Maslow, 1936a, b; Maslow & Flanzbaum, 1936; Carpenter, 1942 ; later Chance, 1956). These studies usually involved pairwise testing pairs of monkeys (otherwise housed singly) in all possible combinations. Experimenters emphasised the typical aggressive behaviour of dominant animals and postulated that dominance was a drive that animals possessed in varying amounts. 'Dominance may be envisaged either as a drive to behaviour or as a social 'attitude'....the factors that seemed to determine dominance in our evenly matched animals seemed to be not so much size, physical strength etc., as an attitude of aggression or confidence' (Maslow & Flanzbaum, 1936, p.307). Yet, if dominance can be considered as a 'drive' which animals possess to varying degrees (or if dominance is achieved as a result of a high aggressive drive, or a high amount of confidence) then it is certainly not appropriate to apply the notion of limitation of behaviour to aggressive behaviour. A subordinate animal may be less aggressive (and therefore less dominant) because of his lack of drive to become dominant, not because of any limitation on the part of the dominant on his aggressive behaviour.

As Hinde (1978) notes, there is often confusion between applying the concept of dominance/subordinance to dyadic relationships and also to the patterning of relationships in a group containing more than 2 individuals, where coalitions may be important for maintenance of rank (Mitchell, 1979; Kawai, 1965), and an individual may enlist the support of another and thus defeat an animal to whom, in a previous dyadic encounter, he had been subordinate (Maslow, 1936b; Wooley, Clark & Stevens, 1978).

A further problem, as Bernstein (1981) notes is that 'some measures of dominance seem to preclude accepting (i.e., not rejecting) the null hypothesis that no dominance relationship exists' (p.426). This is certainly true of aggression; if A aggresses B more than B aggresses A then according to the definition of dominance based on limitation of behaviour, A is the more dominant of the two. Yet this assumes that A and B are equally motivated to behave aggressively, but that B's expression of aggression is limited by A. (The notion that A and B are equally motivated to behave aggressively is too simplistic; A may be more aggressive in a competitive food situation, B may be more aggressive when competing for access to a sexual partner - motivational states will alter). It may be that A is simply more aggressive by nature (i.e., possesses greater drive for dominance) and that the aggressiveness of A and B have nothing to do with their dominance relationship per se. It appears as if the 'drive' hypothesis may prove more useful than the limitation of behaviour notion, at least in explaining agonistic relationships. Before a dominance relationship based on the aggressive interactions between A and B can be called anything other than an aggressive relationship it is necessary to demonstrate that 'A dominant to B' holds for other measures of dominance. In his review of the literature Syme (1974) states that 'if an author wishes to interpret his order as a dominance order in relation to a scale of aggression, this is valid, but such an order should not be interpreted as a general order of social dominance without further measures. If only aggressive behaviour is studied it is simpler to discuss the social order obtained in terms of it being an aggressive order' (p.936). If it can be demonstrated that agonistic dominance relationships influence the pattern of other social interactions then dominance relationships can be viewed as an independent variable influencing identified dependent variables (Bernstein,1981). Yet there is no reason why agonistic dominance relationships need influence all social interactions; if such relationships can determine the outcome of competitive conflicts then they are an important aspect of social interaction, if only in such competitive situations.

(b) Priority of access to preferred incentives

(i) food/water competition tests.

The initial equation of dominance with aggressive behaviour became problematic as it became clear to researchers that measurement of aggression in those species in which it was rare was a slow method by which to arrive at a dominance order. In addition, it was felt that a dominance order based on aggression should generalise to other social behaviour. Richards (1974) provides a summary of the main methods and their respective success. One of the most widely used methods is based on the notion of priority of access to limited resources, on the assumption that a dominance order can be derived from the order to drink/eat etc., which reflects the amount of limitation that each individual has on his behaviour as conferred by his dominance position in the group.

As well as 4 measures of priority to food incentives Richards also studied agonistic interactions, displays and gestures of fear/submission in a group of rhesus macaques (Macaca mulatta). The measures which most consistently ranked all group members and correlated with each other were the 4 measures of priority to food, agonistic interactions (the direction rather than the total), displays and avoidance/yielding ground behaviour. The measures of presentation/mountings and fear grins were poor at ranking individuals as they occurred too infrequently. Similarly Christopher (1972) studied the relationship between dominance as assessed by a water-bottle competition test (after 24 hours water deprivation) and various social behaviours during the test in a group of pigtailed macaques (M. nemestrina); 94.7% of all interactions were oriented in the direction predicted on the basis of the function of these patterns (i.e., the behaviour of subordinate to dominant, dominant to subordinate was consistent with the rank prediction from the water-bottle test). However Deag (1977) believes that measures which maximise the chance of such correlations (in that they are not taken across a variety of social situations) produce results which reflect the method rather than the animals' behaviour.

It may be that animals differ in how highly they value incentives; Baenninger (1970) reports a low correlation between 2 dominance orders in rats, one based on priority of access to food, the other on priority of access to water, which he believes is due to the fact that there are 2 different dominance orders for the 2 rewards. This might reflect the relative value that each animal places on each resource, and the amount of 'limitation' he is prepared to tolerate in his satiation of hunger or thirst. Reviewing the use of competitive orders as measures of social dominance Syme (1974) states that such orders must have both internal validity (proof that they reflect a socially mediated priority of access of one animal over another, rather than some superior individual ability) and external validity (generality to other social behaviours). There are problems of repeated food competition trials in that an animal's motivation may change (Bernstein, 1980). 'If we use multiple measures, we cannot reasonably expect either that the dominant will win on every trial or that wins and losses will be absolutely evenly divided. Neither behaviour nor random events are uniform, and variability is a characteristic of both' (p.74).

(ii) mating success.

If sexual drives can be considered to be a powerful male motivator then access to receptive females can be viewed as one of the reinforcers for animals of high dominance rank (Bernstein, 1976). However evidence that dominant males increase their genetic fitness by successfully competing with other males for access to ovulating females is mixed, and varies both across species and within species between troops in different habitats. It has been demonstrated that mating success is related to aggressive rank in rhesus monkeys (Kaufman, 1965) and in vervet monkeys (Cercopithecus aethiops)(Struhsaker, 1967) but this relationship has not been found in chimpanzees (Pan troglodytes) (Bygott, 1974), chacma baboons (Papio ursinus)(Saayman, 1971) or squirrel monkeys (Saimiri sciureus)(Baldwin, 1968). Saayman (1971) reports in his study of a group of chacma baboons that the 3 adult males of the troop differed significantly in their rank order on a variety of criteria generally employed to assess dominance in a field situation. The most aggressive male was dominant in individual encounters, and initiated significantly more troop progressions than the other 2 males, but completed few copulations, whereas an older adult male, subordinate in individual aggressive encounters was most active in copulatory behaviour. In addition, the different frequencies of grooming and presenting to the respective males indictated that the other baboons discriminated these temperamental differences in the males. Baldwin (1968) attributes the lack of the relationship between dominance rank and mating behaviour in the group of squirrel monkeys which he studied to the particular characteristics of the dominant males; 'The traits of excitability, aggressiveness and persistent interest in dominance activities that made them (adult males) dominant in the hierarchy were responsible for the unsuccessful mating, since mating required quiet, privacy and often long periods of patient consorting' (p. 311). Paterson (1973) found that whereas savannah-living olive baboons (Papio ursinus) competed for females in oestrus, a troop of the same species in a forest habitat showed no such competition. Thus the evidence for a relationship between mating success and dominance is equivocal, and the notion of 'limitation of behaviour' as regards sexual behaviour may not be applicable. However, as Bernstein (1976) notes, it may not be the absolute level of sexual activity that is important, but rather effective reproductive behaviour - 'getting there when it counted'. In a group of langur monkeys (Presbytis entellus) studied by Jay (1963) while there was no correlation between dominance status of the males and the number of successful copulations, there was a tendency for the most dominant individuals to copulate most frequently with females at the peak of their oestrus periods. However, Bernstein (1976) cites equivocal evidence that high-ranking males have greater access to oestrus females than those of lower-rank, although they may be preferred as mating partners by females. Bernstein further suggests that the attributes of an individual who successfully achieves a position of dominance might also prove effective in attracting sexually active females. Thus 'it would be these attributes per se, which would be transmitted to the next generation' (p. 469).

It may be that the individual characteristics of a particular male are more important in determining his mating success than is his dominance rank, particularly as there is also evidence that partner selection is not exclusively a male priority. Females have been shown to express active preferences for particular males as sexual partners, and these preferences may not relate to high male aggressivity or high dominance rank (Jay, 1963; Tutin, 1974). As Bernstein notes, 'rape is rare in non-human primates and an aggressive, assertive male does not automatically gain access to estrous females...' (p. 469).

(iii) competitive avoidance.

Based on the definition of dominance as a priority of access to an approach situation or away from an avoidance situation, Miller & Banks (1962) attempted to determine social dominance using pairs of rhesus monkeys (usually housed singly) in a competitive avoidance task. A small test cage was used, with a perch only large enough to accommodate a single monkey. After an initial training period during which each monkey learned to avoid an electric shock on the grid by climbing on the perch two animals were paired together in the task. The unsuccessful competitor stayed on the grid during the shock period: the other animal was regarded as the dominant. Miller & Banks report the competitive avoidance procedure as being a method subject to minimal interference (timidity on the part of the animals, influence of the investigator) and the results correlate significantly with dominance ranks as determined by a competitive food task. Nowlis (1941) reports similar success using this method with chimpanzees. However Farres & Haude (1976) used 3 methods of dominance testing in pairs of rhesus monkeys; competitive food-getting, competitive drinking and competitive avoidance. With the exception of the competitive avoidance procedure all other methods (including testing after food deprivation in a competitive food test) showed high reliability and high inter-correlations. Van Kreveld (1970) has suggested that in a competitive avoidance paradigm the mechanism for a dominant animal to defend his position over a subordinate may not be released, and that defence is not possible, only flight. It is thus fear which operates, not dominance. The competitive avoidance procedure is limited in use, as it can only be applied in a laboratory situation, and then only to a limited number of animals.

(c) Grooming relationships

If the data on the usefulness of competitive tests in predicting dominance rank is equivocal (summarised in Syme, 1974), the success of grooming and affiliative relations is no better. As is the case with aggressive behaviour its success seems dependent on whether it is used as a predictor in a dyadic or group setting. In a dyad subordinate animals do more grooming than dominants, as found by Crawford (1942) in chimpanzee pairings and Maslow (1936b) in rhesus monkey pairings, although a study by Maslow & Flanzbaum (1936) showed the reverse relationship - dominant individuals of a pair did more grooming. In a group of 6 laboratory rhesus monkeys Varley & Symmes (1966) found no simple correlation between grooming behaviour and dominance position, although the most dominant animal received the most grooming and the amount that each individual groomed Alpha was related positively related to the amount of aggression received from her. They conclude that grooming relationships are determined more by habitual patterns of association and physical proximity than by other mechanisms such as dominance status. In a study of 7 captive groups of six species of monkey Bernstein (1970) failed to find any correspondence between dominance orders based on direction of aggressive behaviour and either mounting sequences or grooming which led him to suggest that these three social responses were not derived from any single social mechanism. Bernstein suggests that these 3 particular interaction patterns may be independently determined by a variety of factors and one may not neccessarily predict the course of the other.

However a study by Kaufman (1967) found that the more dominant male rhesus (based on agonistic criteria) groomed proportionately more females in the breeding season than animals lower in the hierarchy. While maintenance of affiliation with breeding females may be important to a dominant male there is also evidence that more dominant individuals are more attractive as social partners than those of lower rank. In a group of stumptailed macaques (M. arctoides) Rhine (1973) found that the amount of grooming received increased with dominance (and that the amount done decreased). Seyfarth's (1976) study of 8 adult female ursinus baboons (Papio cynocephalus ursinus) indicated that while the number of grooming responses given per solicitation received were greatest in interactions with high-ranking individuals, the amount of grooming in absolute terms was greatest with individuals of similar rank to the groomer. This finding would fit with a theory of the attractiveness but low availability of high-ranking individuals (where the most dominant is the most preferred but the number 2 animal has priority of access to her, and the number 3 animal priority to number 2 etc.).

Clear differences between dyadic dominance relationships and relationships within a group with respect to affiliative interaction can be seen from Simpson's (1973) study of a group of male chimpanzees. Dominance rank was based on several, significantly intercorrelated agonistic measures, and within a dyad, the subordinate of the two groomed his superior more than vice versa, and that dominant individuals tended to groom frequently but in short bouts. The dyadic grooming relationship was clearly established, whilst that between dominance rank in a group and grooming was less so.

Why might it be assumed that grooming behaviour is related to dominance rank and what is the nature of the affiliative relationship between animals of different dominance rank? As Bernstein (1981) notes, one might believe that the groomer is performing a service for the groomee and that dominant animals might claim their grooming 'rights', (and, according to our definition of dominance, be unlimited in respect of this claim). Maslow & Flanzbaum (1936) report that when subordinate monkeys refused to groom a dominant they were attacked by him. Yet there is also evidence that when a dominant chimpanzee is grooming a subordinate it may attack the subordinate if it attempts to leave (Crawford, 1942). It may be that there are 2 drives involved in grooming behaviour, one to groom and one to be groomed, both of which may be limited in the case of more subordinate animals. While it is possible to talk of such drives 'post hoc', there is no a priori reason why grooming behaviour should relate to dominance; one can propose that subordinate animals will do more grooming of dominants than vice versa, according to the notion of the attractiveness of dominants, and the fact that dominants are unlimited in their claim to be groomed. Equally, one can propose that dominant animals will do more grooming of subordinates than vice versa, if one accepts the view that there is a desire to groom which is not limited in the case of the dominants. Thus grooming behaviour is another example of a measure which precludes acceptance of the null hypothesis that no dominance relationship exists (Bernstein, 1981) unless one can establish a reason _a priori_ why such a relationship might exist, and predict the precise nature of the relationship between grooming and dominance rank.

As Chalmers (1981) notes, a dominance relationship, perhaps as expressed by the pattern of competitive interactions between two individuals, is only a subset of the total relationships that exists between the two. 'Dominance may or may not turn out to be the most important aspect of that relationship, but we have no a priori justification for judging all other aspects of the relationship in terms of the competitive interactions of the two animals. We have, therefore no right to assume that grooming, spatial distribution, etc. are 'really' manifestations of dominance' (p. 437).

(d) Submissive behaviour

Rowell (1966) found in a group of olive baboons that the behaviour of subordinate animals in approach-retreat interactions correlated better with rank than agonistic behaviour initiated by high-ranking animals. Similarly Mason (1966) stated that the best indicator of the establishment of a dominance relationship was 'cringing' on the part of the subordinate. In addition to this behavioural evidence Rowell (1974) believes that subordinance (but not dominance) has an endocrinological basis, and that dominance hierarchies are a product of a stressful laboratory situation and are not found in the wild. According to Rowell some animals respond to the stress of captivity with a syndrome of physiological and behavioural changes - 'To explain these observations in terms of dominance (not subordinance) would be less economical, requiring a 2-stage process; captivity elicits dominance behaviour (which has no physiological correlate) which in turn is responded to with submissive behaviour' (p. 141). The dominant-subordinate relationship is viewed by Rowell as a dynamic learning process in which submission by one animal reinforces its subordinate status to the other. Maslow (1936a) however does not believe that the less dominant animal occupies his subordinate position with any evidence of willingness or submission but is forced to assume this attitude by the violence of his superiors (which is linked to the latter's dominance drive).

Rowell emphasises the behaviour of the subordinate animals rather than the aggression or drive of the dominants; dominance hierarchies do not reduce aggressive levels, they exacerbate them, and the hierarchy is only formed because of the subordinates eventually succumbing to the stress (see also Gartlan, 1968). Subordinate animals are considered to take the initiative by for example, non-sexually presenting to a dominant as a gesture of submission and to suppress the likelihood of attack by the dominant.

Rowell claims that 'Dominance relationships are only partly correlated with social behaviour, and there is no evidence for any 'quality of dominance'....submissive behaviour on the other hand can be related to hyperfunctioning of the adrenal gland in response to environmental stress' (Rowell, 1974 p. 151).

This view of dominance hierarchies as being primarily laboratory-found phenomena has not gone without criticism. Deag (1977) holds, contrary to Rowell's view that in wild primates hierarchies are tenuous or absent, that hierarchies are present in wild groups, where little stress as compared to captive animals is concerned. In his study of Barbary macaques (M. sylvanus) he found that both dominant and subordinate animals contributed to the maintenance of the dominance hierarchy. Whereas Rowell (1966) found that in her laboratory study only 'avoidance received' correlated with rank, Deag reports significant correlations of rank with 'avoidance given', 'threats received' and 'threats given'. Indeed there was a greater amount of threatening behaviour by dominants than avoidance on the part of the more subordinate animals, and frequent assertion by dominant animals over their subordinates, at least in a laboratory situation is also reported by Richards (1974). It appears that both dominant and subordinate animals play a role in maintaining a hierarchy - after all, the roles are complementary; one cannot have a dominant without a submitting subordinate, or a subordinate without an assertive dominant (unless the subordinate offers no challenge at all).

(e) Visual monitoring

Visual monitoring behaviour has also been used as a indicator of the dominance hierarchy within a group. Deriving from Chance's work on attention structure (1967) the notion that visual monitoring might reveal the dominance hierarchy of a group stems from the idea that the dominant animals will be the focus of attention for the subordinates; subordinates will monitor the dominant animal closely for reasurrance, in order to follow him if he moves and to make sure he is not too close in case they are attacked by him. Certainly Keverne, Leonard, Scruton & Young (1978) found that visual monitoring in captive talapoin monkeys (Miopithecus talapoin) was greater in subordinate than dominant animals, at least in single-sex groups, and that the animals that received the most monitoring were not necessarily the most aggressive individuals but they were high-ranking. Similar work with rhesus monkeys (Virgo & Waterhouse, 1969) indicated that visual monitoring behaviour may reveal group dominance structure. However this is dependent on group composition; Keverne et al. found that in mixed-sex groups dominant males actually visually monitored more, directing their attention towards females, and that in aggressive situations, visual monitoring increased for all animals, regardless of who gave or received the aggression.

Thus, while visual monitoring behaviour may reveal group structure factors such as group composition, the nature of the situation in which visual monitoring is measured must be taken into account.

1.3 Function of dominance

The evolutionary significance of social dominance hierarchies has been debated. While dominance is relatively easy to observe in the interactions of ground-living primates such as baboons and macaques how significant a role dominance plays in social organization and how structured dominance relations are varies from species to species and troop to troop (Bernstein, 1976). Generally speaking, the more arboreal a species of primate, the less the orientation towards dominance; this may be as a result of lower predation risk, and thus there may be less need for special large , aggressive individuals for group protection (Lancaster, 1975). Wynne-Edwards theory (1965) states that the development of hierarchies arose through group selection; adaptive mechanisms keep group size within limits such that food supplies are exploited without being exhausted. The theory considers the dominance hierarchy as one of these adaptive mechanisms which reduces fighting to death and starvation to fighting for a high position in the hierarchy. Further, the dominance hierarchy serves to integrate the group which is useful in defence from outside threat (Bernstein, 1964) or in protecting group territory, and also reduces inter-group aggression and conserves energy (Struhsaker, 1967; Bernstein & Gordon, 1974). Williams (1966) believes that the predictability of social relationships and the reduction of aggression, both consequences of dominance hierarchies, are the results of individuals adopting strategies maximising fitness, or minimising loss of fitness when disadvantaged in a competitive situation. The individual fitness theory is widely supported by many field studies but with some inconsistencies. The reason that individuals contest dominance relationships may be because the more dominant individual gains advantages in competitive situations (Bernstein, 1981). If such contests occur then this leads to the question of the adaptive significance of being dominant, and how dominant animals achieve greater genetic fitness, which may be related to their success in interactions involving priority of access to incentives (food, drink, escape, access to sexual partners etc.). Several investigators have attempted to determine the benefits conferred on high-ranking individuals, which seem few. Food sources are often dispersed so high status may not mean better access except perhaps in times of privation (Wrangham, 1974). Similarly there is evidence that it may not be the most dominant animal who influences group ranging movements (although the theory of individual fitness does not imply that they will), but they may be preferred partners in travelling activities, and as previously discussed, the evidence that dominant males increase their genetic fitness by successfully competing with other males for access to ovulating females is equivocal.

The establishment of dyadic dominance relationships must have benefits for both individuals, for as Bernstein (1981) states, 'relationships are not readily formed when there is benefit to only one party' (p.427). Yet why should one individual yield to another in a contest for a particular resource if both require the resource for survival or reproduction? This depends on the costs of fighting in relation to the benefits of winning, and if the former greatly outweighs the latter, it is better for the individual to avoid or cease fighting. Gauthreaux (1981) discusses the notion of 'asymmetries' in contests for resources, which may be of 3 types; (1) payoff asymmetries where one contestant may have more to gain by winning, (2) asymmetries in fighting ability,(3) uncorrelated asymmetries, e.g., wins on home territory. The ability of an individual to assess asymmetries in fighting potential and payoff is adaptive (Dawkins & Krebs, 1978); if an individual has reliable cues associated with asymmetries then contests can be settled without resorting to costly aggression, and in the case of dominance it is evolutionary stable to settle a contest on the basis of these asymmetric cues rather than escalate interactions despite marked asymmetries between the contestants (Maynard Smith 1974).

The cues, established by natural selection, may be characteristics such as size, social and fighting skills. And it is perhaps to these cues that we should direct our attentions; we need to identify those factors which enable one individual to dominate another in competitive situations (Chalmers, 1981; Bernstein, 1981).

Dissatisfaction with the functional explanations of dominance has led several authors to advocate the use of other terms to aid in the description of primate social behaviour. Hinde (1978) distinguishes between dominance and 'role', the former being useful for describing dyadic relationships or group structure, whereas role is useful in analysing the determinants of the behaviour of individuals, or the consequences of that behaviour on group structure. Gartlan (1968) and Crook (1970) also advocate the use of 'social role profiles' for individuals as being helpful in describing social systems because of the inadequacy of the dominance terminology.

1.4 Differences in expression of dominance

(a) Species differences

Carpenter (1942) reviews the differences found between primate species in the expression of dominance. Howler males (Alouatta) of the same group feed together without fighting, share receptive females and co-operate together in the defence and leadership of the group. Hamadryas baboons on the other hand show exclusive dominance, and possess harems of 5/6 females per male. Other species lie in between these extremes. The establishment and maintenance of dominance in feral chimpanzees chiefly involves ritualistic display behaviour and overt aggression is rare, and is only resorted to when all else fails (Coe & Levin, 1980). This is in contrast to the extremely aggressive behaviour shown by laboratory rhesus monkeys in the establishment of dominance (Maslow, 1936b).

Usually primate groups are patriarchical, the male dominance being predominant over female dominance, but the degree of overlap between the dominance of the two sexes varies from species to species, and in gibbons (Hylobates spp.) male and females are equally dominant (Carpenter, 1963).

(b) Group composition differences

As previously mentioned, there are differences between dyadic and group dominance. Maslow (1936b) found that new behaviours emerged in groups of animals who had previously only met in pairs. Animals that had been dominant in their pairings were, in groups of 3, often beset by alliances of their subordinates and beaten severely. Similarly Wooley, Clark & Stevens (1978) found that in squirrel monkeys pairs or triads of females could often defeat a male by coalescing. The differences in visual monitoring behaviour according to group composition have already been discussed (Keverne et al., 1978). Evidently the various measures which have been used to determine dominance relationships depend on the particular composition of a group for their success, and what may constitute a reliable measure in one group may not be reliable for another.

(c) Sex differences

Grooming is often more a female activity than a male activity (Sparks, 1967; Rhine, 1973), which holds for single-sex female groups and mixed-sex groups. In rhesus monkeys, while the status of individuals in grooming networks correlates with dominance in females this is not true for males (Sade, 1972).

There are also apparent sex differences in aggressive behaviour. Angermeier, Phelps, Murray & Howanstine (1968) paired female rhesus monkeys and compared the data with that of an earlier study on male pairings (Angermeier, Phelps, Murray & Reynolds, 1967a). Whilst female dominance was established by the initiative of the subordinate animal in avoiding the dominant, male dominance was dependent primarily on the aggressive initiative of the dominant animal, with a higher incidence of vocalisation, fighting and avoidance pairings were, in groups of 3, often beset by alliances of their subordinates and beaten severely. Similarly Wooley, Clark & Stevens (1978) found that in squirrel monkeys pairs or triads of females could often defeat a male by coalescing. The differences in visual monitoring behaviour according to group composition have already been discussed (Keverne et al., 1978). Evidently the various measures which have been used to determine dominance relationships depend on the particular composition of a group for their success, and what may constitute a reliable measure in one group may not be reliable for another.

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(d) Rearing condition differences

Mason (1960; 1961a, b; 1964) has shown that rhesus monkeys lacking social experience show unstable dominance relationships with frequent reversals of ranks, which he attributes to a failure through social restriction to learn the communicative skills necessary for social interaction. Bernstein, Gordon & Rose (1974) studied group formation in 5 groups of rhesus monkeys, one of which was composed of social isolates. Bernstein et al. attribute the cause of the failure of the isolate group to establish a dominance hierarchy to the fact that the animals expressed bizarre behavioural patterns which interfered with this establishment.

Social interaction rates were low, aggression persisted even if one animal submitted and the group failed to act as a unit in the face of an intruding monkey. Richards (1974) suggests that status in a dominance hierarchy may be a measure of an individual's ability to optimise his social position. Certainly if isolates lack the ability to optimise their position then one could understand that dominance hierarchies among groups of isolates might be unstable.

The importance of rearing condition in the establishment of a dominance hierarchy is shown in a study by Angermeier et al. (1967a), which grouped rhesus monkeys in triads, which always included a pair of like-reared animals who were either cage-mates or not. The 4 rearing conditions were; strict isolation, partial isolation (visual and tactile contact between cage neighbours), social (in pairs) and enriched social (in triads). Animals of like-rearing condition always occupied adjacent ranks in the groups of 3, often the top 2 positions, irrespective of whether they were cage mates or not. However in a second experiment, using groups of 3 differently reared animals, previous dominance status was the only significant factor which influenced the formation of dominance hierarchies (Angermeier, Phelps, Oreste, Davies & Reynolds, 1967b).

1.5 Influences on dominance position

In addition to the natural selection theory that individual fitness determines an animal's dominance position, other factors have been found to have important consequences. Biological factors such as state of moult, androgen levels, body weight have bearing on dominance in birds (Collias, 1943). In primates there also appears to be a link between the oestrus cycle and female dominance. Maroney, Warren & Sinha (1959) describe the 'meteoric' rise in dominance of a female rhesus monkey who reached menarche during their experiment on the effects of conditioning on dominance position. Tokuda & Jensen (1969) state that oestrus females associate with dominant males and this affords them an advantage in rank. This has also been found in baboons (Zuckerman, 1932) and rhesus monkeys (Carpenter, 1942). In contrast, Maslow (1936a) reports tentative evidence that a dominant female, when forced to assume the female position (i.e., be mated by a dominant male) will lose her dominance. However this may be as a result of the sudden accession of dominance by the male in the light of new and potent stimuli, rather than loss of dominance on the part of the female as a result of her physiological condition. Maslow also proposes that the assumption of the subordinate role in sexual behaviour is also accompanied by the assumption of the subordinate role in food competition tests and aggressive behaviour.

The effect of conditioning in the form of repeated success or failure in competition for food on dominance position seems negligible, and no permanent changes in dominance position which could be attributed to conditioning were observed (Maroney & Leary, 1957; Maroney et al.,1959). However this procedure has proved to be effective in altering dominance in mice (Ginsberg & Allee, 1942) and previous success or failure in competitive social interaction is a good predictor of dominance in pairs of unfamiliar cats (Baron, Stewart & Warren, 1957).

The importance of social competence on dominance position shown by rearing condition studies has been discussed and field studies have demonstrated the importance of maternal rank for individual rank (Imanishi, 1960; DeVore, 1963a; Sade, 1967; Gouzoules, 1975; Chapais & Schulman, 1980) which is thought to be also due to learning processes (Rowell, 1974). While age correlates significantly for both sexes with dominance position, weight is only correlated with dominance in males and not in females (Tokuda & Jensen, 1969).

Many studies also allude to the importance of qualities of temperament and behaviour for dominance rank (Maslow, 1936a; van Kreveld, 1970; Rowell, 1972; Coe & Levin, 1980). Largely anecdotal evidence purports to the confidence, cockiness, greater motivation and ability and use of superior tactics in dominance attainment of animals, suggesting the importance of individual differences. There has however been little systematic study of the importance of these differences for dominance rank.

1.6 Characteristics of dominant and subordinate animals and the role of individual differences

Maslow & Flanzbaum (1936) talk of dominant and subordinate syndromes associated with pairs of animals. The dominant animal pre-empts most of a limited food supply, assumes a masculine position in copulatory behaviour (regardless of gender), initiates and shows more aggressive behaviour, initiates more play, is more active and exploratory, and shows a tendency to groom rather than be groomed. The subordinate behaves in a role complementary to the dominant (gets little or none of the food supply, assumes a feminine position in copulation and non-sexual presents etc.). Yet Maslow & Flanzbaum also note individual differences in behaviour; in the aggressive behaviour of dominants or the submissive behaviour of subordinates. Varley & Symmes (1966) report differences in the styles of dominance in groups of 2 or more rhesus monkeys, in the boldness of the subordinate or the permissiveness of the dominant in pairings, and in the assertion of dominance in triads, some animals asserting with aggression, others by sexual activity. During periods of dominance change, the interactions between male chimpanzees alter; grooming bouts increase and often occur as reconciliation after display and aggressive encounters, during which dominant males show more directed displays, while subordinates display more frequently at the environment (Coe & Levin, 1980).

As well as differences in social behaviour, some researchers have found differences between dominant and subordinate animals in non-social behaviour. Bartlett & Meier (1971) found differences between rhesus monkeys in rates of bar pressing and duration of response blocks in a reward task which were linked to dominance position in a social group (as assessed by direction of aggression, non-sexual mountings, displacements). More dominant animals pressed at slower rates for longer blocks of time than did subordinates who showed faster rates for shorter blocks of time even when there was no dominant animal present. Bartlett & Meier suggest that dominance status may be related to individual differences in social responsiveness and to individual performances which may themselves have little significance for the social system. Similarly Clark & Gay (1978) found that dominant squirrel monkeys show a higher level of activity as revealed by higher operant rates in an operant task, were more consistent in work output and showed a higher degree of 'frustration' tolerance. This increased tolerance has also been noted in rhesus monkeys; dominant animals attempted more problem solving tasks, with shorter latencies, were more persistent at the tasks and solved the problems more frequently than did subordinate animals (Richards, 1974). Richards concludes 'it is possible that intrinsic differences between dominant and subordinate individuals exist. Previously dominance has been considered to be a social property manifested only when several individuals were together' (p. 289).

Evidence for such non-social differences between dominant and subordinate individuals poses problems for the notion that dominance is a term applying to the relationship between animals in a social setting. If such non-social differences do exist then how might they be accounted for according to the definition and function of dominance? Can such differences be regarded as a basic property of an individual which occur irrespective of his dominance position? Perhaps such characteristics of dominant animals are those which have been selected for, and are important in determining the success or failure of an individual when contesting dominance relationships.

Consideration of the role of individual differences in the study of animal behaviour has not always been given. Too often researchers lump together animals of comparable dominance rank and make comparisons with animals of different ranks, giving overall totals and percentages with a view to defining some universal rank-lined characteristics (Maslow, 1936b; Maslow & Flanzbaum, 1936). It is not surprising that researchers have sometimes failed to discover universal principles of a particular dominance rank; the pattern of individual differences has been recognised by some as a contributing factor in rank attainment.

1.7 The usefulness of the concept of dominance

This brief review of the vast amount of literature on dominance has indicated the lack of consensus existing on how to define and measure dominance. As Bernstein (1981) notes 'the many disparate opinions regarding function and evolution are, at least in part, a consequence of this lack of definition' (p. 426). For some researchers dominance relationships are considered to be a universal principle of primate social organization influencing all social relationships (Maslow 1936a; Jay, 1965; DeVore, 1963b). Others have failed to find evidence of consistent dominance relationships in some species and deny the all-pervasive notion of dominance (Crook, 1970; Winter & Ploog, 1967). The question of the degree to which dominance influences social behaviour is confounded by the lack of universal agreement as to how to measure it (Bernstein, 1981). Dominance can be considered to be a useful term for the description of a particular social structure, by which individuals can be arranged in a hierarchical order. 'Of course, it is the more useful for description the more numerous the aspects of social behaviour to which the rank order is relevant' (Hinde, 1978, p. 31). An individual who is the winner of an aggressive encounter may be called the dominant, yet 'if dominance is only aggressiveness, why not call it aggressiveness?' (Bernstein, 1981, p. 450). If the same animal engages in more grooming behaviour, sexual behaviour etc. than his subordinate counterpart, and this is also true for other dominant animals in other pairings then it may be more economical to refer to him as dominant, rather than use numerous other terms to describe his behaviour. But if each particular primate group is required to have a large number of dominance orders (for different situations and different behaviours) then the concept is effectively useless (Syme, 1974).

One of the many problems associated with the study of dominance is the confusion of dominance relationships with dominance rank hierarchies. Bernstein (1981) acknowledges the usefulness of knowing the relative ranks of 2 individuals in predicting certain aspects of their behaviour (e.g., the nature of their aggressive interactions) but questions whether knowledge of the numerical rank of an animal in a hierarchy will aid in the description of the social behaviour of that individual beyond that in dyadic interactions. 'Inasmuch as all ranks are relational and none absolute, it is hard to conceive of a system in which each specific rank would have predictive power' (Bernstein, 1981, p. 429). Altmann (1981) takes a particularly extreme attitude to dominance relationships; 'they can have no influence, no effects, no function and no adaptive significance....they cannot alter mating success, access to resources, progression orders or any other aspect of social behaviour or life history processes, though they may correlate with it and be predictors of any of these' (p. 431). However as Hinde & Datta (1981) note, denying that position in a numerical hierarchy is important, and that all an animal (or a human observer) needs to know is his rank relative to another, overlooks the evidence that monkeys themselves may discriminate according to relative rank (Cheney, 1978a; Seyfarth, 1976). And numerical rank is obviously important with respect to access to food, water, breeding females etc., where an animals' 'turn' and the chances of his satisfying nutritional/sexual drives may depend on how many individuals rank above him (Lott, 1981).

A further problem is that some researchers have studied dominance in dyadic relationships, others in a group setting; some in a laboratory situation, some in the field; and some have used dominance as a dependent variable, some as an independent variable (Bernstein, 1981). It may be a more profitable approach to use dominance as an intervening variable, 'if we can specify independent variables (size, past experience etc.) that affect dominance; it (dominance) may even have explanatory value if similar independent variables are related to different effects (dependent variables regarded as 'symptoms' of dominance) in different individuals' (Hinde & Datta, 1981, p. 442). Following Hinde & Datta.'s view of dominance as an intervening variable (see Figure 1), the effect of, for example, experience in agonistic encounters (the independent variable) on the directionality of subsequent interactions (dependent variable) can be understood in terms of the effect of the experience on dominance (intervening variable). Thus an animal, having been defeated on a previous occasion by another is likely to respond submissively in future encounters with that animal, because of his previous dominance experience (=subordinance) in that encounter.

Dominance is only one of a number of factors influencing interactions and only one of the principles useful in understanding social structure and behaviour, and as such, cannot explain all aspects of social interaction. There are other important themes of social organisation in primates; the mother-infant bond and the matrifocal sub-unit, the sexual bond between males and females, the separation of roles between adults and young, and the separation of roles by sex and each system has its own scope of explanation in primate behaviour, 'and each species and perhaps each group its own unique combination of emphases on these elements which weave a collection of individuals into a social system' (Lancaster, 1975, p. 41). The extent to which dominance influences social interactions and the extent of its usefulness is controversial. We must identify the independent variables

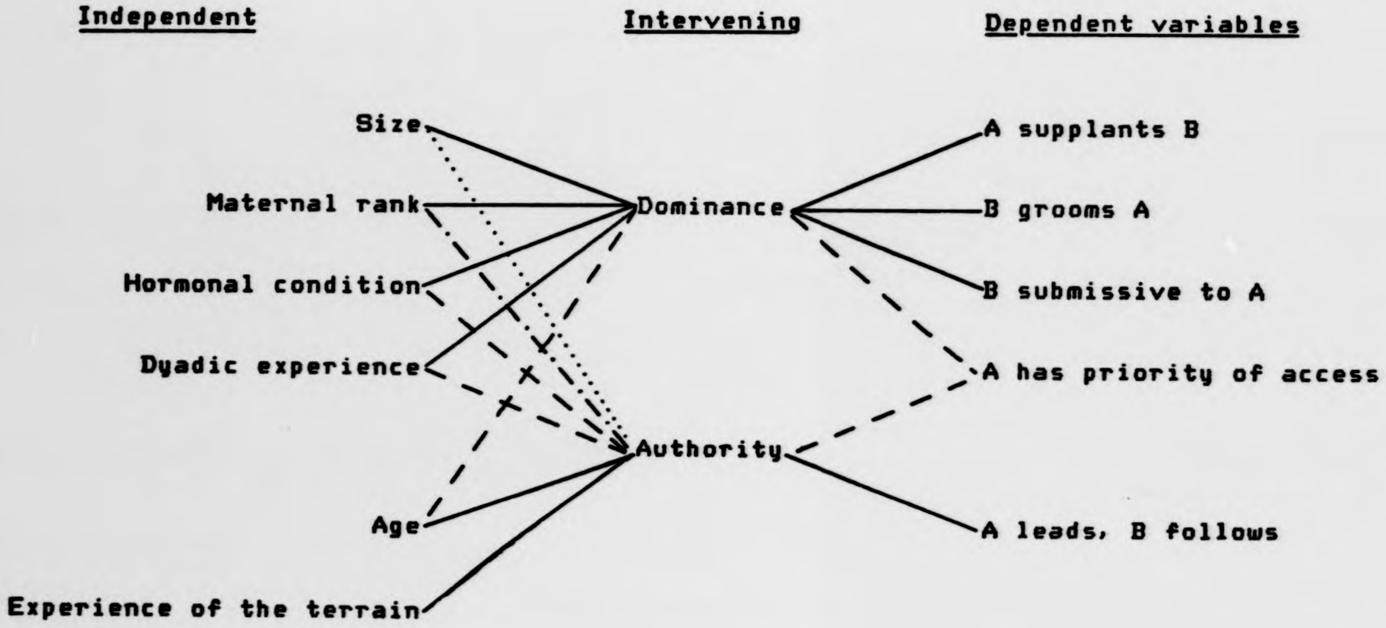

Figure 1 (from Hinde & Datta, 1981). Dominance as an intervening variable, and the possible usefulness of authority as an intervening variable. Continuous vs. dotted lines indicate the relative strengths of the presumed links.

which influence dominance relationships and the dependent variables which it influences (Bernstein, 1981). For example, it is likely that in on initial encounter, the relative dominance of 2 individuals, A and B will be determined by how much aggression each shows, (or how much 'drive' each has to be dominant) and who submits first. During the formation of the relationship it is probable that aggression will be symmetrical - A will show aggression to B, B to A. As the relationship becomes established, B may cease aggressing A, and ultimately, A will cease aggressing B (except when he may re-assert his dominance over B). It may well be that B now grooms A more than A grooms B, or that A's level of sexual activity increases. Yet unless we can offer an functional explanation as to <u>why</u> dominant animals might receive more grooming, or engage in more mating, then we have no reason to expect grooming or sexual activity to correlate with dominance, particularly if grooming and sexual behaviour are more closely to other factors such as affiliative bonds, or individual personality characteristics (Varley & Symmes, 1966; Struhsaker, 1967; Saayman, 1971). All that may be important in the fact that A dominates B is that A aggresses B, or has priority of access over B in situations where it matters to A that he does so. The shotgun approach used by many researchers of attempting to relate almost all aspects of primate social behaviour to dominance without any rationale for so doing has resulted in the concept of dominance suffering under the strain of the criticism that, as a concept, its explanatory value is limited. Yet if dominance is to be used as an exploratory concept, as an intervening variable as Hinde & Datta (1981) suggest, then it is worth discovering how widely it can explain primate behaviour, yet we must work within the scope of its function.

Chapter 2. PERSONALITY IN ANIMALS

2.1 Rodents

Early work on personality in animals using rats focused on differences in levels of 'emotionality' (Hall, 1934,1936; Billingslea, 1940, 1941), 'aggressiveness' (Hall & Klein, 1942; King, 1957), 'learning ability' (Tryon, 1940,1963).

Hall's initial work on emotionality (1934) was concerned with establishing valid and objective measures of this dimension, and involved repeated testing of rats in a unfamiliar open-field task in which food was available. Defecation, urination and eating were recorded in a series of 3 minute tests over 20 days. Initially the percentage of animals defecating was high (69%) and the percentage eating, low (8%). As the percentage of animals defecating increased the percentage eating increased and Hall reports a correlation of +0.82 between days defecating and days not eating, and a similar relationship between days urinating and days not eating (+0.70). Emotional defecation and urination (that is, defecation and urination which cease upon repeated experience in the situation that evoked it) as measures of individual differences in emotionality were thus validated by relating them to eating behaviour; Hall reasoned that eating was related to emotionality, in that the number of trials a rat took before eating in a strange situation was a direct measure of his emotionality.

In subsequent studies, researchers investigated the relationship between emotionality and ambulatory activity, persistence and behaviour disturbance (Hall, 1936; Billingslea, 1940, 1941). In brief, emotional rats were less active and showed more variability in behaviour (i.e., were less stereotyped) than non-emotional rats, while persistence was not related to emotionality.

Hoyenga & Lekan (1970) provide evidence for the importance of rearing condition on emotional adjustment; group-reared rats were less emotional (more active) than isolate rats in an open-field test.

Early social experience also affects aggressive levels, as shown by King (1957). Male mice who had been raised in isolation after weaning were less aggressive as adults than socially reared males, although there were genotypic differences. By selective breeding, Hall & Klein (1942) showed the heritability of aggressiveness in a strain of non-emotional rats and timidity in the emotional strain.

Tryon studied learning in rats in a complex maze task, and selectively bred over many generations a 'maze-bright' and a 'maze-dull' strain of rat, who differed not only in the number of errors they made in a maze learning task, but also in emotionality (1940, 1963).

2.2 Primates

While many researchers have paid lip-service to the existence of individual differences in primates (Maslow, 1935; Crawford, 1938; Nissen, 1956) there have been few quantitative studies which have sought to identify dimensions along which these differences might be grouped. Often, such differences have been noted with respect to dominance rank; 'Observers of primate groups (e.g., baboons and macaques) in the field have concluded that dominance is not related exclusively to size or capacity for physical aggression, but to elusive qualities of temperament and behaviour, which cannot be clearly identified under field conditions' (Clark & Gay, 1978, p.445). There are several anecdotal references to these elusive characteristics of temperament in relation to dominance status; Maslow notes that in cases where there is only a small discrepancy in size between 2 animals then dominance status is determined by other factors, such as confidence, cockiness, boldness, aggressiveness (Maslow, 1935, 1936b; Maslow & Flanzbaum, 1936). Even Schjelderup-Ebbe, who introduced the concept of social dominance (1922,1935) considered each of his birds to have a unique personality related to their dominance ranking.

One of the earliest studies of personality in primates was by Crawford (1938) who devised a behaviour rating scale for chimpanzees. Familiar human observers rated a group of laboratory chimpanzees on 5-point scales on such terms as confidence, excitability, dominance, motor speed, amount of acivity, intelligence. Of the total 22 items, Crawford reports 16 as having inter-observer reliabilities of

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Crawford does however point out that such apparent group factors may simply represent a 'halo effect' operating in the raters judgements, rather than any real relationship in the makeup of the animals. He also offers reasons for the high agreement between the raters; 'the comparable basis of experience with the subjects which is in contrast to the heterogeneous experience which often forms the basis for personality ratings of human beings' (p.86). Also, the raters were all students of psychology - 'they might therefore be expected to be more consistent and discriminating in making their ratings than the relatively untrained persons who often rate human personality'. Crawford also reports 'unavoidable comparison of notes by the staff members' (raters). The analysis showed that the raters most experienced with the chimpanzees agreed most often, and that older animals seemed easier for pairs of raters to agree upon than younger animals. While Crawford's study was a brave first attempt at quantifying individual differences the limitations of rating scales and raters impressions must be considered.

Similarly, Itani's (1959) study of personality as related to the quality and quanitity of paternal care in Japanese macaques (M. fuscata) is limited by the fact that it is based on the subjective impressions of the animals. Itani attempted a classification of personality composed of 3 characteristics, supposedly related to paternal care, on the basis of his observations of the Takasakiyama group of macaques. These 3 characteristics were; (1) whether the individual 'has' sociability or not; some have and are active and cheerful...others...live more or less in solitude among the troop',(2) degree of aggressiveness - 'an individual with a high degree is short tempered and pugnacious while another...has a more peaceful and milder personality', (3) intensity of interest shown by the individual in the central part of the troop, which Itani believes is related to an individual's attitude towards maintaining his status in the troop. 'The intensity of interest can be perceived through a male's activity in the central part during the breeding season and by the position he usually takes in the expansion of the troop'.

On the basis of these measurements, there are 8 possible combinations - high/low sociability, high/low aggression and high/low interest in the central part of the troop, although Itani noted no individuals corresponding to SAc (high sociability, high aggression, low interest) or sAC (low sociability, high aggression, high interest in central part). The males were allocated one of the 6 remaining 'types' according to Itani's observations and also a paternal care

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The first study to measure individual behaviours and their intercorrelations rather than attempt to study differences in sociability or aggressiveness using subjective impressions was Locke, Locke, Morgan and Zimmerman (1964). Their study, designed to determine the basic dimensions of social interaction in 12 1 year old rhesus monkeys, involved testing quadrads of monkeys, who, until the time of testing had been housed individually. The quadrads varied in composition: (1) original group 1 tests - all animals in groups of 4, with 2 males, 2 females per group (OG1); (2) all dominants from OG1 together, all subordinates together, all intermediates together; (3) return to original group (OG2). Ten behaviours were recorded; pass, approach, contact, chase, aggression, passive awareness, avoidance, escape, submission and apparent unawareness, and separate factor analyses computed for behaviour in the 3 different grouping stages. Two factors emerged consistently in all 3 analyses; 'approach-avoidance' (or interpersonal <u>dominance</u> - A's approach causes B's withdrawal) and 'avoidance-approach' (or interpersonal <u>submission</u> - B withdraws as A approaches). Locke et al. report a similarity between these 2 factors and the concepts of dominance and submission found in human personality, which they believe humans recognise as basic dimensions of interpersonal behaviour. But in contrast to human studies, this study found dominance and submission to be independent factors rather than opposite poles of a single dimension. Also, there was no evidence for a dimension of 'love-hostility' as found in human interpersonal behaviour, although this was attributed to the lack of maternal care due to separation at birth and lack of social experience prior to testing. Of greater interest were the individual differences between the animals; factor indexes were computed for each individual in all situations for the 2 factors, and these scores were then correlated with age, sex and weight. Only one significant correlation between individual characteristics and behaviour occurred, between age and approach-avoidance in the OG situation. Evidently such individual differences cannot, for the most part, be explained by differences in age, sex or weight.

It is unfortunate that the study by Locke et al. confined itself to fear and aggressive behaviours, although this choice was limited by the nature of the animals, who were all socially inexperienced, but it did attempt to study social behaviour and individual differences on a sounder basis than relying on rating scales or subjective impressions.

A more comprehensive study of the social behaviour of chimpanzees than that of Crawford (1938) was carried out by van Hooff (1970). He recorded 53 behaviours in a group of 25 captive chimpanzees and subjected the data to component factor and cluster analyses. The first 4 components accounted for 69% of the variance, the first being an affinitive (or socially positive) factor, with high loadings on, for example, touch, cling, groom , embrace. The second factor was labelled a play factor, loading on grasp/poke, relaxed open-mouth, hand-wrestle; the third was labelled an aggressive factor (loading on tug, bite, bared-teeth, bark) and a fourth factor, labelled submissive loaded on flee, crouch, avoid. A fifth factor, accounting for only 6% of the total variance was termed an excitement factor, with loadings on rapid oh-oh, rising hoot. Van Hooff concludes that 'there are 5 (or at least 4) main motivational systems'.

A similar comprehensive study of the social behaviour of rhesus monkeys by Chamove, Eysenck & Harlow (1972) produced 3 indentifiable factors. One hundred and sixty eight rhesus monkeys, separated from their mothers at birth, but socially reared, were tested in a variety of situations, during which the following behaviours were recorded; social explore, social play, non-social play, non-social fear, appropriate withdrawal, inappropriate withdrawal, hostile contact, non-hostile contact, social cling and non-contact hostile (all with inter-observer reliability coefficients of >0.87). Testing was either in a stable group with 4 familiar peers or with a unfamiliar stimulus animal (a 1 month old infant, 6 month old male juvenile, or docile adult male), either alone with the stimulus animal or with one other familiar peer present. Factor analysis of the group test data yielded 3 factors (the amount of variance accounted for by each factor is not reported); a fear factor (loading on social explore, non-social fear, inappropriate fear and appropriate fear), a play factor (loading on non-social play, social play and positive contact) and an aggression-hostility factor (loading on non-contact hostility and contact hostility). Chamove et al. state that these 3 factors 'are not dissimilar to those which gave rise to the 3 major factors in research on human personality - neuroticism-stability, extraversion-introversion and psychoticism ' (p. 502). The results of the stimulus tests are less clear, and different factors emerge from the different situations, which indicate the importance of the situation for behaviour (this will be discussed in Chapter 3). That there appears to be a connection between the 3 factors found in Chamove et al's. study and those found in human personality seems logical - as Chamove et al. note - 'the major possibilities of such (social) behaviour seem to be limited to the 3 patterns we noted; an animal can be friendly-sociable-affectionate, it can be hostile-aggressive-cruel, or it can be fearful-emotional- withdrawing' (p. 502). Chamove et al. also point out that experimental work with monkeys 'seldom pays attention to their personality'.

The factor analytic technique was also applied to social relations in squirrel monkeys by Strayer, Bovenkerk & Koopman (1975). Using 3 groups of 5 squirrel monkeys they measured social interactions such as affiliative, agonistic and display behaviours. Factor analysis of the dyadic interactions revealed 3 primary factors; play (accounting for 11.1% of the variance), social attraction (20.2%) and social power (40%). Strayer et al. also factor analysed the data for 2 groups separately and found that loadings of individual behaviours on the play factor were different for the 2 groups, suggesting between group differences in the significance of social play. Agonistic behaviours loaded primarily on the social power or dominance factor, affiliative behavioural patterns on the social attraction factor. Play was initially assumed to function as an affiliative form of interaction, but emerged as an independent factor. It is unfortunate that Strayer et al. did not measure fear or submissive behaviours; they state that preliminary observations indicated that their behavioural inventory described 'most of the observed social interactions'. While there exist similarities between the types of factors that emerged from Strayer et al's. analysis and those of van Hooff (1970) and Chamove et al.(1972), to be strictly comparable, researchers should measure as far is possible the same behavioural patterns over varying species. It may well be that there are different personality dimensions for different species, but at least as a starting point, the same behavioural repertoire should be recorded.

Despite the move away from rating scales in the area of animal personality to measuring overt behaviour (van Hooff, 1970; Chamove et al.,1972; Strayer et al.,1975), researchers in the field still relied on subjective impressions to quantify individual differences. Strayer et al. (1975) had shown social power or dominance to be a factor that could account for variance in the social relationships of squirrel monkeys and this was also found to be true for baboons and chimpanzees in 2 studies by Buirski et al. (Buirski, Kellerman, Plutchik, Weininger & Buirski,1973; Buirski, Plutchik & Kellerman,1978). The 1973 study involved using rating scales on a group of feral olive baboons, with experienced observers rating the animals on such dimensions as friendly, affectionate, assertive, cautious etc., based on Kellerman & Plutchik's Emotions Profile Index (E.P.I.) (1968). Inter-observer reliabilities are reported as high (all but 2 are >0.74) and individual differences in emotions profiles were apparent; more dominant animals (as estimated by observers) showed less sociability and more aggression than did submissive animals, who showed a great deal of both sociability and fearfulness (although none of the correlation coefficients are significant). In addition to collecting observer ratings on the animals' personalities, Buirski et al. recorded detailed grooming interactions. The more dominant animals were groomed longer per grooming bout and had more total time devoted to their grooming than did low ranking animals. Additionally, there were significant correlations between mean time being groomed and a number of the E.P.I. personality dimensions. Animals rated as low on fearfulness were groomed more, as were animals rated as sullen and jealous, defiant, belligerent and aggressive. As none of these traits (fearfulness, jealousy) correlated significantly with dominance rank, it may be that there are animals who are 'attractive' (as a groomee) by virtue of their personality, without necessarily being dominant.

In 1978, Buirski et al. applied a similar rating scale to 23 chimpanzees, again using familiar observers. Buirski et al. report low reliability correlations between observers for male chimpanzees, which they believe may have been due to the instability of the males' dominance positions within the group. There were apparent sex differences in personality; females were more timid, less aggressive and more trustful than males. There was a negative correlation between dominance rank (where 1=dominant) and aggressiveness (-0.51) and a positive correlation between rank and timidity (0.39), indicating that dominant animals are more aggressive and less timid. However, Buirski et al. do not report whether these correlations are significant, but based on an n=10, this is unlikely. Buirski et al. follow a rather curious line of reasoning, by stating that they validated the E.P.I. trait descriptions by correlating them with dominance rank. Validating ratings on, e.g., a trait of aggression by correlating them with dominance rank (based on the notion that dominant animals are more aggressive) is a dangerous and circular procedure. What is needed is an <u>objective</u> measure of aggression (or timidity, or trust etc.) against which to validate rating scales, rather than preconceived and subjective notions of the personality of dominant and subordinate animals.

Buirski et al. state that there are high correlations between profiles drawn from an earlier study on human personality and chimpanzee and baboon personality profiles which they believe is surprising, given that for the chimpanzee and baboon studies, small numbers of individuals were involved, and that 3 different versions of the E. P. I. were used in the 3 studies - a self report for the humans, a rating form for the baboons and a modified version of this form for the chimpanzee study. They conclude that 'there may in fact be a similar 'normal' personality pattern in higher primate groups' (p. 128) and that where social structures are similar, so are the modal personality requirements (gregariousness, trust, low aggression). This notion is in line with Chamove et al.'s (1972) idea of the 3 possibilities of social interaction (social, hostile, fear) but Buirski et al.'s findings of such similarities are somewhat tenuous in nature - important correlations and significance levels are not always given.

A study by Stevenson-Hinde & Zunz (1978) also used rating scales, but analysis was along the lines of human personality research, using a principal components analysis. Familiar observers rated a colony of rhesus monkeys over a 3 year period, using behaviourally defined adjectives on a 7-point scale, such as confident, sociable, active, excitable, sensitive. 3 main components emerged, acounting for over 60% of the variance; components 1 and 2 were stable over the 3 year period, whilst component 3 emerged as a result of the introduction of new items in the 3rd year. Component 1 ranged from *confident* to *fearful*, with adult males scoring higher on it than adult females or juveniles. Component 2 ranged from *active* to *slow*, again adult males scored higher on it than adult females. Component 3 ranged from *sociable* to *solitary*, with adult males scoring lower on it than adult females or juveniles. In addition, the scores of mothers on components 1 and 3 correlated positively with the scores of their 1 year old infants on the same components. Stevenson-Hinde and Zunz note that, since loadings on components 1 and 2 were significantly correlated over all 3 years of assessment, the emergence of component 3 in the 3rd year was probably due to the introduction of new items, rather than any change in the behaviour of the monkeys or the observers. 'This emphasizes that the components are not entities independent of the method of assessment. Comparison of the present components with components found by others is therefore of questionable value' (p. 480).

In a later paper, Stevenson-Hinde, Stillwell-Barnes and Zunz (1980) studied the stability of personality characteristics over time. In addition to the results of the 1978 study, they also present data from a fourth year of study, which again used rating scales based on behaviourally defined adjectives. A principal components analysis produced 2 main components in each of the 4 years, and with the addition of new items in the third and fourth year, a third component emerged. Using their principal components analyses as a guide, 12 items were selected to provide summary scores; those 6 items loading most heavily on component 1 formed the basis for a confident score, the 4 loading most heavily on component 2 formed the basis for an excitable score, and 2 from component 3 formed a sociable score. At all ages, confident scores were stable from year to year, whereas excitable and sociable scores were not stable until adulthood. One year old males who had adverse experiences during their first 8 months (e.g., loss of mother, maternal rejection) were more excitable but no less confident or sociable than control males. Correlations between scores of mothers and their yearlings showed that confident mothers had confident infants, sociable mothers had sociable infants, and that excitable mothers had infants who were not confident. 'Since adult female scores were so stable from year to year, it is tempting to infer a causal influence of mothers' characteristics on infants' characteristics and behaviour' (p.81).

The authors conclude that the significant correlations between personality dimensions over the years reflect true behavioural consistency, rather than observer bias, as different pairs of observers were used over the 4 years, and inter-observer reliability was high. In addition they state that 'a few' of the items on the rating scales were validated by correlating them with overt behaviour (for 1 year only), for example, ratings on the aggressive scale were correlated with the sum of occurrences of hits, threats, chases; ratings on the effective scale with the sum of occurrences of displacements of others and avoidance by others; excitable with the sum of displays and threats directed outside the pen; fearful with the sum of fear grins; playful with the sum of occurrences of playful behaviour, and sociable with the total number of monkeys any individual was in contact with (sampled every 10 minutes). All 6 Spearman correlation coefficients are reported as being significant and positive ($p<0.001$ 1 tailed). It is certainly an innovation to see rating scales being validated in this way, yet why not simply record overt behaviour to determine personality dimensions, rather than rely on the use of rating scales?

As Chamove (1974) showed, different results may be obtained from recording overt behaviour according to the particular analysis used. Chamove recorded the detailed social behaviour of 2 groups of 4 laboratory rhesus monkeys, using a keyboard linked to an adding machine and printout counter. The data was subjected to 4 factor analyses, one based on the frequency of each behaviour, one based on the duration, one on a modified frequency (frequency per 15 seconds) and one on duration per frequency of each behaviour. Two primary factors resulted from each of the frequency, duration and modified frequency and one from the duration per frequency which was clearly different from those derived from the other 3 analyses. The strongest common factor between the first 3 analyses was one which he labelled <u>assertiveness</u>, and there were higher-order factors of <u>fear</u>, <u>hostility</u>, <u>explore and play</u>, <u>explore-assertive</u> (explore directed to assertive animals), <u>bully</u> and <u>play-assertive</u>, but these factors were not common to all analyses. As Chamove notes 'the results of these analyses should stress the importance of careful selection of category and of the time base utilised in recording the category' (p.97).

2.3 Overview

The work to data on personality in animals has been somewhat mixed with studies which have varied in their approaches, some relying on subjective impressions, some on behaviourally defined rating scales, others on overt behaviour. The characteristics that have been investigated have varied from study to study, from species to species, and there is a wide variety of statistical techniques used in analysis. Several of the studies purport to finding what might be termed a confident or assertive dimension of personality (Itani, 1959; Locke et al., 1964; Strayer et al., 1975, Buirski et al., 1973, Stevenson-Hinde et al., 1978,1980); other dimensions reported are aggression (Itani, 1959; van Hooff, 1970; Chamove et al., 1972), sociability (Crawford, 1938; Itani, 1959; van Hooff, 1970; Chamove et al., 1972; Strayer et al., 1975; Stevenson-Hinde et al., 1978,1980) and a dimension that might be termed emotional stability or instability (Crawford, 1938; van Hooff, 1970; Chamove et al.,1972; Stevenson-Hinde et al., 1978,1980). Two studies (van Hooff, 1970; Strayer et al.,1975) also report finding play factors. However, as Stevenson-Hinde et al. (1978) note '...components are a product not only of the subjects behaviour, but also of the instrument of assessment. Indeed, by definition, components are a product of the subject, the instrument and even the observers' (p.481). In the light of the apparent incompatability in the areas of the dimensions studied, methods of measuring and statistical techniques it is surprising that there exists a certain degree of overlap between the various studies of primate personality.

If we are selective in the sorts of behaviours we choose to record, or the dimensions we chose to study in the field of personality, then the results we acheive may only partly reflect the complete personality of the individual. They are more likely to reflect the particular method of measurement used, and as such, are not representative of the animal's personality. In addition, it should be borne in mind that an individual's behaviour may be influenced by the situation in which he finds himself, and may be constrained or facilitated by that situation. Therefore we should also take into account the diversity of situations in which an animal may find himself (competitive situations, situations of novelty etc.) if we are to build up a complete picture of an individual's personality.

Chapter 3. PERSONALITY THEORY

3.1 Human personality theory

The literature on human personality is as plentiful if not more so than that on dominance in non-human primate research. But the problems and debates concerning the two concepts are somewhat different. While researchers differ as to their views concerning the function, definition, measurement and the usefulness of the concept of dominance, the disagreement amongst personality theorists is primarily at the measurement level. Since the literature on the topic of personality is so large, this section will selectively focus on the aspects which are pertinent to the present study.

Baughman (1972) provides a simple model by which we might view the processes involved in the behaviour of an organism (Figure 2). Past, present (and future events) are seen as affecting the individual who behaves in some particular way. But rather than the simple stimulus-response Skinnerian view of behaviour, there are, additional 'within-organism' processes which interact with situational or stimulus factors to determine an individual's behaviour. That such within-organism processes exist (also called 'covert behaviour' or 'intrapsychic processes') is not, for the most part, a contentious issue amongst personality theorists; it is evident that 2 individuals may respond differently to the same events. The debate concerns the emphasis that the various theorists place on these processes, the ways of measuring them, and the nature of the contribution of

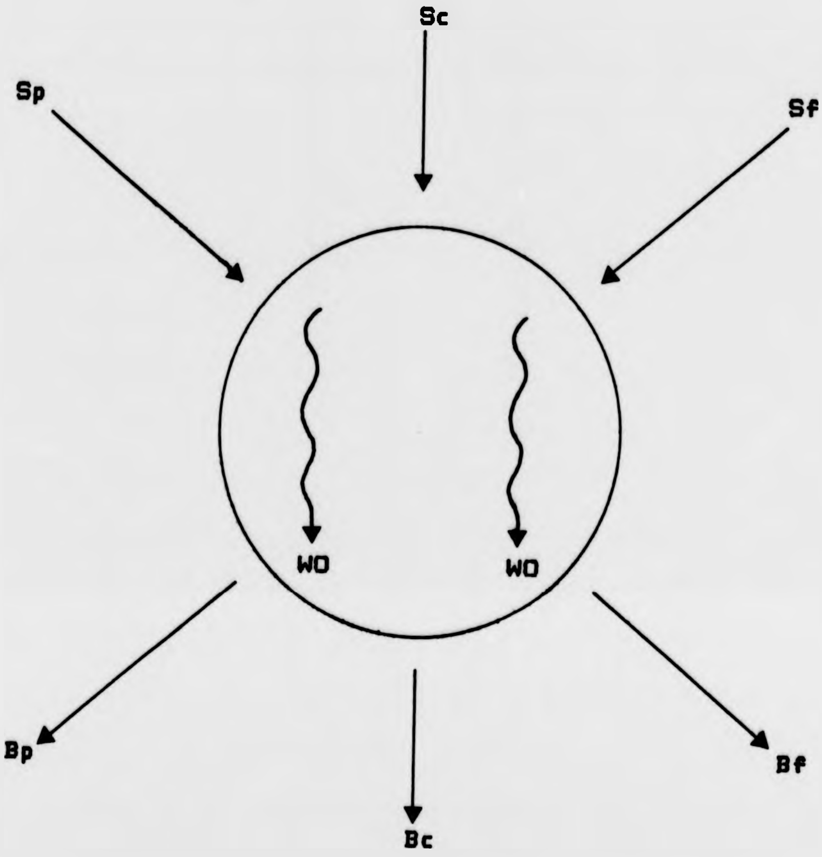

Figure 2 (from Baughman, 1972). A behavioural model. S = situation or stimuli. B = behaviour. p = past. c = current. f = future. WO = within-organism processes.

situational variables to behaviour. Baughman (ibid.) provides a summary of several personality theories; this section will concern itself with evaluating two main theories which have had the greatest influence on personality assessment – 'trait' and 'state' theories, and will discuss the social behaviour theory (or situational specificity model) of personality.

Cattell's trait theory (1950) emphasises prediction in its definition of personality. 'Personality is that which permits prediction of what a person will do in a given situation...personality...is concerned with all the behavior of an individual, both overt and covert and under the skin' (Cattell, 1950, pp. 2-3). To achieve the ability to predict, Cattell believes that we must learn how to describe and measure accurately the many traits of personality, and that one can describe an individual's personality by his position on a number of scales or dimensions, each of which represents a trait. Cattell initially identified 171 traits (on the basis of words which are used to distinguish one person from another) and, by factor analysis, identified from these 16 primary source traits, or higher-order factors, of which 2 – general anxiety level and exvia-invia (comparable to Eysenck's extraversion-introversion factor) are reliably found in populations of all ages. Cattell differentiates 3 types of data; life record, questionnaire, and objective test, but there is some disparity in the source traits derived from analyses of the 3 different types. Cattell believes that both primary traits and higher-order factors should be measured in personality assessment, and his approach is essentially atheoretical; 'only when we know what factors actually do emerge is Cattell (sic.) prepared to try to interpret them in the light of previous theorizing' (Cattell & Kline, 1977, p. 75).

Eysenck's type theory (1960) was based on the theory that there exist four types of personality; sanguine, phlegmatic, melancholic, and choleric. His approach used factor analysis to define the major dimensions of personality and to permit him to construct a personality inventory that would yield the appropriate methods of assessing an individual's level of these 4 types. Eysenck has identified 3 higher order factors of personality, namely <u>neuroticism</u>, <u>introversion-extraversion</u> and <u>psychoticism</u> (the first 2 are similar to Cattell's factors of anxiety and exvia-invia) and each of these 3 factors may be regarded as a 'syndrome' of traits. Thus the neurotic is characterised by worry and moodiness, the extravert by sociability, friendliness, activity, excitability and impulsivity, and the psychotic by hostile and troublesome behaviour and a liking for powerful sensations (Eysenck, 1967; Eysenck & Eysenck, 1968). Both Cattell and Eysenck recognise the descriptive value of their primary traits (which show a considerable degree of overlap) as well as the existence of type or higher order factors, but Cattell prefers the use of his 16 trait factors for obtaining a more accurate and detailed picture of personality, whereas Eysenck believes that his 3, more inclusive type factors have the greater advantage in economy of explanation.

Social behaviour theorists are critical of both trait and type factor theories of personality, believing that they are both too broad and do not sufficiently recognize the importance of the context in which behaviour occurs. Theorists of this type (e.g.,Mischel, 1968) are more concerned with the effects of the situation on an individual's behaviour and, as such dispense with trait concepts altogether as they hold that since behaviour is a function of the situation, traits which assume cross-situational stability are redundant. Social behaviour theory is more concerned with the prediction of behaviour change than with descriptive analysis of personality. Mischel (1973) states that trait/type theories focus on personality as a theoretical construct and try to infer the unobservable internal predispositions, attributes, and motives of the individual. 'Social behavior theory...focuses on direct samples of behavior itself' (Mischel,1973 p.161). A further distinction between trait/type theories and social behaviour theories is that trait/type theories view test data primarily as cues by which to infer underlying dispositions (thus, according to trait/type theory, an individual's personality may be inferred from his response to a Rorschach inkblot, or from the story he relates in response to a Thematic Apperception Test card), whereas in social behaviour theory, the individual's responses themselves are of main interest. As Mischel notes, the trait/type theories aim to identify the position of an individual on particular dimensions by comparing him with norms based on other individuals under standardized conditions. Trait/type theories assume that such traits (e.g.,neuroticism) will be stable over time, yet, despite the amount of effort invested in the development of reliable instruments to tap these presumed stable, enduring traits, 'voluminous research...shows that performances on all tests are affected by a variety of stimulus conditions, can be modified by numerous environmental manipulations, and provide little support for the existence of stable, broad unchangeable personality traits' (Mischel, 1973, p.163).

Cattell, in defence, holds that situational determinants are accounted for in his 'specification equation' (Cattell & Child,1975) which defines how a person's traits might combine with situational variables to determine behaviour. Eysenck & Eysenck (1980) defend their position against Mischel's criticisms, and state that Mischel has ignored the distinction between the idea of consistency at the intervening-variable level and consistency at the behavioural level. The central criticism made of the trait approach to personality is that the apparent inconsistency of behaviour contrasts with the predictions deriving from a trait approach of behavioural consistency. Yet Eysenck & Eysenck (1980) state that trait theories argue for consistency at the intervening-variable level, rather than at the behavioural level and therefore such criticism is undamaging. Eysenck & Eysenck summarise the main tenets of the trait theories of personality; individuals differ with respect to their location on traits which can be measured by using questionnaires; the interactive influence of traits and situations produces states, which, like traits, are intervening or mediating variables; the relationship between states or traits and behaviour is typically indirect, being moderated by the interactions that exist among traits, states and other salient factors. Since both trait and state concepts are intervening (mediating) variables it is possible that behavioural inconsistency may co-exist with consistency at the mediating level. As Magnusson & Endler (1977) note, anxiety at the mediating level may lead to excessive talking (behavioural level) in one situation or to minimal talking and withdrawal in another situation. Thus inconsistency of behaviour may be quite compatible with consistency at the mediating level in terms of how information is selected, interpreted and treated by the mediating system. A further criticism by Eysenck & Eysenck (1980) is that a social learning theory of personality cannot account for the evidence for the significant involvement of heredity in personality differences, which can be incorporated in a trait theory of personality. There is also evidence that there is consistency, at least in some behaviours over varying situations, and this poses problems for the notion of situational specificity. Mischel (1969) argues that such consistency can be explained by the fact that such behaviours fall into the cognitive domain and not personality, and cognitive styles are indeed resistant to change. In reply, Hilgard, Atkinson & Atkinson (1971) state that 'because cognitive aspects are indeed central to a conception of the total personality...they cannot be sharply distinguished from the personality domain. If not distinguished, then any generality in cognitive aspects is critical of the specificity theory of personality' (Hilgard et al.,1971, p.411).

The question of the generality or specificity of behaviour will now be considered in greater detail.

3.2 The individual and the situation in human personality research

As Meltzer (1961) notes, there is no lack of studies which examine the inter-relationships of situation and personality variables, but generally they attempt to show the importance of one level of data in explaining the other. This has led to what Endler (1973) terms a 'pseudo-issue' in that the personality versus situation issue is usually conceptualised in terms of which is more important, rather than in terms of how the two interact in affecting behaviour (rather like that of the nature-nurture issue in the I.Q. controversy). The issue is further complicated by the complex relationship between the two variables, namely that individual behaviour and attitudes are developed/modified in response to the situation (e.g., Asch, 1956) and in turn, group behaviour can often be changed by an individual (e.g., Kelman & Hovland, 1953).

Mischel (1969) summmarises the findings on cognitive and intellectual dimensions of personality which he concludes are highly consistent and resistant to change, once established (e.g., the self-concept, impression formation in person perception, cognitive style). Consistency in personality and social behaviour he states are much less consistent and cites evidence to support this claim, most of this evidence resting on the poor correlations between social behaviour or personality over time or over different situations. Certainly the lack of correlations between behaviour or personality over time would appear to pose problems for the trait theories of personality which argue for trans-situational consistency, i.e. that personality is basically stable and continuous, regardless of the situation. On the other hand, social behaviour theory emphasizes situational specificity and states that 'a person will behave consistently across situations only to the extent that behaviour leads, or is expected to lead, to similar consequences across those situations' (Mischel, 1971). There is evidence for specificity (change according to the situation) for such traits as dependency, aggression, social non-conformity, rigidity, attitudes to authority and other non-cognitive personality variables (Mischel, 1968). 'We may have to tolerate more dissonance than we like in our personality theory. To be more than nominally dynamic our personality theories will have to have as much room for human discrimination as for generalisation, as much place for personality change as for stability...' (Mischel, 1969, p.1017).

In reply to Mischel, Alker (1972) states that situational specificity of response is itself a personality variable. He attacks Mischel's interpretation of the data which he states is 'an abortive guide for future personality research' (p.1). Alker re-examines the papers which Mischel studied and found that in many cases, the person-situation interaction often accounted for more of the variance in behaviour than either variable alone. Similarly he criticizes Mischel's view that personality coefficients are too small, as 'he (Mischel) ignores many factors attenuating the size of these coefficients'. Alker argues for a personality paradigm which incorporates facts of situational specificity, by using 'moderator' variables, the use of which is also supported by Bem (1972) who defines a moderator variable as 'any variable which affects the relationship between two other variables'. An example of the application of this approach is Kogan and Wallach's study (1964,1967) on rational versus irrational risk taking. Test-taking anxiety and a defensive need for social approval were used as moderator variables. Persons exhibiting large amounts of test-taking anxiety and need for social approval were analysed as a separate population from persons exhibiting minimal anxiety and need for approval. Convergent validity correlations of various risk taking measures were then computed for each separate population. For the high-anxiety, high-defensive population substantial correlations emerged; these individuals were consistently risky regardless of the task at hand. This was not so of the low-anxiety, low-defensive individuals, who showed inconsistent levels of risk taking according to the situation. Alker (1972) states that the situational specificity of personality is the dependent variable while the personality variables are the independent variables which explain the varying situational specificity. There has been criticism of the use of moderating variables in explaining behaviour, summarised in Endler (1973); they are often identified on a post-hoc 'hunting expedition' and attempts to validate their existence have not been successful. Mischel (1968) similarly criticises the use of such moderator variables; the more moderating variables that are required to qualify a trait the more a trait theory of personality resembles a relatively specific description of a behaviour-situation level of analysis. Eysenck & Eysenck (1980) reply that 'while it is true that trait-state conceptualisations have become increasingly complex over the last few years, it could very well be argued that in view of the complexity of human functioning that this is a necessary, and indeed inevitable development' (p. 195).

Since 1969, several studies have looked at the importance of the person/situation with respect to social behaviour (rather than self-reports, self-ratings) summarised in Argyle & Little (1972) who conclude that the person x situation interaction accounts for more variance than either situations or persons alone. Bowers (1973) comes to a similar conclusion in his review of 11 articles which evaluated the relative magnitude of person and situtional variables. The data used in the 11 articles derive from either S-R inventories (in which the subjects were asked to respond to various hypothetical situations), self-reports in real situations or recording of actual behaviour. Bowers concludes that self-report measures are more subject to weightier person effects than measures of overt behaviour, and that in no category (inventory, self-report or overt behaviour recording methods) was there a greater effect of situation versus person variables; the interaction of person and situation variables accounted for a higher percentage of variance than either person or situations alone.

However Sarason, Smith & Diener (1975) review a similarly large number of studies and conclude that the predominant source of variance was error variance, which was greater than the variance attributable to person, situation or person x situation interaction effects. There is criticism of the method of apportioning variance; as Epstein (1977) notes, 'it is logically inescapable that, depending on how studies are conducted, any one of the 3 sources of variance can be demonstrated to be most important' (p.96). Epstein gives an example to demonstrate this fact; by selecting sprinting races that vary very little in distance and runners who vary greatly in speed it can be shown that individuals account for almost all of the variance; by selecting runners of close to equal ability and varying the lengths of the races it can be shown that the situation (races) account for almost all of the variance; by varying the type of race (dashes, long distance and hurdle) and the specialities of the runners, such that some do well in some events, poorly in others, it can be shown that interactions account for almost all of the variance. Mischel (1973) makes the same point, namely that estimates as to the relative contributions to total variance from persons, situations and their interaction will vary markedly depending on the persons sampled and the situations selected.

The trait/state versus situational specificity theory debate is primarily at the measurement level. Eysenck & Eysenck (1980) argue for consistency at the mediating level of traits and states (which they measure using questionnaires) and they argue that consistency at the trait/state level does not imply consistency at the level of specific behavioural responses (which Mischel prefers to measure and argues is inconsistent). If we take Magnusson & Endler's (1977) example of the relationship between anxiety and talking - an anxious person may talk a lot in one situation and not in another; if we ask that person the question 'would you call yourself a tense or highly strung person?' (Eysenck Personality Inventory, question 26) in both situations then we will obtain consistency of response. If we measure that person's overt behaviour (talking) we will not obtain such consistency. Yet if Eysenck & Eysenck argue for apparent consistency at the mediating level despite inconsistency at the behavioural level then they must account for why one situation results in one behavioural response (talking) and another situation a different behavioural response (not talking), hence bringing in the notion of the situation into the question of personality! Eysenck relies on questionnaires, rather than recording overt behaviour in his personality assessment, but he needs to specify the characteristics of situations which interact with traits and states to produce a certain behavioural response to account for behavioural inconsistency. If situationism ignores the person, the trait/state theories are equally guilty of ignoring the situation.

Bem & Allen (1974) state that we must study both situational and personality variables and their interaction, and that neither situation nor personality alone can of themselves explain behaviour. If there is evidence for such interaction between situation and personality variables then it follows that we must offer explanation as to the nature of the interaction. While Eysenck, Cattell and Mischel are coming round to the idea that behaviour is a product of the person in the situation only Mischel (1973) offers any explanation as to how one might characterise such interaction. In his 1973 paper, Mischel abandons references to social learning theory and instead proposes that the interaction between personality variables and situations might be analysed within the framework of a cognitive social learning approach, measuring encoding strategies and personal constructs, behaviour-outcome and stimulus-outcome expectancies, subjective stimulus values and self-regulatory systems and plans. Thus the influence of the situation on a person's behaviour will depend on how he processes the information input from the situation in terms of his past experience, desires, expectancies etc.

It follows that if we are to understand the interaction between personality variables and situations then we must be able to describe and characterise persons and situations. While there has been much work on the measurement of personality variables, there has been little on the measurement of situations. Bem & Funder (1978), in a paper entitled 'assessing the personality of situations' use a Q-sort procedure which permits the prediction of individuals within certain situations. This technique determines the criterial behaviour in a given situation and obtains a personality pattern or template of persons who behave criterially. They then compare the personality templates of those people whose behaviour they wish to predict with those of the criterial templates; those persons whose personality template most closely matches the ideal template is then expected to display the criterial behaviour. The template of each subject is thus compared with several criterial templates, each of which is characteristic of a different pattern of behaviour in a given situation.

Epstein (1979) argues that the 3 approaches of personality theorists (trait, situation and interactionist approach) do not conflict, since they identify not 3 different solutions to the same problem, but 3 different problems. The trait theorist wishes to study consistent behavioural tendencies in individuals over a sample of situations; the situationist is concerned with the _general_ effects of situations over a sample of individuals and the interactionist wishes to study consistent behavioural tendencies in individuals over a sample of situations. Epstein states that underlying all approaches is the need to consider that error of measurement is apt to be high and temporal reliability or replicability low when findings are based on small samples of behaviour.

Further, as Endler (1973) notes, the methodology one uses often influences the results one obtains. The situationist model uses experimental techniques which fasten our attention on behaviour change in a way that makes us inattentive to whatever behavioural stability exists (Bowers, 1973). Indeed, in employing an experimental approach subjects are usually assigned at random to treatment conditions that are _not_ selected at random, but are selected because it is presumed they will make a difference to the behavioural outcome. 'Few investigators try to prove the null hypothesis' (Bowers, 1973, p. 323). The trait theorists argue that had those experiments which found no evidence for the stability of behaviour across situations been done differently, stability might have been demonstrated; behavioural stabilities are more apt to emerge when correlational analyses are applied to naturalistic and clinical data, since it is under these non-experimental circumstances that a person is able to engender interpersonal circumstances which are characteristic of him - circumstances which can in turn sustain and lend consistency and stability to his behaviour (Bowers, 1973). Consistency will be more apparent when we study the behaviour of individuals over situations which they themselves have selected, rather than in situations to which they have been assigned, as in many of the studies which have found no stability (Epstein, 1979).

As Bowers (1973) notes, instances in which studies using experimental methods reveal that *apparently* changed environments do not lead to corresponding changes in behaviour are often considered non-events, and seldom are such studies taken as evidence regarding the stability of behaviour across situations (or indeed published, according to Bowers). Yet if 'truly' changed environments can only be inferred from changed behaviour then the situationist model becomes circular; when does behaviour change? - when the situation does. How do you know when the situations has changed? - when the behaviour does. 'Viewed this way, behaviour becomes situationally specific because it is impossible for it not to be situationally specific' (Bowers, 1973, p. 317). Frederiksen (1972) suggests that instead of assigning situations to clusters based on their mutual possession of various attributes we should group situations on the basis of their tendency to elicit similar behaviours. Yet because 2 individuals apparently behave similarly in the same situation may not mean that the situation is perceived in the same way by both individuals; one individual may talk alot in one situation because he is sociable and relaxed in that situation, while another may talk alot because he is nervous and anxious in that situation. The situation is not equivalent for the 2 individuals.

It follows that the conclusions that may be drawn from any study of personality with respect to the presence or absence of stable traits, the influence of the situation on behaviour will be dependent on the method of measurement. If we use self-report techniques we might expect consistency, since such studies only demonstrate that peoples' beliefs about themselves are consistent (Mischel, 1968). If we measure overt behaviour but only in one or two situations then we can expect not to find consistency, since there is a high component of error of measurement (Epstein, 1979). This high error of measurement may also account for why self-rating, ratings by others and personality inventories correlate poorly with overt behaviour (Epstein, 1979). Epstein concludes that given an adequate sample of behaviour we can predict 'most of does. 'Viewed this way, behaviour becomes situationally specific because it is impossible for it not to be situationally specific' (Bowers, 1973, p. 317). Frederiksen (1972) suggests that instead of assigning situations to clusters based on their mutual possession of various attributes we should group situations on the basis of their tendency to elicit similar behaviours. Yet because 2 individuals apparently behave similarly in the same situation may not mean that the situation is perceived in the same way by both individuals; one individual may talk alot in one situation because he is sociable and relaxed in that situation, while another may talk alot because he is nervous and anxious in that situation. The situation is not equivalent for the 2 individuals.

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3.3 The individual and the situation in animal behaviour research

While there has been much work done on the influences of sex, rearing condition, age, dominance rank etc. on primate social behaviour, or on behaviour in a non-social setting, few researchers have considered the importance of personality and the situation (and their interaction) in behaviour. Early work on personality in rats noted the influence that particular situations had on emotionality and aggressive levels. Hall (1936) studied the relationship between emotionality and ambulatory activity in a variety of situations; testing in an open-field (i) without prior food deprivation, no food in field, (ii) without prior food deprivation, food in field, (iii) prior food deprivation, food in field. In all situations, emotional rats (high defecators) were less active than non-emotional rats, but the correlation between emotionality and activity was higher in period (iii) (hunger, food) than in period (i) (no hunger, no food). In the hunger-food period the emotional rats were even less active and the non-emotional rats even more active. Hall concludes that one result of emotionality will be to hinder the elimination of needs (e.g., hunger); whenever increased activity is of service to the animal, emotionality will interfere with performance; whenever activity is of disservice to the animal, emotionality will facilitate performance. Billingslea (1940,1941) also demonstrated the importance of the situation on the behaviour of emotional and non-emotional rats. In familiar situations, the performance of the emotional rat was superior to that of the non-emotional rat, but in strange situations, performance was inferior to that of the less emotional animal because fear inhibits the expression of adequate adjustment (p.324). Hoyenga & Lekan (1970) found that group-reared rats were less emotional (more active) than isolate rats in an open-field test. In addition, when a group-reared rat was paired with an isolate in a competitive-food test, the group-reared rat was dominant, but as the isolate rat became familiar with the test situation and the group-reared rat, so it began to compete more vigorously for the food.

As well as affecting emotional levels, the situation has also been shown to affect aggressive behaviour. Galef (1970) found that wild rats were more aggressive towards humans, mice and fellow rats than were docile domesticates, but in a novel situation, the wild rats were timid and shy compared to the curiosity of the domesticates. Evidently, any conclusions regarding an animal's level of emotionality, or aggressiveness will be dependent on the situation in which the animal is observed, and we may not be able to generalise his aggressiveness to other situations.

If complex situation/personality interactions have been demonstrated in humans and rats, then it seems reasonable to assume that this is also true of non-human primates, yet there has been little quantitative work in this area. Yet there is evidence for such interaction, even if rather anecdotal. Maslow (1935) noted the differences in the aggressive levels of animals in positions of dominance, and Varley & Symmes (1966) found that animals differ in their 'styles' of dominance, some showing a lot of aggression, others showing high levels of sexual activity. Situational effects have been noted with respect to aggressive behaviour (Maslow, 1935; Locke, Locke, Morgan & Zimmerman, 1964; Chamove, Eysenck & Harlow, 1972), fear behaviour and stress levels (Chamove & Bowman, 1976; Locke et al.,1964) and affiliative interaction patterns (Strayer, Bovenkerk & Koopman, 1975) as well as with respect to dominance rank (Bernstein & Gordon, 1980).

Maslow (1935) reports differences between the behaviour of rhesus monkeys when in pairs and when in triads. In groups of 3, a middle ranking animal was often aggressive to his subordinate despite the fact that he was not aggressive when alone with him. In groups of 4, an animal would frequently enlist the support of another in aggressing a third animal to whom he had been subordinate in a pairing. Aggressive levels were therefore dependent on the particular size of the grouping and dominance rank. Locke et al. (1964) found a similar finding in their study of the behaviour of rhesus monkeys in a variety of groupings; consistency of behaviour over changes in group composition were not found, and the pattern of approach-avoid and avoid-approach differed according to the particular format of each group. Locke et al. concluded that animals do not carry these behaviour patterns with them to all situations. Chamove et al. (1972) tested the behaviour of rhesus monkeys either in groups of familiar peers, or in a dyadic setting with one of 3 unfamiliar stimulus animals (infant, juvenile or adult) or in a triad with a stimulus animal and a familiar peer. Factor analysis of the data resulted in the emergence of different factors in the stimulus animal tests, depending on whether there was a familiar peer present or not (dyad versus triad). In the triad situation, animals showed less hostility towards a juvenile stimulus animal, less fear and more hostility to an adult stimulus animal, and less non-social fear than in dyadic situations with the same stimulus animals. In many cases, animals substituted partner-directed clinging for non-social fear.

Chamove & Bowman (1976) tested the behaviour of 4 rhesus monkeys over different dominance positions in dyads, triads or quadrads with the same partners. There were differences between the animals both in their behaviour over dominance positions and in their levels of 17-OHCS secretion (related to stress). One animal showed more stress the more subordinate a dominance position she occupied and the more she was the object of aggression. For another animal, there was a similar relationship between dominance position and amount of stress, but stress was also positively correlated with the more social behaviour he exhibited.

In a later paper, Chamove & Bowman (1978) found that corticosteroid elevations during social stress are related to fear and not to amount of aggression shown, and are dependent on dominance rank, the level of dominance competition and previous dominance history.

Strayer et al. (1975) demonstrated the importance of particular situations for affiliative relations. As well as recording the behaviour of squirrel monkeys in a free-social situation, they made experimental assessments of social preference, where each animal had a free choice in a test chamber as to which animal from his normal, social group he maintained the greatest proximity to. The experimental assessments of social preference did not correspond with affiliative patterns evident in the free-social behaviour group setting. There was a trend for animals to prefer maintaining proximity with the dominant animal in the test situation, and Strayer et al. hypothesize that 'in conditions of perceived external threat animals do not seek out their normal affiliative partners, but instead look to specific group members that are most likely to assume a defensive role' (p. 317).

Situations can also affect an individual's dominance rank. Bernstein & Gordon (1980) repeatedly introduced male rhesus monkeys of one group (group 1) into another (group 2). The dominance ranks of the introduced males were random with respect to the original ranks. As each male was introduced into group 2, he immediately submitted to the group 2 males and received more aggression than he gave. A second experiment introduced the alpha and beta males of group 2 into group 1, where they occupied the bottom two ranks, and submitted to all group 1 males, despite the fact that they had dominated them the previous week. The other males in group 2, during the absence of alpha and beta increased their amount of sexual behaviour with the females, although they immediately submitted to alpha and beta on their return. Thus dominance ranks were specific to the social context and were not fixed attributes of any of the males.

3.4 Implications for future personality research

The aforementioned studies demonstrate the importance of the situation in determining behaviour. It follows that we may come to different conclusions about an individual's personality depending on the situation in which we choose to measure his behaviour and the method we choose for measurement (self-reports or overt behaviour). If we only measure an individual's behaviour in one particular situation, then we cannot say anything about that individual's personality, since his behaviour may be a function of the particular situation. In order to obtain a more complete description of his personality, we must study the behaviour of an individual over a variety of different situations. Only then can we assess the usefulness of the trait, state and situational specificity theories of personality.

Chapter 4. AIMS OF THE STUDY, METHODS AND RESULTS OF PHASE 1

4.1 Aims of the study

The present study was conducted with 3 questions in mind;

(i) How much of an individual's behaviour is a function of his dominance position?

(ii) How much of an individual's behaviour is a function of his personality?

(iii) How much of an individual's behaviour is a function of the interaction between his dominance position and his personality?

Thus the aim was to assess the usefulness of dominance and personality as _explanatory_ variables, in terms of how much each variable (or their interaction) contributes to an individual's behaviour. To date, the research on the concept of dominance in non-human primate research has, in general, avoided discussing the notion of causality when two or more variables are found to correlate. Thus, dominance is reduced to a descriptive level; a dominant animal is described as being aggressive, as the animal who pre-empts a food supply, who receives more grooming than his subordinate etc. Of course, in demonstrating a relationship between dominance rank and behaviour we cannot infer anything about the nature of that relationship in terms of the direction of causality (and those studies which address themselves to problems of causality do not always reach the same conclusions regarding the direction). It may be that dominant animals are more aggressive, more attractive as groomees etc. by nature (i.e., by reason of their personality), not because they are dominant. Conversely, subordinate animals may be submissive, may like to groom etc. by nature, not as a result of their being subordinate. It follows that if we can isolate those behaviours which dominance rank <u>influences</u> then we have considerably increased the value of the concept of dominance, beyond that of a purely descriptive term, to that of an explanatory concept. In doing so, we may be able to arrive at a more satisfactory functional definition of dominance.

In order to identify personality dimensions we must show that behaviour is not purely a function of dominance rank, and that there are aspects of an animal's behaviour which are characteristic of that animal, irrespective of his dominance rank. By studying behaviour over changing dominance position (changing situation) it was hoped to evaluate the usefulness of the trait/type theories of personality and the social behaviour theory of personality; how much of an individual's behaviour can be considered to be reflective of stable personality characteristics and how much of his behaviour can be considered to be situationally (dominance) dependent?

The study is divided into 3 separate phases.

<u>Phase 1</u> was a pilot phase, designed to discover those sorts of behaviours which seemed to reflect (1) dominance position in a stable group of 13 animals and (2) personality. In this phase many different sorts of experiments were designed, not all of which proved useful in the above respects, but which tested behaviour over a variety of situations. The experiments designed to measure dominance were based on those behaviours which are considered as dominance-related,

e.g., aggression, fear etc. The rationale behind the experiments designed to measure personality was based on the personality dimensions found in humans as reported by Eysenck, i.e., extraversion, neuroticism and psychoticism. Measurement of these dimensions was conducted at the primary trait level; for example, extraverts, according to Eysenck, display primary traits of sociability, activity, liveliness, impulsiveness and excitability; the experiments designed to measure extraversion were designed to tap these behavioural correlates.

The results of Phase 1 (hereafter referred to as P1) indicated those sorts of behaviours which correlate with dominance position in a stable group of 13 animals. It was evident that many behaviours were related to dominance rank, but it was not clear whether these behaviours were indicative of dominance position or personality; there being only 1 animal in each of the 13 dominance positions the two variables (dominance and personality) were confounded. Phase 2 was designed to separate these effects.

Phase 2 (hereafter referred to as P2) was a manipulative stage, designed to separate dominance effects from personality effects. Each of the 13 animals was studied in a number of different dominance positions in groups of 5 animals (thus they could experience up to 5 different dominance positions). It was reasoned that if the amount of certain behaviours expressed by an animal remained constant over changing dominance position then these behaviours reflect those aspects of personality which are unaffected by dominance; if behaviours changed with changes in dominance position then such behaviours may be said to reflect either the effect of dominance per se, or reflect the interaction between dominance position and personality.

Phase 3 (hereafter referred to as P3) was run after the completion of P2 and was designed to measure the behaviour of the animals in their stable group of 13 in greater detail than had been possible in P1, primarily to assess the affiliative patterns of the animals which it was felt had some effect on the behaviour of the animals in P2.

4.2 Method

(a) Subjects

The subjects used throughout this experiment were 13 group-living, laboratory-bred stumptailed macaques (*M. arctoides*). Each animal had been used in previous experiments (Chamove, 1978, 1980; Walker-Leonard, 1980) and had, from birth experienced varying rearing conditions. Animal number, sex, rearing condition, weights, age and dominance positions at the various stages of the experiment are given in Table 1.

All subjects had been separated from their mothers at approximately 8 days of age, removed to an incubator and taught to self-feed (Chamove, 1975). Until 3 months of age they were housed in individual cages where they had auditory but no visual or tactile contact with other monkeys. When the average age of animals who were to receive similar rearing experience was 3 months their appropriate social stimulation

Table 1

Animal number, sex, rearing condition, age, weight and dominance positions throughout the study

Animal number	Sex	Rearing condition	At onset of Phase 1 Age y/m	Phase 1 Dominance rank (1=high)	Phase 2 Dominance rank	Phase 3 Dominance rank	Weight kg.
2	F	Peer-dark	5/2	8	8	8	15.8
3	M	Peer-dark	5/2	10	10	10	22.8
4	F	Peer-dark	5/2	9	9	9	18.8
5	F	Peer-light	5/2	3	3	3	18.3
6	M	Peer-light	5/2	11	13	13	14.8
8	F	Peer-light	5/1	6	7	7	13.8
10	F	Isolate	5/1	5	5	5	13.8
11	F	Isolate	5/1	4	4	4	13.8
13	F	Isolate	5/0	7	6	6	13.3
15	M	Adult-peer	4/11	1	1	1	23.2
17	F	Adult-peer	4/11	2	2	2	16.3
25	F	Peer-dominant	3/7	12	11	11	11.3
27	F	Peer-dominant	3/7	13	12	12	9.3

was begun (apart from the isolate group who remained in individual cages until 12 months of age). This social experience was a minimum of 1 hour per day with animals from like-rearing condition, in groups of 2 or 4.

The <u>peer-dark</u> group were put together daily in a single cage, but always in the dark so that they experienced vocal, tactile and olfactory contact but no visual contact with each other.

The <u>peer-light</u> group were put together daily in a single cage, but in the light, thus experiencing vocal, tactile, olfactory and visual contact.

The <u>isolate</u> group remained in their individual cages.

The <u>adult-peer</u> group were put together daily in with a group of feral adult animals.

The <u>peer-dominant</u> group were put together daily with peers in groups of 2 or 3 such that they were always dominant in these groups (i.e., put with younger animals).

At 1 year of age all animals began living continuously with their like-reared peers (thus the peer-dark group now had visual contact with each other and the isolates met for the first time). At 2.5 years of age the peer-dark, peer-light, isolate and adult-peer groups were integrated into one large group, the peer-dominant group joining them after 2 years.

The group lived in an indoor stainless-steel caging system (21.6 square metres) with access to an outside enclosure ('North Pen', 16.1 square metres), (see Figure 3). They were fed twice daily, had permanent access to drinking water, and were rarely removed from the group.

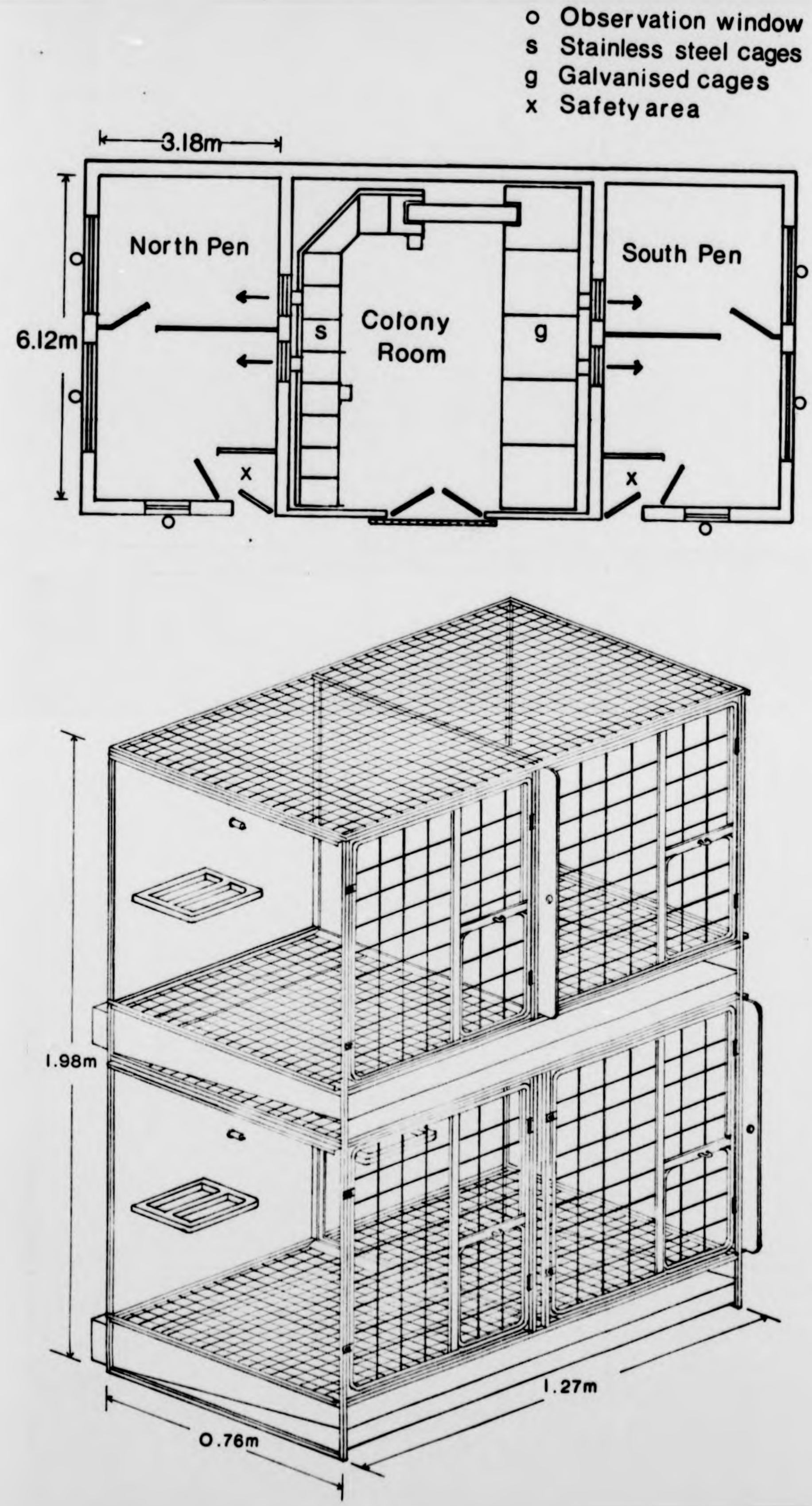

Figure 3 top - plan of colony room
bottom - a unit of 4 stainless steel cages

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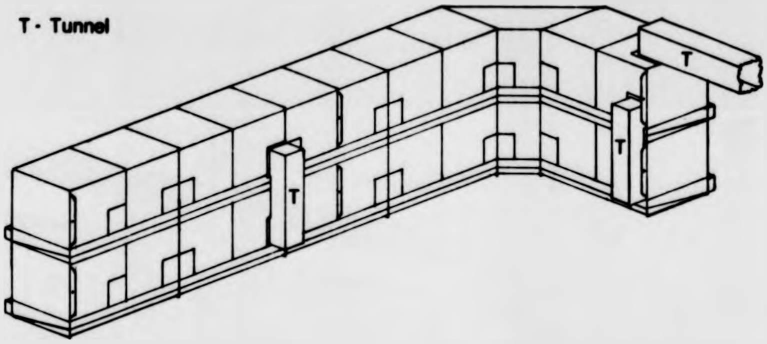
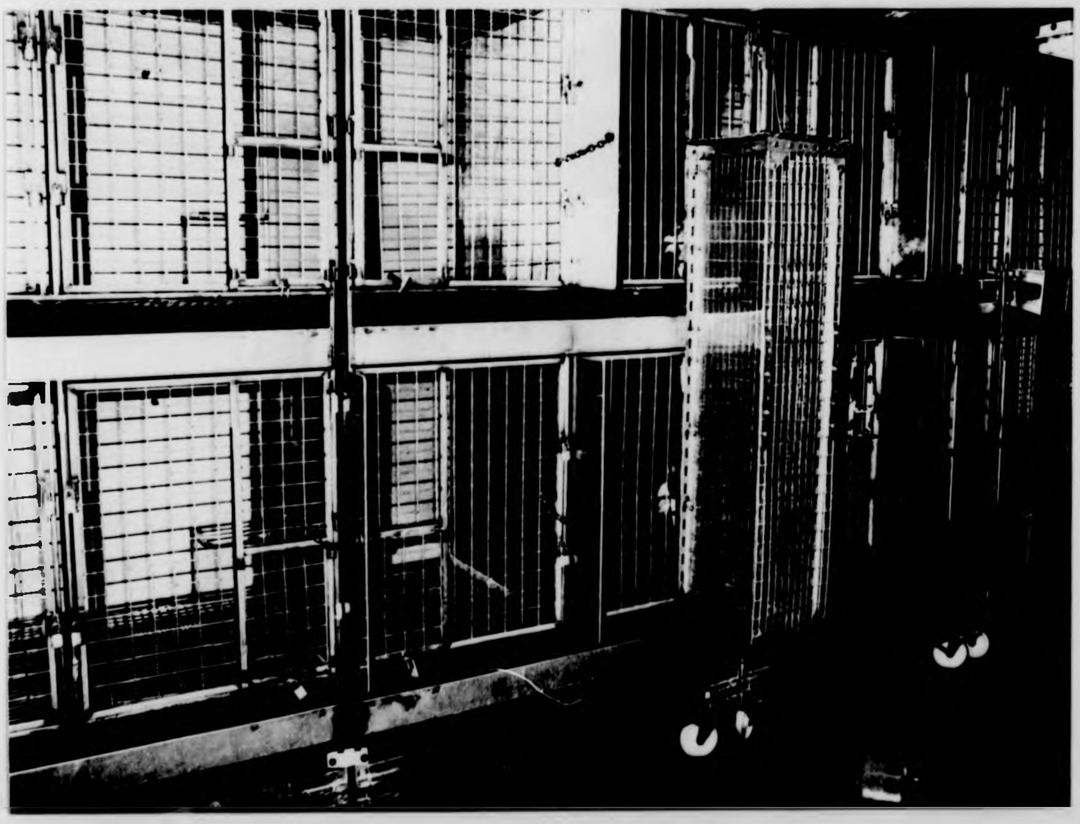
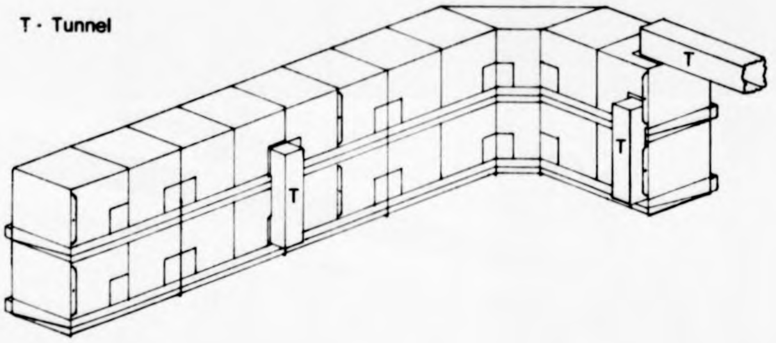
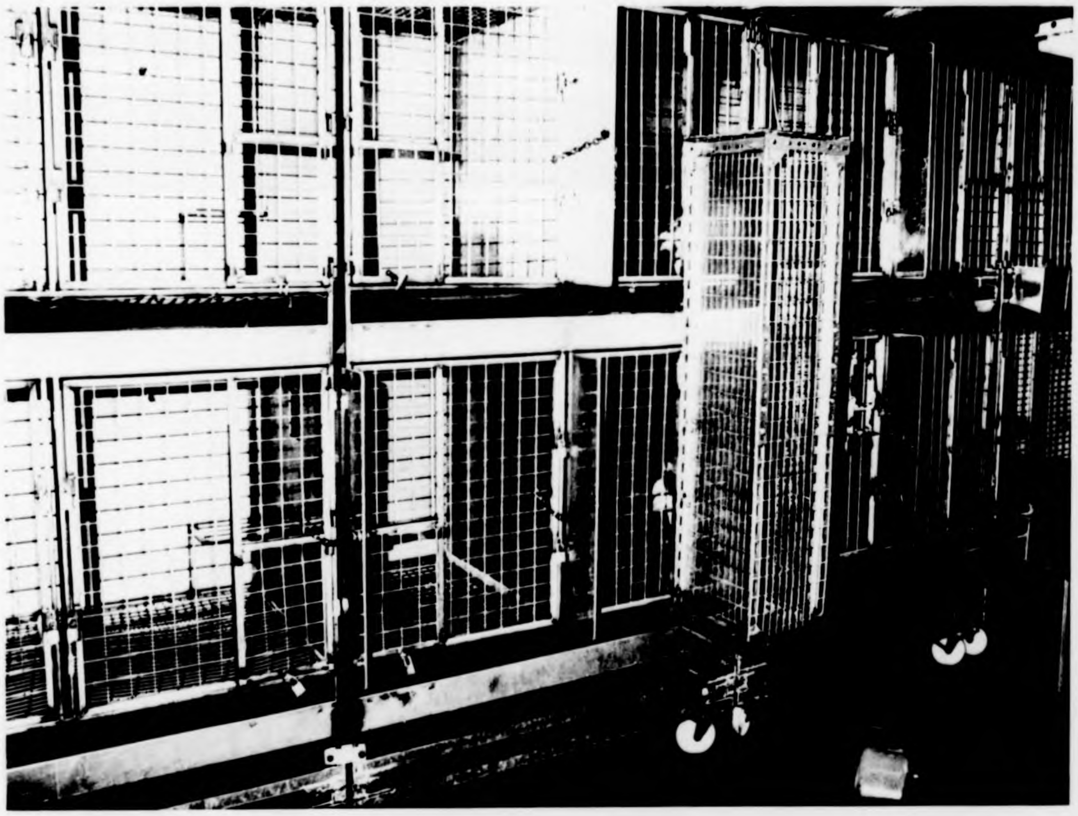




top – the stainless steel caging system
bottom – photograph of stainless cages showing tunnel





top - the stainless steel caging system
bottom - photograph of stainless cages showing tunnel

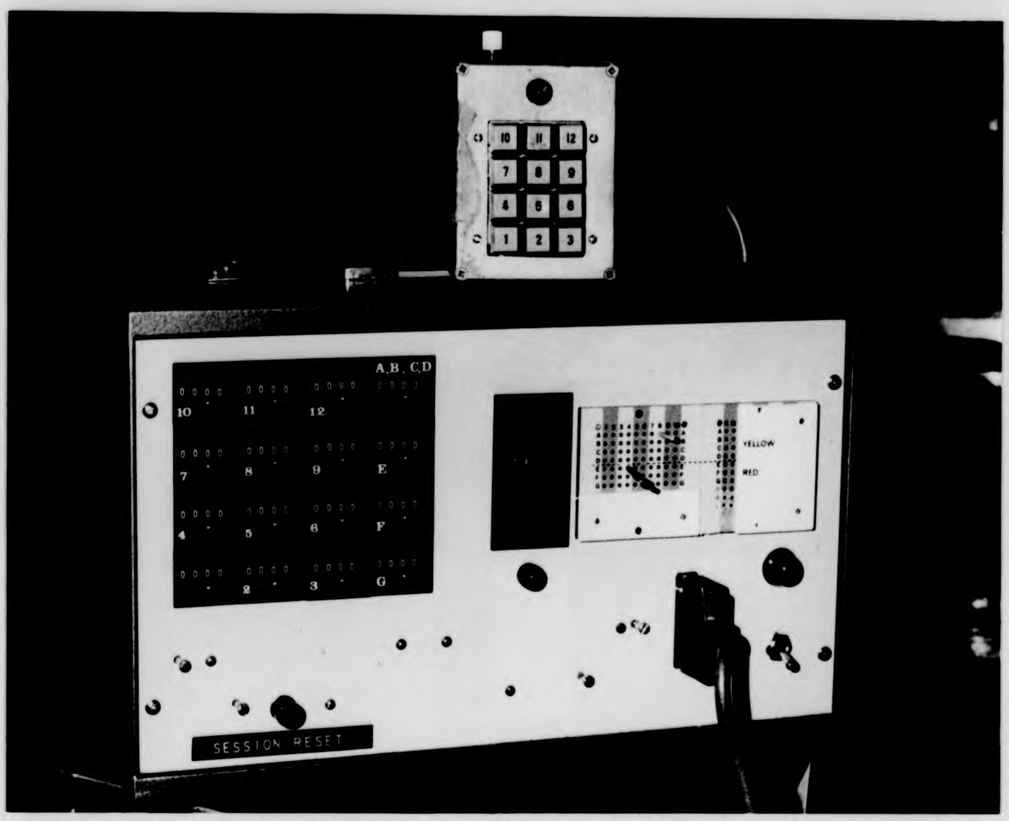
(b) Data collection and recording equipment

(i) Clock and counter box (see Figure 4).

Using the clock and counter box, behaviour is recorded by depressing one of 12 microswitches which activate both a counter which records the frequency of presses and a clock which records the total duration during which the switch was depressed. Behaviour was recorded in terms of 0.25 second time periods and tests using the clock and counter were typically 10 minutes duration.

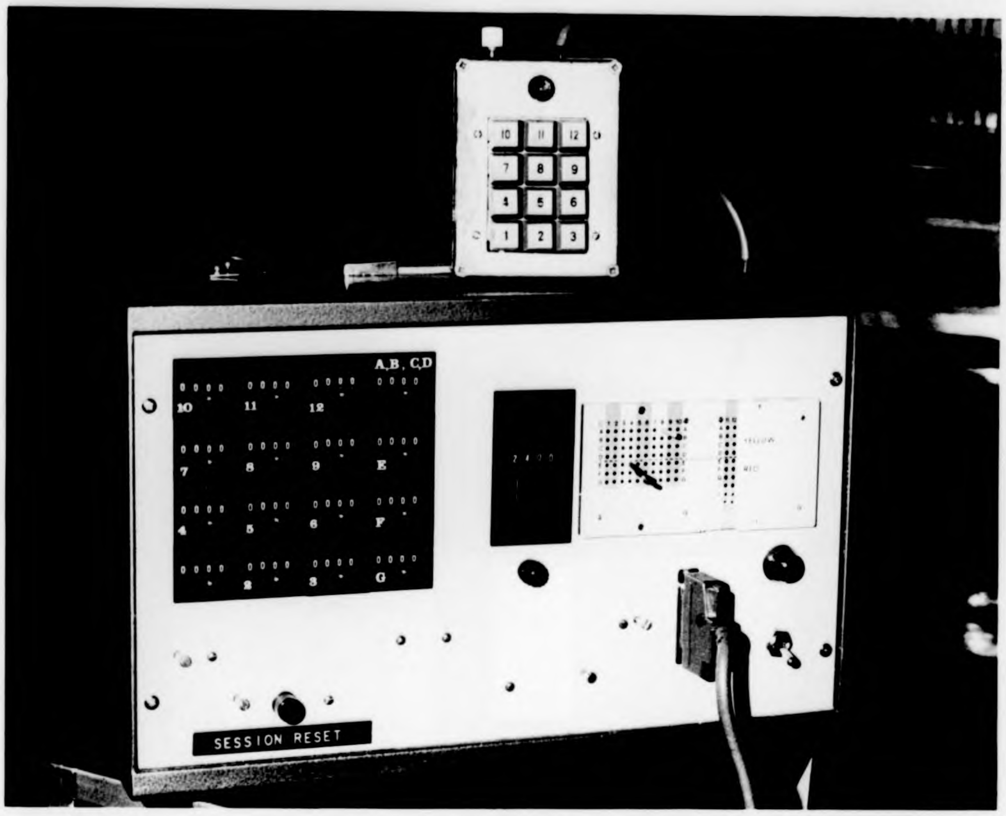
(ii) Data Transfer Unit (DTU) (see Figure 5).

The DTU permits recording of the detailed behaviour of any 1 animal using a keyboard which is linked to a data logger. It enables recording of up to 6 'levels' in any behavioural sequence (Chamove 1974) and is time-linked in that it records the time of onset and termination of any new sequence. The record is mutually exclusive and exhaustive, and ends when a new sequence is input. The levels used in recording behaviour were; general behavioural category (e.g., affiliation, aggression), sub-behaviour (e.g., affiliative-huddle, aggressive-bite), direction (e.g., to environment, self or a particular animal) and initiator (e.g., self or other animal). Details of the behaviours recorded, an example of some DTU output are given in Appendix 1, and the definition of the behavioural categories in Appendix 2.



keyboard

Figure 4 Clock and counter box



keyboard

Figure 4 Clock and counter box

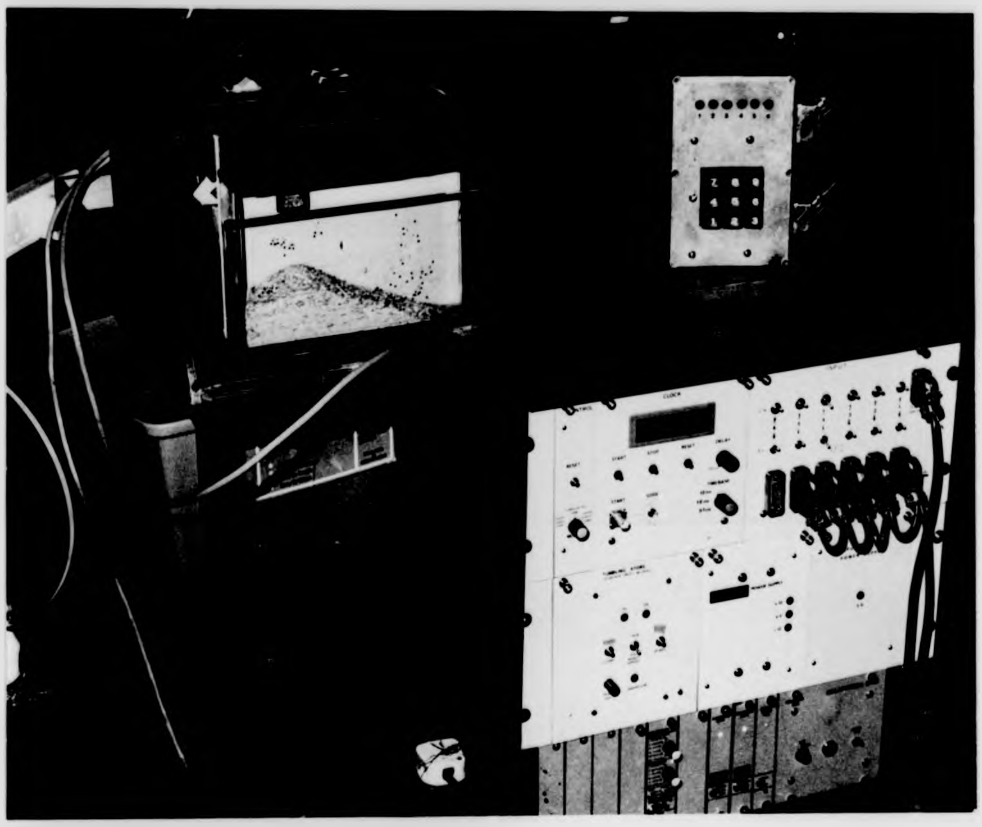


Figure 5 Data Transfer Unit (DTU)

paper tape punch keyboard

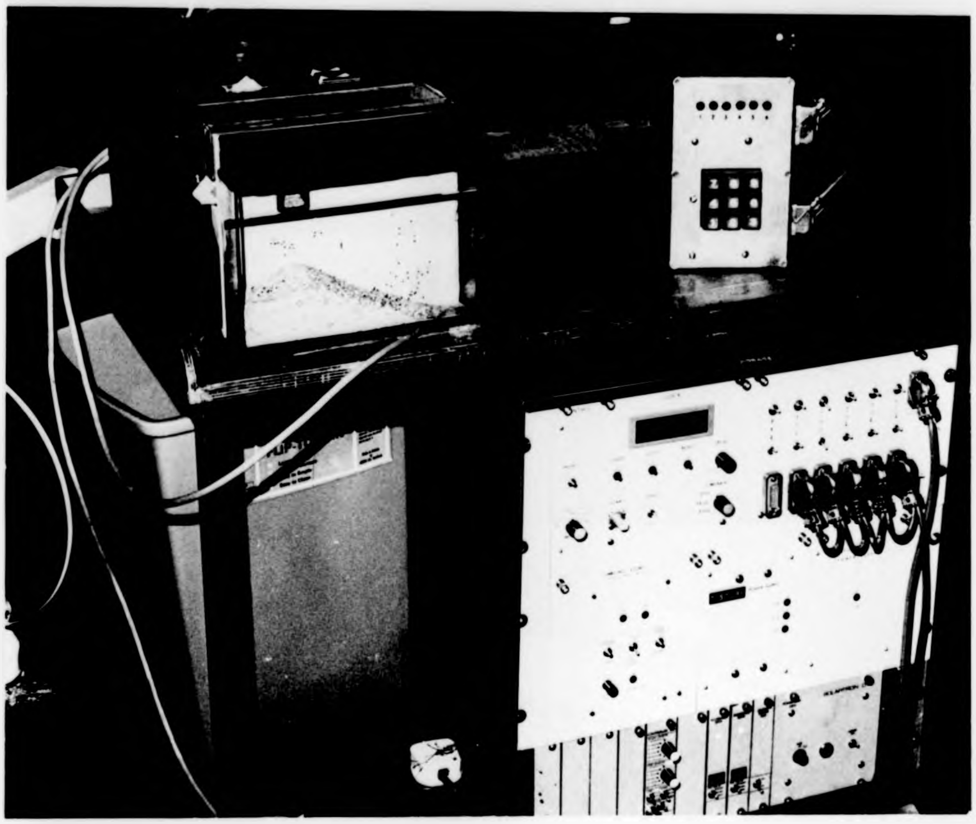


Figure 5 Data Transfer Unit (DTU)

Data is recorded to 2 decimal points in time, thus:

time	event
000420	7177
000830	5612
001070	2577

indicates that sequence 7177 (self-groom) began at 4.20 seconds of testing and continued until 8.30 seconds when sequence 5612 began etc. Output is on paper tape which is then analysed by computer and yields the following information:

(a) total number of events within that testing period

(b) different sequences occurring within the testing period

(c) percentage of total testing period those sequences occurred

(d) frequency per 30 seconds of each of those sequences.

Thus for any given event sequence (which corresponds to a certain behaviour e.g., self groom) there is information on what percentage of time a given animal spent doing that behaviour, and the frequency of occurrence per 30 seconds. A daily diary was also kept during periods of DTU testing, to record 'non-standard' events, i.e., events for which there was no standard coding, such as when an animal was engaged in more than one behaviour (e.g., being huddled by one animal whilst grooming another, see section 5.3). The DTU was not available for testing free-social behaviour in P1 but was used in P1 persistence tests, and in P2.

Footnote 1:
using the Primate Observational Data (POD) program, written by Graham Cameron with support from S.R.C. grant B/RG 98910 to Arnold Chamove.

(iii) Scan sampling

Scan data was collected primarily in P1 of the experiment by scanning the entire group of animals and recording in no fixed order the behaviour of each animal. This is referred to as random scanning where the experimenter went into the unit on occasion and scanned the group of animals. The behaviours recorded varied with the particular scan test (see below). Certain tests also involved the use of an auditory metronome which was typically set at 15 seconds. The behaviour of the animals was recorded on a 1-0 basis, using checksheets to record what behaviours had occurred within each 15 second period, the end of those periods being marked by a tone.

4.3 Procedure - P1

(i) Novel object tests

This test was designed to measure each animal's behaviour when faced with a novel and potentially frightening object, which, it was thought, might reflect level of emotionality. Each animal was separated from the rest of the group by an opaque partition for a period of 10 minutes in the lower left-hand cage of the home cages and a novel object was introduced. The object was a die-cast metal box, 7 by 11.5 by 8.5cm (see Figure 6) with 3 intermittently flashing lights accompanied by a short buzzing noise. The behaviours of each animal during this test were recorded using the clock and counter box, accumulating 0.25 second intervals. Animal numbers 25 and 27 were not tested with the object as they had experienced previous contact with it, hence it would not be

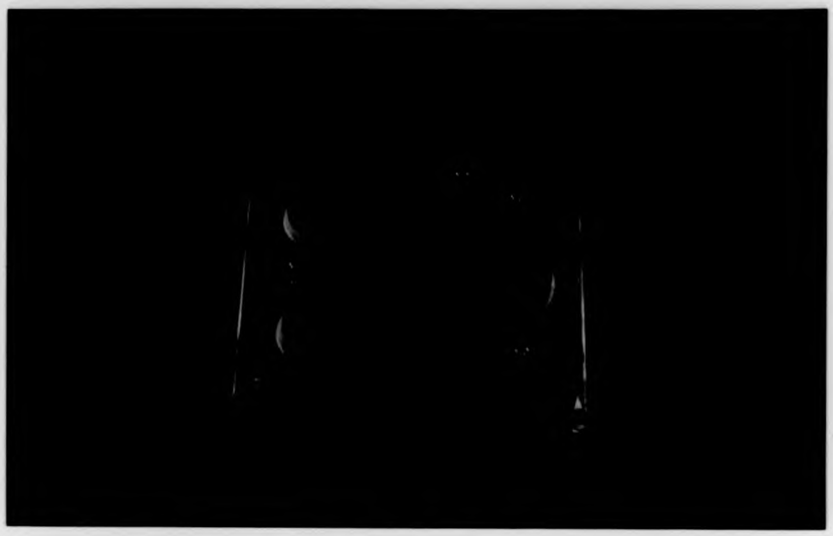


Figure 6 The box used in the novel object tests

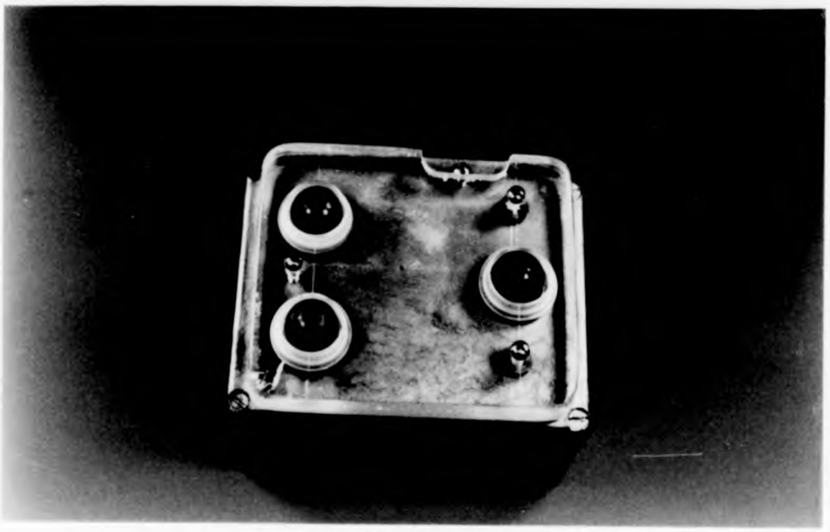


Figure 6 The box used in the novel object tests

novel to them. The behaviours recorded during the novel object tests were:

self-aggression (duration) stereotypy (duration)

dominance to the environment (e.g., hitting divider) (duration)

visual dominance to the object (e.g., visual threat) (duration)

contact dominance to the object (e.g., hitting the object) (duration)

play, not including the object (duration)

play contact with the object (duration)

locomotion (duration and frequency)

explore object visual (duration and frequency)

explore object contact (duration and frequency)

fear shown to the object (duration)

epimeletic object (duration)

(For definitions of behavioural categories, see Appendix 2). Also recorded was the time taken to first contact the object.

(ii) Isolation tests

This test measured how disturbed each animal was at being isolated from the rest of the group, which would perhaps reflect his level of sociability or emotionality (more sociable or emotional animals may be more upset at being isolated from other animals). The procedure was as for the novel object tests but without the novel object.

The behaviours recorded (using the clock and counter box) were:

self-aggression (duration)
stereotypy (duration)
self groom (duration)
self huddle (duration)
masturbate (duration)
dominance to the environment (duration)
play (duration)
locomotion (duration and frequency)
explore environment visually (duration)
explore environment contact (duration and frequency)
whimper (duration and frequency)
scream (duration and frequency)

(For definitions of behavioural categories, see Appendix 2).

(iii) Random scan sampling.

Throughout the period of February to July 1979, several scan periods of the stable group of 13 animals were conducted which were designed to measure various aspects of the animals' personalities. The sorts of behaviours recorded varied according to each particular scan test but were chosen to reflect some underlying personality trait as conceived by Eysenck. The periods of scan collection, the behaviours recorded in each of these different periods and the rationale behind the collection of each particular behaviour are listed in Table 2. The measures recorded throughout this scan period were designed to measure (a) how sociable each animal was, (b) how active each animal was, (c) how excitable each animal was,

Table 2 **Behaviours sampled during scan periods**

* S=Sociability, A=Activity, E=Excitability,
D=Disurbance, P=Psychoticism.

Scan period	Measure	Code (in Tables)	Reflects*
February	alone	Falone	S, P
	sit with others	Fsitwt	S
	do huddling	Fdohud	S
	do groom	Fdogm	S
	within arms length of other animals	Farms	S
	receive huddle	Fbehud	S
	receive groom	Fbegm	S
	forage	Fforage	A
March	locomotion	Mloco	A
	forage	Mforage	A
	sit	Msit	A
	climb	Mclimb	A
	masturbate	Mmast	D
	self-aggression	Msagg	D
April	alone	Aalone	S, P
	be positive	Abe+ve	S
	locomotion	Aloco	A
	forage	Aforage	A
	self-aggression	Asagg	D
	be negative	Abe-ve	P
	visual monitor	Avimon	Dominance?
May	forage	Myforage	A
	sit	Mysit	A
	locomotion	Myloco	A
	pace	Mypace	A, E
	climb	Myclimb	A
	self-aggression	Mysagg	D
June	alone	Jalone	S, P
	be positive	Jbe+ve	S
	locomotion	Jloco	A
	self-aggression	Jsagg	D
	be negative	Jbe-ve	P
July dominance test 1-0 sampling per 15 second bout interval			
	alone	Jlalone	S, P
	be positive	Jlbe+ve	S
	locomotion	Jlloco	A
	sit	Jlsit	A
	forage	Jlforage	A
	be negative	Jlbe-ve	P
	visual monitor	Jlvimon	Dominance?
Familiar observer ratings (1=high)			
	sociability	Socrate	S
	excitability	Excrate	E
	activity	Actrate	A
Opportunistic measures			
	pace	Excpace	E
	scream	Excscrm	E

(d) how much disturbance he reflected and (e) how psychotic he was.

(a) sociability. This is perhaps reflected in how much time each animal spends in affiliative interaction (e.g., huddling, grooming) with other animals. An unsociable animal would be one who spent little time with other animals, and was generally on his own.

(b) activity. This is reflected in how much time the animal spends walking around, climbing, pacing etc. An inactive animal would be one who spent most of his time sitting.

(c) excitability. This was to measure the excitability of each animal and involved opportunistic recording of the animals' responses to a potentially arousing situation (e.g., an animal being removed from the other group of animals in the colony room, fights amongst the other group of animals etc.) An excitable animal would be one who reacted by pacing or screaming to an arousing situation. A non-reactive animal would remain passive under such situations.

(d) disturbance. It is possible that how disturbed an animal is is reflected in the amount of abnormal behaviour he expresses, for example, the amount of self-aggression, masturbation, stereotypy etc.

(e) psychoticism. This was an attempt to determine how psychotic each animal was, based on Walker-Leonard's (1980) interpretation of Eysenck's idea of psychoticism as being determined by some measure of solitariness combined with aggression. That is, animals are psychotic to the extent that they spend time alone and when they do interact with others it is primarily in an aggressive manner. During the scan period which sought to measure psychoticism the following measures were taken: number of scans the animal was observed to be;

(i) alone

(ii) being positive to other animals (e.g., affiliative, play)

(iii) being negative to other animals (e.g., aggressive)

From these measures, the animals were ranked according to the following criterion; percentage of scans seen alone plus being negative to others divided by the percentage of scans seen alone plus positive to others plus negative to others.

(iv) Dominance tests. January, February, May 1979.

Several dominance tests were conducted throughout the period of testing in P1, using Boelkin's (1967) criterion of 30 seconds accumulated drinking time. The order of animals to drink to this criterion level was recorded (the liquid was either milk or orange juice). Also recorded in the July dominance test were several other behaviours, using the 15 second 1-0 sampling technique (see Table 2).

(v) Familiar observers ratings.

Several ratings on all animals were made by individuals who were familiar with the animals, namely the technical staff in the unit. The technicians were asked to rank order the animals on the following criteria (1 = most);

(a) how sociable the animal is (i.e., how much does he like being with other animals)

(b) how active the animal is (i.e., how much of the day does he spend walking, pacing or climbing as opposed to simply sitting)

(c) how excitable the animal is (i.e., how prone the animal is to react to potentially disturbing situations, e.g., removal for medication)

(vi) Persistence tests.

It was decided to devise a test which might measure the level of persistence of each animal, as persistence is purported to be a characteristic of introverts (Eysenck & Eysenck, 1968). Each animal was observed attempting to reach a highly-valued food item. The animal was isolated from the rest of the group in the home cage by an opaque partition; another partition, with a small hole (11 x 20cm) was inserted in the cage between the animal and a small shelf, on which the food item was placed (an orange segment). Each animal was allowed to obtain a segment by inserting his hand through the partition hole and given 6 segments as trials before testing began. The E gradually increased the distance each S had to reach to grasp the orange segment until an distance at which the piece was just out of reach was attained (see Figure 7). Testing then began and lasted for 10 minutes, behaviours being recorded using the DTU (one sequence events only). From the data the following scores were obtained per animal: time spent;

(i) looking through the divider hole at the orange piece (and frequency of occurrence).

(ii) inserting arm through the divider hole in an attempt to grasp the orange piece (and frequency of occurrence).

(iii) pushing the divider separating the animal from the orange segment.

(iv) self-aggressing.

(v) locomoting.

(vi) showing dominance to the environment.

(vii) showing stereotypic behaviour.

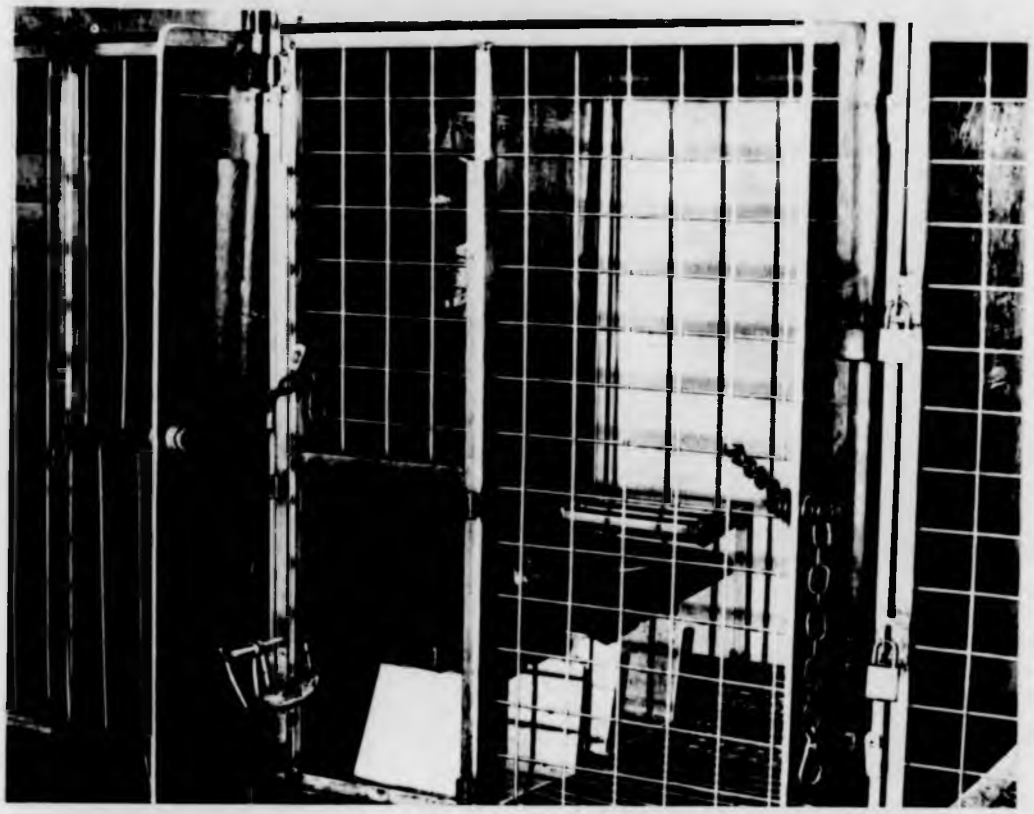


Figure 7 An animal attempting to reach the orange piece in the persistence test

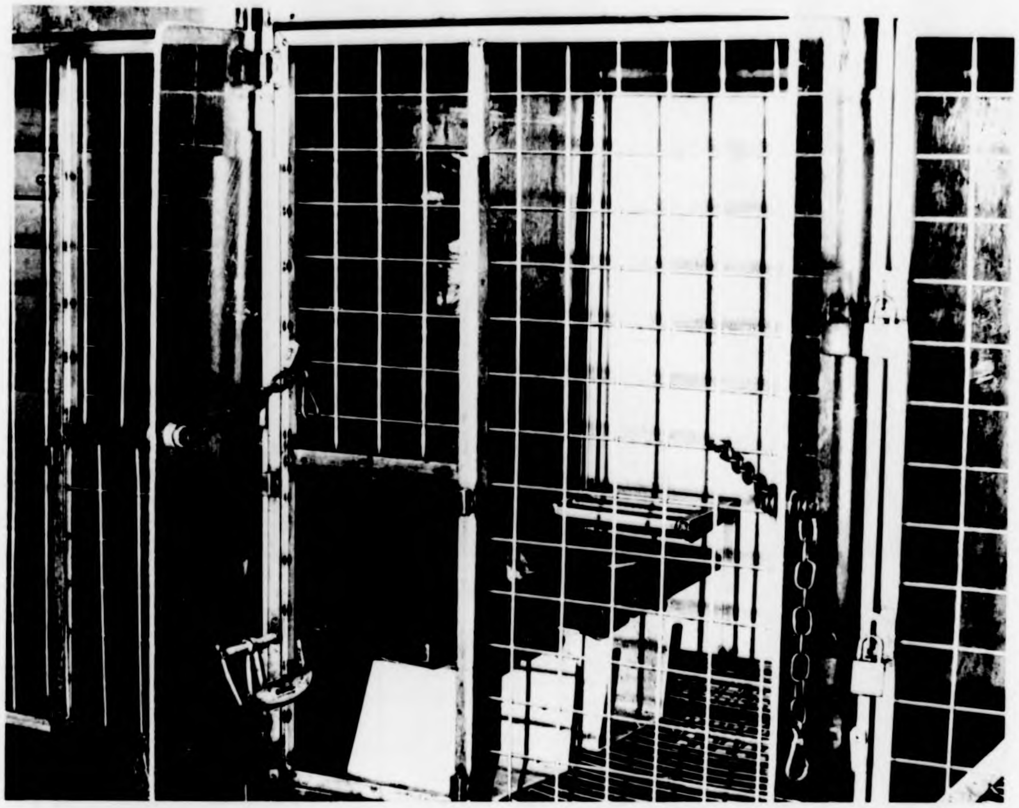


Figure 7 An animal attempting to reach the orange piece in the persistence test

4.4 Results - P1

(i) Novel object tests.

Most animals showed little interest in the object, glancing at it occasionally and blinking when it buzzed and flashed, although actual fear of the object was rarely shown. Table 3 gives a correlation matrix between behaviours recorded during the test and between dominance position and behaviour (Kendall correlation coefficients, 2 tailed). Animals who were slow to contact the object rarely showed visual dominance to the object ($r=-0.66$, $p<0.05$), and showed low levels of explore object contact ($r=-0.89$, $p<0.01$). Animals who showed a lot of explore object contact also showed a lot of visual dominance to the object (e.g., threats) ($r=0.75$, $p<0.05$), and played with the object a lot ($r=0.89$, $p<0.01$) ($n=11$ for all correlations). In general there were two sorts of reactions to the object - some animals avoided contact with it all together, others explored the object and showed dominance behaviour towards it. The test did not offer any insight as to differences in emotionality; those animals who avoided contact with the object did not appear to frightened of the object, but simply disinterested. The only significant correlation between dominance position and behaviour in the novel object test was between dominance position and dominance environment ($r=-0.53$, $p<0.05$, $n=11$), the more dominant animals showing more environmentally directed dominance behaviour, a finding also reported by Stamm (1961) with respect to behaviour in isolation.

Table 3
Matrix of correlation coefficients between behaviours in the novel object test

Kendall correlation coefficients   2 tailed tests

n = 11 *p=<0.05 **p=<0.01

n.b. some coefficients, while apparently high, are nevertheless non-significant, due to ties.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 self-aggression	-															
2 stereotypy	-0.18	-														
3 dominance env.	0.14	-0.26	-													
4 dom obj visual	-0.06	-0.33	0.18	-												
5 dom obj contact	-0.46	0	0.35	0.37	-											
6 play exc. obj	0.28	-0.46	0.07	-0.46	-0.46	-										
7 play with object	0	-0.26	0.47	0.66**	0.35	-0.36	-									
8 locomotion (dur)	0.38	-0.02	0.15	-0.23	-0.08	0.26	0.03	-								
9 locomotion(freq)	0.26	0.21	-0.16	-0.29	-0.31	0.17	-0.34	0.66**	-							
10 expl obj vis (d)	0.21	0.34	-0.09	0.03	-0.03	-0.13	-0.03	0.09	0.18	-						
11 expl obj vis (f)	0.04	0.34	-0.22	-0.08	-0.03	-0.04	-0.15	0.35	0.44	0.75**	-					
12 expl obj cont(d)	0.07	-0.26	0.37	0.75**	0.26	-0.36	0.89**	-0.03	-0.28	0.03	-0.09	-				
13 expl obj cont(f)	0.07	-0.26	0.37	0.75**	0.26	-0.36	0.89**	-0.03	-0.28	0.03	-0.09	1.00**	-			
14 epimeletic obj	-0.05	0.30	-0.14	0	-0.18	-0.25	0.07	-0.43	-0.11	0.30	0.08	0.15	0.14	-		
15 fear object	0.07	0.35	-0.21	-0.26	-0.26	-0.07	-0.21	0.09	0.31	-0.09	-0.09	-0.21	-0.21	0.22	-	
16 time to contact	0	0.26	-0.47	-0.66**	-0.35	0.36	-1.00	-0.03	0.34	0.03	0.15	-0.89**	-0.89**	-0.07	0.21	-
dominance rank	-0.04	-0.34	-0.53**	0.23	-0.18	0	-0.09	-0.27	-0.07	-0.16	-0.13	-0.03	-0.03	0.17	0.03	0.09

(ii) Isolation tests.

The isolation tests were repeated 6 months after the first set of isolation tests in order to obtain test-retest reliability correlation coefficients. In the 2nd set of tests, one animal (number 4) was not tested as she was heavily pregnant and markedly lethargic. These reliability coefficients (Kendall 1 tailed tests), correlation coefficients between all behaviours in the 1st test (Kendall 2 tailed tests) and correlations between dominance position and behaviours in the 1st test (Kendall 2 tailed tests) are given in Table 4. There are significant test-retest correlations ($r>0.37$) for the following behaviours; masturbate, locomotion (duration and frequency), explore environment visual and whimper (duration and frequency). The behaviours which show significant test-retest reliability also correlate with each other to some extent and these may be indicative of a disturbance reaction to isolation.

From the first set of tests there are significant correlations between several behaviours; animals who showed alot of dominance environment also masturbated a lot ($r=0.76$, $p<0.01$) and showed little self grooming ($r=-0.48$, $p<0.05$). Animals who self-aggressed a lot showed a high frequency of locomotion ($r=0.46$, $p<0.05$); highly stereotypic animals also screamed a lot ($r=0.49$, $p<0.05$) and frequently whimpered ($r=0.48$, $p<0.05$) ($n=13$ for all correlations). Correlations between the two vocalisations, screaming and whimpering were also significant. That there appear to be various 'clusterings' amongst the items may be

Table 4
Matrix of correlations between behaviours in 1st isolation test (2 tailed tests, n = 13) and test-retest correlations (1 tailed tests, n = 12)

Kendall correlation coefficients
Diagonal correlations are between behaviour in 1st test and behaviour in 2nd tests
*p=<0.05 **p=<0.01
\+ = correlation not in predicted direction

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 dominance env	0.23															
2 expl env vis	-0.37	0.37*														
3 stereotypy	0.46	-0.21	0.19													
4 play	0	-0.24	0.02	-0.03												
5 expl env con(d)	-0.42	-0.11	-0.16	-0.12	0.17											
6 expl env con(f)	-0.36	-0.34	-0.10	0.05	0.67**	-0.15+										
7 self-aggress	0.34	-0.17	0.36	0.07	-0.29	-0.01	0.18									
8 locomotion (d)	-0.14	0.21	0.07	0.07	-0.09	0.05	0.30	0.39*								
9 locomotion (f)	0.12	0.13	0.33	0.02	-0.17	-0.05	0.46*	0.78**	0.38*							
10 whimper (d)	0	-0.05	0.47	0.07	0.28	0.13	-0.05	0.11	0.21	0.69**						
11 whimper (f)	0	-0.06	0.48*	0.07	0.29	0.15	-0.05	0.13	0.23	0.99**	0.59*					
12 scream (d)	0.39	-0.42	0.49*	0.46	0.03	0.06	0.03	-0.06	0.10	0.52*	0.54*	0.21				
13 scream (f)	0.39	-0.42	0.49*	0.46	0.03	0.06	0.03	-0.06	0.10	0.52*	0.54*	1.00**	0.21			
14 self groom	-0.48*	-0.12	-0.17	0.07	0.42*	0.50*	-0.03	0.07	-0.17	-0.05	-0.03	-0.18	-0.18	0.08		
15 self huddle	0.26	-0.27	0.33	0.43	-0.32	-0.14	0.40	0.04	0.09	-0.01	-0.03	0.06	0.06	0.08	0.30	
16 masturbate	0.76**	-0.40	0.24	0.16	-0.45	-0.43	0.12	-0.21	-0.07	-0.30	-0.29	0.24	0.24	-0.41	0.26	0.75**
dominance rank	-0.26	-0.18	-0.30	0.38	0.29	0.34	-0.30	0	-0.13	-0.15	-0.13	0.19	0.19	0.41	-0.12	-0.02

indicative of different reactions to an isolation situation; some animals respond to being isolated by showing dominance towards the environment and masturbation, others by self-aggressing and locomoting, and others by stereotypy and high amounts of vocalisation. Surprisingly, none of the behaviours show significant correlations with dominance position. This is contrary to the findings of Stamm (1961) who found that dominant animals showed greater behavioural disturbance than subordinates in an isolation situation, in terms of more rapid pacing, jumping, somersaulting, cage-shaking and 'yelling'.

(iii) Scan sampling.

(a) Sociability.

Table 5 gives a matrix of correlations (Kendall 1 tail tests) between the various behaviours sampled during the scans which it was considered might be reflective of sociability, and their correlations with dominance position (Kendall 2 tailed tests). Though not all are significant, all but one of the correlations go in the direction predicted if the behaviours are reflecting some common underlying trait of sociability. The correlation between 'February do groom' and 'February be groomed' is negative, although not significant; it may be that the attractiveness of an animal as a grooming partner is independent of how sociable he himself is. There are many significant correlations between the items themselves, and a general picture emerges of a trait which could be termed sociability, characterised by how much time an animal spends on his own versus in affiliative interaction. In addition

Table 5
Matrix of correlations between sociability items from scan tests and observer ratings

Kendall correlation coefficients, 1 tailed tests
Bottom row shows correlation of each item with dominance rank,
Kendall correlation coefficients, 2 tailed tests
n = 13 *p=<0.05 **p=<0.01
+ = correlation not in predicted direction

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Falone	-													
2 Fsitwt	-0.88**	-												
3 Fdohud	-0.65**	0.73**	-											
4 Fdogm	-0.57**	0.44*	0.56**	-										
5 Farms	-0.35	0.35	0.27	0.13	-									
6 Fbehud	-0.69**	0.69**	0.68**	0.43*	0.28	-								
7 Fbegm	-0.30	0.32	0.30	-0.13+	0.45*	0.33	-							
8 Aalone	0.25	-0.37*	-0.34	-0.14	-0.20	-0.42*	-0.16	-						
9 Abe+ve	-0.20	0.32	0.34	0.04	0.21	0.45*	0.21	-0.91**	-					
10 Jalone	0.43*	-0.52**	-0.58**	-0.39*	-0.27	-0.51**	-0.29	0.66**	-0.58**	-				
11 Jbe+ve	-0.39*	0.49*	0.58**	0.38*	0.29	0.42*	0.31	-0.65**	0.55**	-0.87**	-			
12 Jlalone	0.33	-0.36*	-0.38*	-0.14	-0.20	-0.28	-0.33	0.56**	-0.59**	0.29	-0.36*	-		
13 Jlbe+ve	-0.29	0.44*	0.35	0.12	0.29	0.35	0.04	-0.63**	0.61**	-0.27	0.37*	-0.60**	-	
14 Socrate	-0.61**	0.75**	0.74**	0.43*	0.37*	0.55**	0.11	-0.44*	0.39*	-0.64**	0.57**	-0.37*	0.47*	-
dominance	0.72**	-0.81**	-0.75**	-0.37	-0.33	-0.72**	-0.44*	0.50*	-0.45*	0.67**	-0.63**	0.31	-0.33	0.73**

there are several significant correlations with dominance position; dominant animals spent significantly less time alone in the February scan period ($r=0.72$, $p<0.01$), in the April scan period ($r=0.50$, $p<0.05$) and in the June scan period ($r=0.67$, $p<0.01$). During the February scans dominant animals spent more time sitting with other animals ($r=-0.81$, $p<0.01$), huddling other animals ($r=-0.75$, $p<0.01$), being huddled ($r=-0.72$, $p<0.01$) and being groomed ($r=-0.44$, $p<0.05$); more time being positive to other animals in the April scan period ($r=-0.45$, $p<0.05$) and in the June scan period ($r=-0.63$, $p<0.01$). Thus dominant animals show more positive social interaction versus solitary behaviour than do subordinates, and are also rated as more sociable by familiar observers ($r=0.73$, $p<0.01$), ($n=13$ for all correlations). Interestingly, while there are several significant correlations between dominance rank and sociability in a free social behaviour situation (i.e., in the February, April and June scan periods) the correlation between dominance rank and time spent alone in the July dominance test is not significant (although positive), and neither is that between rank and time spent in positive interaction during the July dominance test (although negative). Thus the degree to which an animal is sociable is situation-dependent.

(b) Activity

Table 6 gives a matrix of correlations (Kendall 1 tailed tests) between the various items chosen to measure activity levels, and their correlations with dominance position (Kendall 2 tailed tests). All but 3 of the correlations

Table 6

Matrix of correlations of activity measures from scan tests

Kendall correlation coefficients, 1 tailed tests
Bottom row shows correlation of each item with dominance rank.
Kendall correlation coefficients, 2 tailed tests
n = 13 *p=<0.05 **p=<0.01
+ = correlation not in predicted direction

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 Fforage	-																
2 Mloco	0.28	-															
3 Mforage	0.12	0.08	-														
4 Msit	0.17	-0.62**	-0.21	-													
5 Mclimb	0.08	0.31	0.35	-0.35	-												
6 Aloco	0.22	0.41*	-0.05	-0.32	0.18	-											
7 Aforage	0.35	-0.11	0.24	-0.21	0.27	-0.06	-										
8 Myforage	0.54*	-0.03	0.29	-0.03	0.43	-0.32	0.40*	-									
9 Mysit	0.07	-0.51**	-0.38*+	0.68**	-0.43	-0.27	-0.36*	-0.52*	-								
10 Myloco	0.40*	-0.02+	0.33	-0.31	0.24	0.14	0.28	0.36*	-0.44*	-							
11 Mypace	-0.21	0.44*	-0.16	-0.27	0.29	0.76**	0.07	-0.22	-0.32	0.08	-						
12 Myclimb	-0.38*	0.36*	-0.34	-0.22	0.06	0.66**	-0.18	-0.34	-0.05	0.03	0.59**	-					
13 Jloco	-0.37*	0.25	-0.24	-0.09	0.24	0.47*	-0.02	-0.23	-0.03	-0.13	0.55**	0.64**	-				
14 Jlloco	0.21	0.05	-0.19	0.05	0.23	0.19	0.22	0.28	-0.65**	0.22	0.46*	0.27	0.26	-			
15 Jlsit	-0.49*	0.24	-0.44*	-0.01+	0.01	0.05	-0.23	-0.37*	0.28	-0.53**	0.20	0.31	0.44*	-0.05	-		
16 Jlforage	0.16	-0.11	0.18	-0.09	0.01	0.14	0.29	0.13	-0.03	0.36*	0.09	-0.01	0.04	-0.08	-0.41*	-	
17 Actrate	0.36*	-0.36*	0.04	0.17	-0.17	-0.50**	-0.11	0.28	0.26	0.28	-0.61	-0.32	-0.55**	-0.12	-0.30	0.06	-
dominance	-0.29	0.27	0.09	-0.41	0.34	0.55**	0.30	-0.17	-0.05	-0.01	0.58**	0.40*	0.52**	0.01	0.27	0.19	-0.52**

between the items are in the direction predicted (if they can be said to reflect activity level) and several are significant; e.g., time spent locomoting during the March scan period with time spent sitting ($r=-0.62$, $p<0.01$), or climbing during the May scans ($r=0.36$, $p<0.04$); time spent locomoting during the April scans with pacing in the May scans ($r=0.76$, $p<0.01$), or with climbing during May ($r=0.66$, $p<0.01$) or with time spent locomoting in the July dominance test ($r=0.47$, $p<0.05$) ($n=13$ for all correlations). There appears to be a trait of activity, characterised by how much time an animal is active (e.g., walking, climbing) as opposed to inactive (sitting) and from the pattern of correlations with dominance position it appears that the more subordinate animals are the more active, (e.g., there is a significant correlation between dominance rank and locomotion during the May scan period ($r=0.55$, $p<0.01$), rank and pacing during May ($r=0.58$, $p<0.01$), rank and locomotion during June ($r=0.52$, $p<0.01$) (2 tailed tests, $n=13$).

(c) Excitability.

Table 7 gives a matrix of correlations (Kendall 1 tailed tests) between the excitability measures and their correlations with dominance position (Kendall 2 tailed tests). All but 2 of the correlations are in the direction predicted and significant and there are two significant correlations with dominance position (rank and observer rating ($r=0.54$, $p<0.01$), rank and pacing during May scans ($r=0.58$, $p<0.05$ (ties), $n=13$ for all analyses). Excitable animals (as rated by familiar observers) pace

Table 7
Matrix of correlations between excitability items from scan tests and observer ratings

Kendall correlation coefficients, 1 tailed tests
Bottom row shows correlation of each item with dominance rank,
Kendall correlation coefficients, 2 tailed tests
n = 13 *p=<0.05 **p=<0.01
+ = correlation not in predicted direction

	1	2	3	4
1 Mypace	-			
2 Excpace	-0.18+			
3 Excscrm	-0.38+	0.65**		
4 Excrate	-0.48*	-0.38*	-0.38*	-
dominance	0.58*	-0.28	-0.38+	0.54**

Table 8
Matrix of correlations between disturbance items from scan tests

Kendall correlation coefficients, 1 tailed tests
Bottom row shows correlation of each item with dominance rank,
Kendall correlation coefficients, 2 tailed tests
n = 13 *p=<0.05 **p=<0.01
+ = correlation not in predicted direction

	1	2	3	4	5
1 Mmast	-				
2 Msagg	-0.16+	-			
3 Asagg	0.16	-0.20+	-		
4 Mysagg	-0.19+	0.42+	-0.19	-	
5 Jsagg	-0.23+	0.05	0.04	0.31	-
dominance	0.20	-0.21	0.40	-0.15	-0.29

(r=-0.38, p<0.05) and scream a lot (r=-0.38, p<0.05) (n=13) in reaction to arousing stimuli and are also more dominant.

(d) Disturbance.

Table 8 gives a matrix of correlations (Kendall 1 tailed tests) between the disturbance items and their correlation with dominance position (Kendall 2 tailed tests). The correlations between the items are low and several of them are in the opposite direction from that predicted and only one is significant. There are no significant correlations with dominance position. This suggests that the trait of disturbance is not characterised by these behaviours.

(e) Psychoticism.

Table 9 gives a matrix of correlations (Kendall 1 tailed) between the items designed to measure psychoticism and their correlations with dominance position (Kendall 2 tailed tests). There are significant correlations between the 'alone' items but not between the 'be negative' items. The ranking of psychoticism, from the April scans does not correlate significantly with any items other than those from which it was directly computed. Psychoticism may not be a personality dimension in primates or if it is, it is evidently not composed of negative and solitary behaviour.

(iv) Persistence tests.

The persistence tests were repeated 6 months after the first set of tests in order to obtain correlations indicative of test-retest reliability coefficients. coefficients. These reliability coefficients (Kendall 1 tailed tests), correlation

Table 9

Matrix of correlations between psychoticism items from scan tests

Kendall correlation coefficients, 1 tailed tests
Bottom row shows correlation of each item with dominance rank,
Kendall correlation coefficients, 2 tailed tests
n = 13 *p=<0.05 **p=<0.01
+ = correlation not in predicted direction

	1	2	3	4	5	6	7	8
1 Falone	-							
2 Aalone	0.26	-						
3 Abe-ve	-0.27	-0.17	-					
4 Psychot rating	-0.27	-0.97**	0.12	-				
5 Jalone	0.43*	0.66**	-0.15	-0.69**	-			
6 Jbe-ve	-0.55**	-0.17	0.02	0.18	-0.47*	-		
7 Jlalone	0.32	0.56**	-0.23	-0.52*	0.28	-0.21	-	
8 Jlbe-ve	-0.13	-0.25	0.29	0.20	-0.23	0.22	0.03	-
dominance	0.72**	0.50*	-0.36	-0.51*	0.67**	-0.39	0.31	-0.36

Table 10
Matrix of correlations between behaviours in the 1st persistence test (2 tailed tests, n = 13) and test-retest correlations (1 tailed tests, n = 13)

Kendall correlation coefficients
Diagonal correlations are between behaviour in 1st test and behaviour in 2nd tests.
*p=<0.05 **p=<0.01
+ = correlation not in predicted direction

		1	2	3	4	5	6	7	8	9
1	look through divider (f)	0.43*								
2	look through divider (d)	0.78**	0.23							
3	arm through divider (f)	0.71**	0.55**	0.39*						
4	arm through divider (d)	0.65**	0.55**	0.80**	0.54**					
5	push divider	-0.10	-0.02	-0.10	0.03	0.15				
6	locomotion	0.08	0.08	0.03	-0.03	-0.21	-0.09+			
7	dominance environment	-0.17	-0.12	-0.14	-0.10	0.12	0.11	-0.05+		
8	self-aggression	-0.33	-0.42*	-0.32	-0.37	0.23	-0.34	0.35	0.03	
9	stereotypy	-0.15	-0.21	-0.09	-0.11	0.01	0.30	0	0.07	0.28
	dominance rank	0.09	0.01	0.06	-0.05	-0.35	0.12	-0.17	-0.22	0.05

coefficients between all behaviours in the 1st test (Kendall 2 tailed tests) and correlations between dominance position and behaviours in the 1st test (Kendall 2 tailed tests) are given in Table 10. The test-retest reliability coefficients are low, and are only significant for look through (f) ($r=0.43$, $p<0.05$), arm through (d)($r=0.54$, $p<0.01$), and arm through (f) ($r=0.39$, $p<0.05$), ($n=13$ for all correlations). These 3 items also inter-correlate highly ($r> 0.55$, $p<0.05$, $n=13$) in the first set of tests. There are no significant correlations with dominance position. It may be that the reliable items and those which intercorrelate highly (look through and arm through) are reflective of persistence or perhaps some other factor like food motivation.

(v) Factor analysis of P1 data.

The results from P1 indicated those items which seemed to reflect similar traits and which were reliable. There were many correlations of behaviour with dominance position, and several apparent traits (e.g., sociability, activity). As an exercise, all the items from the P1 data were factor analysed; analysis 1 included only the social behaviour data (i.e., scan data, observer ratings and July dominance test data); analysis 2 included all the P1 data (i.e., all the data included in analysis 1 plus novel box, isolation and persistence test data). The results from these two analyses are given in Table 11, but must be treated with caution. The use of multivariate techniques, particularly factor analysis for analysing data with such a small sample size (13) is questionable, and often the results vary according to what

Table 11

Factor loadings for behaviours from P1

Analysis 1 - Scan data, observer ratings and dominance test data

Behaviour	Factor 1	Factor 2	Factor 3
Dominance rank	0.95	-0.04	-0.15
Avimon	0.81	0.16	0.17
Jlvimon	0.83	-0.12	0.09
(i) sociability measures			
Falone	0.83	-0.28	-0.05
Fsitwt	-0.88	0.11	0.12
Fdohud	-0.84	-0.18	0.02
Fdogm	-0.35	-0.02	-0.47
Farms	-0.60	0.27	-0.07
Fbehud	-0.83	0.07	0.17
Fbegm	-0.53	0.48	0.48
Aalone	0.83	0.34	-0.34
Abe+ve	-0.80	-0.21	0.40
Jalone	0.85	0.13	-0.07
Jbe+ve	-0.76	-0.23	0.12
Jlalone	0.62	0.13	-0.40
Jlbe+ve	-0.44	-0.47	-0.04
Socrate	0.86	0.10	0.06
(ii) activity measures			
Fforage	-0.16	0.59	-0.09
Mloco	-0.04	-0.06	0.14
Mforage	-0.02	0.77	-0.31
Msit	0.15	-0.58	-0.17
Mclimb	0.33	0.04	0.23
Aloco	0.81	0.11	0.50
Aforage	0.38	0.56	-0.42
Myforage	-0.24	0.42	0.11
Mysit	-0.41	-0.43	-0.44
Myloco	0.30	0.43	0.24
Mypace	0.61	0.17	0.67
Myclimb	0.63	-0.24	0.48
Jloco	0.70	-0.46	0.19
Jlloco	0.50	0.15	0.75
Jlsit	0.13	-0.92	0.05
Jlforage	0.37	0.64	-0.41
Actrate	-0.67	0.36	-0.19
(iii)excitability measures			
Excpace	-0.26	0.70	0.30
Excscrm	-0.29	0.79	-0.08
Excrate	0.70	-0.21	-0.32
(iv) disturbance measures			
Mmast	0.45	0.22	0.65
Msagg	-0.27	0.32	-0.22
Asagg	0.31	-0.17	-0.21
Mysagg	-0.10	0.21	-0.28
Jsagg	-0.14	-0.03	-0.09
(v) psychoticism measures			
Abe-ve	-0.25	0.43	0.61
Psychot rating	-0.75	-0.43	0.28
Jbe-ve	-0.60	-0.04	0.25
Jlbe-ve	-0.13	-0.12	0.19
Eigenvalue	15.31	6.66	4.78
% variance	33.30	14.50	10.40
	'dominance'	'activity' ?	?

Analysis 2 - Scan data, observer ratings, dominance test data, novel object, isolation and persistence test data.

Behaviour	Factor 1	Factor 2	Factor 3
Dominance rank	-0.90	0.01	0.22
Avimon	-0.77	0.29	-0.06
Jlvimon	-0.79	0.18	0.09
(i) sociability measures			
Falone	-0.80	-0.37	0.25
Fsitwt	0.83	0.17	-0.29
Fdohud	0.69	-0.23	-0.37
Fdogm	0.12	-0.01	-0.22
Farms	0.62	-0.02	0.23
Fbehud	0.78	0.13	-0.37
Fbegm	0.61	0.39	0.10
Aalone	-0.79	0.38	0.25
Abe+ve	0.82	-0.30	-0.15
Jalone	-0.76	0.36	0.08
Jbe+ve	0.66	-0.55	0.04
Jlalone	-0.66	0.27	0.04
Jlbe+ve	0.30	-0.43	-0.27
Socrate	-0.80	0.10	0.23
(ii) activity measures			
Fforage	0.31	0.40	0.53
Mloco	-0.13	-0.03	-0.43
Mforage	0.01	0.37	0.72
Msit	0.15	-0.52	-0.43
Mclimb	0.22	-0.21	0.85
Aloco	-0.70	0.30	0.01
Aforage	-0.29	0.37	0.55
Myforage	0.46	-0.02	0.82
Mysit	0.28	-0.18	-0.43
Myloco	0.27	0.63	0.31
Mypace	-0.59	0.24	-0.04
Mclimb	-0.45	0.14	-0.54
Jloco	-0.56	-0.26	-0.06
Jlloco	-0.35	0.24	0.03
Jlsit	-0.15	-0.67	-0.46
Jlforage	-0.33	0.53	0.38
Actrate	0.69	0.29	-0.02
(iii)excitability measures			
Excpace	0.24	0.77	-0.10
Excscrm	0.34	0.87	0.17
Excrate	-0.67	-0.07	-0.13
(iv) disturbance measures			
Mmast	-0.56	0.24	-0.04
Msagg	0.30	0.54	-0.12
Asagg	-0.58	-0.03	-0.20
Mysagg	0.06	0.38	-0.13
Jsagg	0.12	-0.11	0.32
(v) psychoticism measures			
Abe-ve	0.30	0.34	0.10
Psychot rating	0.77	-0.44	-0.25
Jbe-ve	0.60	-0.27	0.12
Jlbe-ve	-0.06	0.09	-0.40

continued/

Behaviour	Factor 1	Factor 2	Factor 3
(vi) novel object tests			
self-aggression	-0.07	0.26	0.20
stereotypy	0.39	-0.53	0.44
dominance environment	0.50	0.68	-0.40
dominance object visual	-0.69	0.25	-0.09
dominance object contact	0.40	0.49	-0.51
play, excluding object	0.01	-0.27	-0.42
play with object	0.46	0.70	-0.38
locomotion (d)	0.14	0.18	0.20
locomotion (f)	0.20	-0.06	0.34
explore obj visual (d)	-0.14	-0.55	-0.22
explore obj visual (f)	0.01	-0.67	-0.24
explore obj contact (d)	-0.37	0.47	-0.18
explore obj contact (f)	-0.56	0.25	-0.05
epimeletic object	-0.13	-0.22	0.45
fear object	0.13	-0.10	0.71
time to contact	-0.47	-0.69	0.38
(vii) isolation tests			
dominance environment	0.56	0.65	-0.34
explore environ visual	-0.27	-0.03	0.36
stereotypy	0.75	-0.10	0.36
play	0.04	-0.28	-0.30
explore env contact (d)	-0.51	-0.27	0.03
explore env contact (f)	-0.46	-0.40	-0.08
self-aggression	0.73	0.47	-0.22
locomotion (d)	0.02	0.33	0.59
locomotion (f)	0.27	0.27	0.50
whimper (d)	0.56	-0.38	0.52
whimper (f)	0.51	-0.37	0.53
scream (d)	0.53	-0.23	0.31
scream (f)	0.53	-0.24	0.32
self groom	-0.58	-0.02	-0.26
self huddle	0.33	-0.11	-0.52
masturbate	0.50	0.68	-0.38
(viii) persistence tests			
look through (f)	0.05	-0.53	0.35
look through (d)	0.13	-0.73	0.15
arm through (f)	0.12	-0.43	0.29
arm through (d)	0.09	-0.38	-0.35
push divider	0.26	-0.03	0.18
locomotion	0.05	-0.34	0.40
dominance environment	0.43	0.46	0.33
self-aggression	0.05	0.70	0.40
stereotypy	0.19	0.20	0.54
eigenvalue	20.22	13.33	10.69
% variance	23.30	15.30	12.30
	'dominance'	'excitability' ?	?

items are included in the analysis, the factors emerging being a function of what goes in. These analyses were an attempt to merge all the data from P1, and to see if factors emerged which might be explicable in terms of some Eysenckian notion of personality. The only clear factor which emerges from both analyses is one which will be labelled a dominance factor, accounting for 33.3% of the variance in analysis 1, 23.3% in analysis 2. This factor loads highly on dominance position (0.95 on analysis 1, -0.90 on analysis 2), several sociability items (e.g., time spent alone in April scan period; 0.83 on analysis 1, -0.79 on analysis 2: time spent being huddled in February scan period; -0.83 on analysis 1, 0.78 on analysis 2), activity (e.g., April locomotion score; 0.81 on analysis 1, -0.70 on analysis 2), excitability (e.g., observer rating; 0.70 on analysis 1, -0.67 on analysis 2), visual monitor (e.g., time spent visual monitoring in July dominance test; 0.83 in analysis 1, -0.79 in analysis 2). Of the items added in analysis 2 (novel box, isolation and persistence tests), several load highly on the dominance factor, e.g., dominance to the environment (0.50), visual dominance to the novel object (-0.69), stereotypy in isolation (0.75) and self aggression in isolation (0.73).

Thus dominant animals spend little time alone, a lot of time being huddled, are relatively inactive, are rated as highly excitable, and show low levels of visual monitoring. They show high levels of environmentally-directed dominance behaviour in a novel object test, low levels of visual dominance to the object and show more stereotypic and self-aggressive behaviour in isolation than do more subordinate animals. It appears from this that perhaps much of animal's behaviour can be explained without reference to any personality traits such as sociable, active etc., but simply in terms of how dominant the animal is, which can be considered a 'higher order' type-factor, characterised by these traits. Behaviour appears to be closely linked to dominance position, and it is not possible from the data to separate the two and offer any explanations as to causality. What are the influences of dominance position on behaviour, what are the personality characteristics that exist independent of dominance position, and what is the relationship between the two? The rest of the study aims to answer these questions.

Chapter 5 PHASE 2 - MANIPULATION PHASE - METHODS, EVALUATION OF DOMINANCE MEASURES, EFFECTS OF GROUP FORMATION AND SUCCESS OF MANIPULATION PHASE

5.1 Aims of P2

P1 had indicated the reliability of various measures of social behaviour (e.g., sociability, activity) and behaviour in test situations. There was no clear evidence for any higher order factors of personality such as extraversion, neuroticism etc. Rather, many behavioural characteristics seemed to be closely related to dominance rank, but as an exploratory phase, the results from P1 did not offer any explanantions as to the precise nature of the relationship between personality and dominance position, although they did suggest that dominance was an important variable. How does being in a given dominance position affect an animals behaviour? An individual's behaviour is likely to be a function of the dominance position he occupies; for example, a dominant animal can be as aggressive as he chooses; a subordinate animal's level of aggressive behaviour is constrained by the position he occupies. Similarly, a dominant animal is unlikely to show fear to his subordinates, whereas subordinate animals may show fearful reactions. An animal's behaviour in a given dominance position may, in turn, be affected by his personality; one animal may be very aggressive when dominant, another in a similar position of dominance may be less so. Similarly there may be individual differences in the amount of fearful behaviour shown by different animals when in the same subordinate position.

P2 was a manipulative stage, designed to separate dominance effects from personality effects, to answer questions concerning the relationship between dominance and personality, and to determine individual differences in behaviour in various dominance ranks. It was reasoned that if behaviours remained stable over changing dominance position then such behaviours must reflect those aspects of personality which show cross-situational stability. If behaviours changed with dominance position then this might be in one of two ways; (1) every animal shows similar changes in in behaviour with changing dominance position (e.g., all animals are more affiliative as dominants than subordinates, even though individual _levels_ of affiliative behaviour may differ) or (2), there are individual differences in the way behaviour changes with changing dominance position - some animals are more affiliative as dominants, some are more affiliative as subordinates. In the former case (1), changes in behaviour may be considered to be a function of changes in dominance rank per se; in the latter case (2), changes in behaviour are a function of the interaction between dominance rank and personality.

Accordingly, the group of 13 animals was manipulated to form smaller regroups of 5 animals, which existed for a period of 4 weeks. By removing different animals to form these regroups it was possible to give varying dominance position experience to each animal. The format of regroupings is given in Table 12, totalling 9 regroups in all.

Table 12 Proposed regrouping of animals in P2

Numbers in groups refer to intended dominance position of each animal within that regroup of 5
* = male animal

Animal number	15*	17	5	11	10	8	13	2	4	3*	25	27	6*
Dominance position in group of 13	1	2	3	4	5	6	7	8	9	10	11	12	13
Regroup number													
1	1	2	3	4	5								
2		1	2	3	4	5							
3			1	2	3	4	5						
4				1	2	3	4	5					
5					1	2	3	4	5				
6						1	2	3	4	5			
7							1	2	3	4	5		
8								1	2	3	4	5	
9									1	2	3	4	5

This intended format of regroupings results in 5 animals experiencing all 5 dominance positions in the groups of 5 (animal numbers 10, 8, 13, 2, 4), 2 animals experiencing 4 dominance positions (animal numbers 11 and 3), 3 animals experiencing 3 dominance positions (animal numbers 5 and 25), 2 animals experiencing 2 dominance positions (animal numbers 17 and 27), and 2 animals experiencing only 1 dominance position in the groups of 5 (animal number 15 experiences position 1 only and animal number 6 experiences position 5 only). This was the ideal format of regroupings, yielding the maximum number of available data points for subsequent analysis (45). However the actual format was slightly different, due to animals not conforming to their expected dominance positions in the various regroups, and changes in the relative dominance positions of animals in the group of 13 over the 12 month period of the experiment. This necessitated deviation from the planned format of regroups and forming regroups of animals so as to maximise as far as possible the number of data points, given the altered circumstances. The actual dominance positions observed in the regroups resulted in duplication of data points, and there was therefore some redundant data where animals were occupying dominance positions for which data had already been collected. Data was therefore not collected on these animals in these repeated positions, and some groups (e.g., Group 6) were abandoned altogether because they duplicated totally data which had been collected already. Table 13 lists the actual regroups resulting from manipulation of the group of 13, the expected dominance positions within those regroups and the

Table 13 Actual regrouping of animals in P2

Order regroups run was random and not in order listed
Numbers in groups refer to animal number expected to occupy that dominance position, underneath is the observed animal in that position for that regroup
** Data not collected on this particular animal in this regroup, as it repeats previous data points

Dominance position in regroup number	1	2	3	4	5	reversals?
1	15	17	5	11	10	
	15	17	5	11	10	No
2	17	5	11	10	13	
	17	5	11	10	13	No
3*	5	11	10	13	8	
	5	11	10	13	8	No
4*	11	10	13	8	2	
	11	10	13	8	2	No
5*	10	13	8	2	4	
	10	13	8	2	4	No
6*	13	8	2	4	3	
	3	13	8	2	4	Yes(abandoned)
6b*	13	8	2	4	25	
	13**	8	2	4	25**	No
7	13	2	4	3	25	
	13	2	4	3	25	No
8	2	4	3	25	27	
	3	2**	4**	25	27	Yes
8b	2	4	25	27	6	
	2	4**	25**	27**	6**	No
9	4	3	25	27	6	
	3**	4	25	27	6	Yes

*Animal number 8, previously dominant to number 13 in the group of 13 had, by the time this regroup was formed, dropped below her, so her expected position was beneath number 13 in this regroup observed dominance positions within those regroups.

From the observed format of animals in their respective dominance positions in the various regroups there were only 3 animals instead of the anticipated 5 who experienced all 5 dominance positions (animals numbers 10, 13 and 2). Three animals experienced only 4 dominance positions (animal number 11 experienced positions 1,2,3, and 4; animal numbers 8 and 4 experienced positions 2,only 3,4 and 5), 2 animals experienced only 3 dominance positions (animal number 5 experienced positions 1,2 and 3; animal number 25 experienced positions 3,4, and 5), 3 animals experienced 2 dominance positions (animal number 17 experienced positions 1 and 2; animal number 3 experienced positions 1 and 4; animal number 27 experienced positions 4 and 5) and 2 animals experienced only 1 position (animal number 15 experienced position 1;animal number 6 experienced position 5). The available data is shown in Table 14.

The data collected in P2 involved recording behaviour in much greater detail than in P1, and included recording some behaviours which had not been recorded in P1 (e.g., fear behaviour which was rarely observed in the group of 13 animals, but which may reflect emotionality). Several new tests were introduced, and the novel object test from Phase 1 abandoned, as it had not proved to be very efficient in terms of differentiating the emotionality levels of the animals.

Table 14 **Available data for each animal in the regroup dominance positions**

M = missing data point + = available data

Animal	Dominance position in group of 13	Regroup dominance position				
		D1	D2	D3	D4	D5
15	1	+	M	M	M	M
17	2	+	+	M	M	M
5	3	+	+	+	M	M
11	4	+	+	+	+	M
10	5	+	+	+	+	+
8	6 (7)*	M	+	+	+	+
13	7 (6)*	+	+	+	+	+
2	8	+	+	+	+	+
4	9	M	+	+	+	+
3	10	+	M	M	+	M
25	11	M	M	+	+	+
27	12	M	M	M	+	+
6	13	M	M	M	M	+

* Animal number 13 and 8 reversed their dominance positions in the group of 13 animals mid-way through Phase 2 testing

5.2 Procedure - P2

See Table 15.

(1) Day 1 - Formation of regroup.

On Day 1 of each regroup period the 5 animals that were to form that regroup were moved to the left hand side of the stainless steel cages in the colony room (2.5 cage modules - see Figure 3), the remaining animals having access to the right hand stainless steel cages, 2 of the galvanised South Pen caging and half the South Pen outside area. The animals in the regroup were then immediately shut outside in the North Pen outside area and a milk dominance test was performed.

(2) Day 1 Milk dominance test, duration 30 minutes.

Dominance order was determined using the criterion 'time to accumulate 30 seconds of drinking at the milk bottle'. Using a 1-0 recording method per 15 second time period (indicated by a metronome), instances of aggression and fear, specifically which animal expressed them and to whom, were also recorded.

(3) Daily DTU testing.

Throughout the period of each regroup each animal within that group except those animals for which data had already been collected in that dominance position, were tested daily for a period of up to 15 minutes in a free-social situation. This involved observing each animal for a given period, wherever he might be and recording his behaviour, using a

Table 15 **Format of testing procedures P2**

Day	Week	Morning	Afternoon DTU testing period, per animal (minutes)
1	1	Group formed Milk dominance test	15
2			15
3			15
4			15
5			15
			Total DTU=75
6			
7			
8	2		10
9			10
10			10
11			Persistence tests
12			10
			Total DTU=40
13			
14			
15	3		10
16			10
17			10
18			Isolation tests
19		Milk dominance test	10
			Total DTU=40
20			
21			
22	4		10
23			10
24		Introduction of SSA	10
25		Introduction of DSA	10
26		Orange juice dominance test	10
			Total DTU=50
			DTU total=205
27			
28			
29	End of regroup	All animals reunited into group of 13	
33	Milk dominance test on group of 13		

4-sequence category system; general behaviour, sub-behaviour, direction (specific animal, environment or self), and initiator. (see Appendix 2 for details.) The order of testing each animal was randomly determined, alternating observations commencing inside the colony room with those taken in the outside pen from day to day. The following restrictions to a random order were imposed: on a day commencing inside, for example, if the first animal to be tested was not in view, the second animal was tested (or the 3rd if the 2nd was not in view). When every animal that was inside had been observed, testing began outside to observe those animals not already tested. The order of testing on a given day was never changed, i.e., if an animal had 'missed' his turn, he had to wait until all other animals had been tested within the given order. If an animal disappeared from view whilst being tested then the DTU code 'don't know' was punched; if that animal reappeared within 20 seconds, observation continued, if not, testing of that animal for that observation session was terminated and resumed after all other animals had been observed. Observation of that animal then continued until the allocated period of testing for that day had accumulated. If an animal was asleep at the start of his testing period, testing of that animal was abandoned until a later time. If an animal fell asleep during testing, testing was not abandoned - in fact both situations rarely occurred. Data was analysed by weekly sessions, total minutes given in Table 15.

(4) Day 11 Persistence tests.

Each animal was tested in the persistence test in each of the dominance positions he occupied. Procedure as for P1 tests.

(5) Day 18 Isolation tests

Each animal was tested in isolation in each of the dominance positions he occupied. Procedure as for P1 tests.

(6) Day 19 Milk dominance test Duration 30 minutes

To keep a check on the stability of the dominance order within each regroup, a milk dominance test was run on Day 19, again with all animals shut outside in the outside area and the procedure as for the Day 1 dominance test.

(7) Day 24 Introduction of subordinate stimulus animal (SSA test)

A subordinate stimulus animal (younger than any regroup member) was introduced into a small section of the stainless cages, shut off initially from the animals in each regroup by an opaque divider. The divider was then removed and the SSA introduced to the regroup animals. The test lasted for a period of 30 minutes, during which instances of affiliation and aggression between regroup members were noted, affiliation and aggression to SSA, self-aggression, dominance behaviour on the part of the regroup animals (e.g., dominance yawns, bounces). Behaviour was recorded using the 15 second 1-0 sampling technique as outlined in section 4.2.(b)(iii).

The test was designed to assess the varying reactions of each regroup member, according to his dominance position, to the introduction of a new, subordinate animal. (It was expected that, for example, the most subordinate animal of each regroup would ensure his dominance over the newly introduced animal by aggression or dominance assertion). Unfortunately, in the middle of P2 circumstances beyond experimental control necessitated using a different subordinate stimulus animal for the remaining regroups than had been used for previous regroups. Regroup numbers 3,4,5,7,8,9 experienced SSA number 46, a 3 year old female, calm and non-aggressive, while regroup numbers 1,2, 6b and 8b experienced SSA number 77, a 9 month old infant female, who was a highly confident individual as she had previously been living with an adult male animal.

(8) Day 25 Introduction of dominant stimulus animal (DSA test)

A dominant stimulus animal (older than all regroup members) was introduced in a similar manner to the introduction of SSA, with the exception of regroup 1 where he was first introduced to the dominant animal of this regroup (animal number 15) alone (in an attempt to make 15 subordinate to DSA by not allowing any support for him from the rest of the regroup animals). The DSA was a feral-born adult male, approximately 15 years old, weighing 15.3 kg., (unfortunately considerably less than animal number 15). The test lasted for a period of 30 minutes, and the behaviours recorded were the same as those recorded in the SSA test, with the addition of matings and harrassment of matings, again using a 15 second 1-0 sampling technique. The test was designed to assess the varying reactions of each regroup member, particularly the dominant, to the introduction of a new, dominant animal, in terms of amount of affiliation and aggression expressed towards DSA, and the effect of an 'intruder' on the behaviour of the regroup animals.

(9) Day 26 Orange juice dominance test

A final check on the dominance order was made on Day 26 of the regroup, with an orange juice dominance test. The animals were shut out in the outside area, as in previous dominance tests, and the same behaviours recorded as in the Day 1 and Day 19 tests, using the same procedure.

(10) Day 29 Reuniting of all animals

On Day 29 of each regroup phase all animals were reunited into one large group (n=13). (No testing was done on this day).

(11) Day 33 Milk dominance test

As a check on the stability of the dominance hierarchy within the group of 13 animals, a milk dominance test was run, 4 days after the group had been re-united, all animals being shut outside in the North Pen. The dominance order was determined by using the 30 second criterion as in previous tests. This test was necessary in order to determine the possible success or failure of future regroups; if the dominance ranks of the animals in the stable group of 13 had altered, then the intended format of regroupings had to be modified accordingly.

5.3 Data analysis - P2

The daily DTU testing of each animal in every regroup yielded a vast amount of detailed information on the behaviour in a free social situation of the 13 animals over a variety of dominance positions. The data for some animals is more complete than for others, as not all animals were observed in all 5 regroup dominance positions. Where data for a particular dominance position for a particular animal is available it is always in a standard form; the % time per week (4 weeks in total) that each animal was observed engaged in fear, exploratory, play, affiliative, aggressive, sex, self (or solitary) and other behaviour. In addition to the data for these gross behavioural categories there is also data on % time observed 'fear grimacing', 'affiliative lipsmack', 'self-aggression' etc., which, in the case of the social behaviours can be further sub-divided into % time fear grimacing to or grooming a particular animal in the same regroup (see Figure 8).

The behaviour of the animals was usually mutually exclusive, i.e., rarely was an animal performing 2 behavioural sequences that might be scored separately on the DTU at the same time. An exception to this occurred on occasion in affiliative interaction, where an animal was, for example, grooming one animal whilst being huddled (dorso-ventral) by another. In this case, a unique code was punched on the DTU, and a diary entry for that day recorded (e.g., 5959 - huddled by animal x, grooming animal y). If the sequence 5939

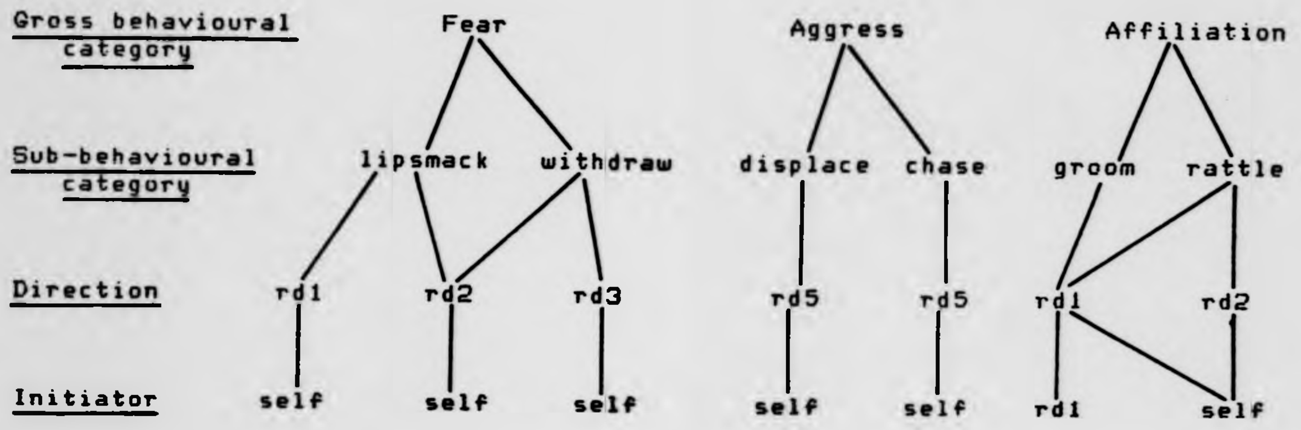


Figure 8 Breakdown of the DTU data on free-social behaviour

accounted for 10% of the weekly DTU data, 'grooming animal x' and 'huddled by animal y' both scored 10%. This has the effect of inflating the % affiliation score for that particular animal for that week, but rather than decide which behaviour (grooming or being huddled) was the more important to score (and since both behaviours were of interest) this method of data breakdown gave better representation of how affiliative an animal was, by scoring both interactions. Self-aggressive episodes were always scored, in preference to other activities in which the animal might be engaged (e.g., huddling) as self-aggression was of particular interest.

Appendix 3 is a table of means over the 4 week periods during which each regroup existed of the gross behaviour of each animal in every dominance position which he experienced. In the following sections, the DTU data is analysed in many different ways, according to the purpose of each analysis. Accordingly, it is felt that the readers task should be simplified by standardising the format of analyses and by introducing the rationale behind each analysis by posing simple questions at the beginning of each section.

5.4 Results - P2

5.4.1. How efficient and valid are various measures of dominance?

Central to the debate on the usefulness of the concept of dominance is the controversy surrounding its measurement. From the data collected in P2 it is possible to assess the 'efficiency' of various methods of dominance measurement (in terms of how well from such measures we are able to assign dominance ranks to each individual) and their 'validity' (in terms of their correlations with other measures of dominance). Appendix 4 lists the relative ranks assigned to each animal in each regroup based on several measures which include 3 competitive 'drinking order' measurements, direction of aggressive and fear behaviour during the 3 competitive drinking tests and in the 2 stimulus animal tests and during free social behaviour (DTU testing), visual monitoring behaviour, initiate groom and receive groom during free social behaviour (DTU testing).

(1) Efficiency of the measures

Appendix 4 also lists the number of regroups where all animals were assigned an unequivocal dominance rank on a particular measure (maximum = 9, except for DTU measures, where total is 6 as DTU data was not collected on every animal in every regroup).

(i) Competitive drinking orders. These were taken on 3 separate occasions, Day 1, Day 19 and Day 26, using the criterion 'time to accumulate 30 seconds of drinking time'. (The first animal to accumulate 30 seconds was given rank 1 etc.) These measures were relatively efficient; for the Day 1 measure it was possible to assign ranks to every animal in 7 of the 9 regroups, for the Day 19 and Day 26 measures 6 out of 9 regroups. Occasions when it was not possible to assign ranks to all animals occurred when not every animal drank to criterion, or did not drink at all, in which case they were not assigned any rank.

(ii) Aggression orders during:

(a) competitive tests.

A rank order based on the direction of aggression in each of the 3 competitive tests was computed for each subject in each regroup. To avoid circularity (A aggresses B, B aggresses C, C aggresses A) it is desirable to demonstrate a linear dominance hierarchy (A aggresses B and C more than B and C aggress A, B aggresses C more than C aggresses B). This was only possible in 3 out of 9 regroups for the Day 1 measure, 2 out of 9 for the Day 19 measure and 4 out of 9 for the Day 26 measure. In other regroups, it was only possible to rank 2 or 3 individuals (e.g., regroup number 7, Day 19 measure) on the basis of direction of aggression, whilst in other regroups (e.g., regroup 3, Day 1 test) it was possible only to a limited extent (A, B and C aggress D and E but no aggression between A, B and C). Hence there are a lot of missing ranks on this measure. This is because aggression during the competitive tests was infrequent.

(b) stimulus animal tests.

A similar order based on the direction of aggression was computed for each regroup during the stimulus animal tests. Interactions of an aggressive nature were recorded between all regroup members during (1) dominant stimulus animal test (DSA) and (2) subordinate stimulus animal test (SSA). However, in none of the 9 regroups was it possible to rank order all the animals during these tests on the above criterion. In 4 out of 9 regroups during the DSA test and 6 out of 9 in the SSA test no ranks were assignable for any of the animals. The efficiency of this measure, at least in these situations, can be considered very low, as aggression between regroup members was infrequent.

(iii) Submissive orders during:

(a) competitive tests.

A rank order based on submissive/fear interactions was computed for each regroup for each of the competitive drinking tests. As for the aggressive orders, it was hoped to derive a linear hierarchy, where E,D,C,B show fear to A, E,D,C show fear to B etc. but this was not possible for any of the regroups in any of the 3 tests. Only occasionally was it possible to infer any dominance relationship between the animals (e.g., regroup 1, Day 1 test, animal number 11 submits to animal number 15).

(b) stimulus animal tests.

Again, using the same criteria in an attempt to acheive a linear ranking it was not possible to assign ranks to every animal in every regroup on this measure, and only occasionally to several animals (e.g., regroup 2, SSA test).

The efficiency of the measure using direction of submissive behaviour to rank order animals is low, at least in these situations (competitive and stimulus animal tests), as it occurs infrequently.

(iv) Free social behaviour (DTU data)

(a) aggressive orders

Because of the great amount of data collected for each animal during free social behaviour it proved much easier to rank every animal in every regroup on an aggression order than on the same measure in the competitive and stimulus animal tests.

Rank orders based on (1) total amount of aggression (highest level= dominant animal) and (2) direction of aggression (using the same criteria as in the competitive and stimulus animal tests) were computed for each regroup. Both measures show high efficiency in ranking all regroup members, although the aggression total measure results in ties for 2 animals in regroup 4, and the aggression direction measure only ranks unequivocally all animals in 4 out of 6 regroups. (Not all animals were tested in free social behaviour in all regroups because of duplication of existing data).

(b) submissive orders

Rank orders based on (1) total amount of fear/submissive behaviour (highest level=most subordinate animal) and (2) direction of fear/submissive behaviour were computed for each regroup. The rank order based on submission total enabled unequivocal (i.e., no ties) ranking of every animal tested in free social behaviour in all 6 regroups. The order based on direction of submission ranked 4 out of 6 regroups unequivocally (example of equivocal ranking is regroup 5, where animal numbers 13,8,2, and 4 showed submissive behaviour to number 10, and numbers 2 and 4 to numbers 13 and 8, but 13 and 8 never showed submission to each other and neither did 2 and 4, hence ranking = 1 (number 10), 2.5 (numbers 13,8), 4.5 (numbers 2 and 4).)

(c) other free social behaviour measures - visual monitoring, initiate groom, receive groom.

Rank orders based on amount of visual monitoring (highest level= most subordinate animal), initiate groom (highest level=most subordinate animal) and receive groom (highest level=dominant animal) were computed for all regroups. All 3 measures proved efficient in unequivocally ranking all animals tested in every regroup (6 out of 6).

In terms of their efficiency in ranking every regroup member without ties, the various dominance measures rate as follows; the free social behaviour measures (visual monitor ranks all animals in 100% of regroups, initiate groom 100%, receive groom 100%, aggression (total 83%, direction 67%), submission (total 100%, direction 67%)) are the most efficient, rankings based on competitive drinking orders the next (average over 3 tests=70%), aggression in competitive tests (direction, average over 3 tests=33%), with aggression in stimulus animal tests and submission in both competitive and stimulus animal tests the least efficient, due to the low frequency of these behaviours in these situations.

The efficiency of a dominance measure when judged in terms of its ability to rank all regroup members unequivocally can therefore be viewed as a function of the situation it is tested in. This point has perhaps not always been borne in mind by researchers who have sought to investigate various methods of dominance assessment. However, the overall efficiency of a measure must also take into account its validity, that is, how valid is a ranking based on a given measurement in terms of reflecting the 'true' dominance order? (assuming that there is only one such order, which is questionable). As dominance can only be measured by these various different methods, it becomes a circular issue, but it can be argued that it is those measures which correlate best with other measures which seek to measure the same concept (dominance order) which have the highest validity.

(2) Validity of the measures

(i) internal validity or reliability

Table 16 shows the correlation coefficients between various measures of dominance which are based on the same criteria (competitive drinking, aggression, submission), averaged over all regroups (excluding those where the correlation coefficient was based on an $n < 2$). Table 16 shows that the highest mean correlations are between the various competitive drinking measures of dominance, (averaging 0.94), followed by the measures based on aggression (averaging 0.74), with the submissive order measures showing the lowest, and often negative, correlations (averaging -0.01).

(ii) external validity

Table 17 shows the percentage number of significant correlations of all correlations of each measure with every other measure for each regroup (Kendall correlations, 1 tailed tests, $p<0.05$), (e.g., in regroup number 1, measure number 1(Day 1 drink order) correlates significantly with 64% of other measures), and the mean correlation for each measure over all regroups. The best correlate with all other dominance measures is the Day 19 competitive test aggressive order(direction); where an order could be determined in a particular regroup on this measure then this measure correlates significantly, on average, with 71% of other measures. The aggressive order (direction) derived from the dominant stimulus animal test is the next best correlate, on average correlating significantly with 68% of the other items.

Table 16 Average correlation coefficients over all regroups between dominance measures

Averages based on Kendall correlation coefficients, 1 tailed tests, p=<0.05 d.f. varies
* not computable - no overlap between rankings on two measures for any regroup

(a) Competitive drinking order measures

		Measure	
	1	4	11
1 Day 1	-		
4 Day 19	0.95	-	
11 Day 26	0.93	0.93	-

(b) Submissive measures

			Measure			
	3	6	8	10	13	14
3 Day 1 Fear direction	-					
6 Day 19 Fear direction	*	-				
8 DSA test Fear direction	*	-1.00	*			
10 SSA test Fear direction	*	*	*	-		
13 Day 26 Fear direction	*	*	*	*	-	
14 DTU data Fear total	0.83	-1.00	1.00	-1.00	*	-
15 DTU data Fear direction	0.50	-1.00	1.00	0	*	0.54

(c) Aggression measures

			Measure			
	2	5	7	9	12	16
2 Day 1 Agg direction	-					
5 Day 19 Agg direction	0.95	-				
7 DSA test Agg direction	0.53	0.67	-			
9 SSA test Agg direction	0.72	0.96	1.00	-		
12 Day 26 Agg direction	0.91	0.78	0	0.94	-	
16 DTU Agg total	0.64	0.66	0.24	0.86	0.69	-
17 DTU Agg direction	0.87	0.88	0.77	0.86	0.82	0.78

Table 17 Percentage number of significant correlations between dominance measures (of total correlations) per group

Percentage as a function of all correlation coefficients based on n= or > 4 (not computable for regroup 6b or 8)

* = no correlations possible

Measure Number	Method	Regroup 1	2	3	4	5	7	9	mean	validity rank
1	Day 1 Drinking order	64	64	62	0	67	55	73	55	9.5
2	Day 1 Aggression (direction)	*	64	62	0	67	55	82	55	9.5
3	Day 1 Fear (direction)	*	*	*	*	*	*	*	*	
4	Day 19 Drinking order	64	64	62	27	67	*	82	61	3
5	Day 19 Aggression (direction)	64	*	62	*	*	*	86	71	1
6	Day 19 Fear (direction)	*	*	*	*	*	*	*	*	
7	DSA test Aggression (direction)	*	*	*	*	*	50	86	68	2
8	DSA test Fear (direction)	*	*	*	*	*	*	*	*	
9	SSA test Aggression (direction)	*	*	*	*	*	56	*	56	7.5
10	SSA test Fear (direction)	*	*	*	*	*	*	*	*	
11	Day 26 Drinking order	64	64	62	0	67	50	82	56	7.5
12	Day 26 Aggression (direction)	0	64	0	*	50	*	*	29	11
13	Day 26 Fear (direction)	*	*	*	*	*	*	*	*	
14	DTU data Fear (total)	64	0	8	0	0	8	56	19	12
15	DTU data Fear (direction)	64	64	62	27	67	55	83	60	4.5
16	DTU data Aggression (total)	64	64	62	45	0	0	0	60	4.5
17	DTU data Aggression (direction)	64	64	62	36	58	55	*	57	6
18	DTU data Visual monitor (total)	9	9	0	9	0	0	55	12	13
19	DTU data Initiate groom (total)	9	0	0	0	58	0	0	10	14
20	DTU data Receive groom (total)	0	0	0	0	0	0	64	9	15

Then follows the Day 19 competitive drinking order (61%), the fear direction order and aggression total order from the free social behaviour data (60%), the aggression direction order from free social behaviour (57%), the aggressive order from the subordinate stimulus animal test and the Day 26 competitive drinking order (56%), the Day 1 competitive drinking order and the Day 1 competitive aggression order (55%), Day 26 competitive aggression order (29%), fear total order from free social behaviour (19%), visual monitor (12%), initiate groom (10%) and receive groom(9%). Several measures failed to show any significant correlations with any other measures for any of the regroups (e.g., Day 19 competitive submission order). The success of these measures, be they competitive drinking orders, aggression orders, submissive orders etc. as indicators of dominance rank seems therefore to be a function of the type of situation in which they are used (e.g., competitive test, stimulus animal test etc), and the specific group of animals under investigation. For example, where aggression in a competitive test occurs for a given group, then a dominance order based on the direction of this aggression correlates, on average, with 71% of other dominance measures. The measures derived from the free social behaviour testing, although the most efficient in ranking all the animals in every group, proved to be the poorest correlators with other measures of dominance. There was no evidence of a correlation between dominance and the amount of grooming done by the animals, contrary to the finding of Crawford (1942), although his study was with pairs, rather than groups of animals. Neither was there a relationship between the amount of grooming received and dominance, unlike that found by Maslow & Flanzbaum (1936), Varley & Symmes (1966) (both using pairs of animals) but is in line with a later finding by Maslow (1936b). There was no evidence of a dominance order based on amount of visual monitoring generalising to other dominance orders derived from different measures, contrary to Chance (1967), Keverne et al. (1978) and Virgo & Waterhouse (1969).

The dominance orders based on aggression are, in general, quite efficient in ranking all animals, although this does depend on the situation in which it is measured, as in some situations aggression is relatively rare, supporting the worK of King (1965a). The correlations between the various dominance orders based on aggression are high, and, given these orders are taken from a variety of situations, is a finding contrary to those of Collias (1943) and King (1965b). In addition, the aggressive dominance orders do generalise to other measures of dominance : the aggressive order (direction) derived from the Day 19 competitive drinking test shows the highest average number of significant correlations (71%) with other measures over all groups than any other single measure, although it was not possible to rank every animal in every group on this measure. Aggression in the stimulus animal tests was rare and therefore not a very efficient measure, although it correlates well with other aggressive orders and with orders derived from other methods of assessment.

The dominance orders based on submissive behaviour, both total and direction show poor, often negative correlations with each other, and, in general, show low efficiency in their ability to rank all animals in each regroup, apart from the submissive total order from the free social behaviour. The rarity of submissive behaviour in competitive and stimulus animal tests makes it impossible to assess the validity of submissive orders derived from these situations. The use of submissive orders in explaining dominance orders amongst a group of animals is limited by the fact that submissive behaviour rarely occurs, a fact also noted by Richards (1974). Whilst present findings cannot offer any serious criticism to the theory proposed by Rowell (1966) that the dominance order can best be explained by studying submissive behaviour, the use of submissive orders in explaining dominance orders amongst a group of animals is limited by the fact that submissive behaviour rarely occurs, at least in most situations. Unless one can measure submissive behaviour over a long time period, as here in the free social behaviour data, using submissive behaviour to explain dominance hierarchies could be a time-consuming activity!

Possibly the most useful method of measuring dominance hierarchies is an order based on performance in competitive drinking tests, using a 'time to accumulate 30 seconds of drinking time' as criteria for determining a dominance order. These measures are relatively efficient, on average ranking all animals in 70% of regroups, show the highest internal validity of any of the measures used in assessing the dominance order, and relatively high validity in terms of their correlations with other measures of dominance (averaging 58% over all 3 tests). It appears that priority of access measures of dominance do generalise to other methods of dominance assessment (Syme, 1974), and may therefore reflect a true dominance order rather than any individual differences in ability to control the food source. It can be argued that, if the definition of dominance includes a notion of 'priority of access to incentives' then it is only in a competitive situation that one can reasonably control the level of incentive (by using highly desirable food rewards). In other situations, different animals may have different incentives; one animal may like to groom a dominant, another may prefer not to, and the amount they groom may not be related to their dominance rank.

In summary, the success of the various measures of dominance seem to be dependent on the type of situation in which they are measured (competitive- or stimulus animal tests, or free social behaviour). The best method of assessment seems to be a rank order based on priority of access to a limited resource (bottle dominance test), then rankings based on measurement of aggressive behaviour (both direction and total), with affiliative and visual monitoring behaviour and submissive behaviour being the poorest measures of an underlying dominance hierarchy.

5.4.2. Are there any changes in the behaviour of the regroup animals over time?

An indication as to the presence or absence of behavioural stability of the regroupings can be obtained by studying the effects of weeks on behaviour. In all groups, the relative dominance hierarchy was established on Day 1, as assessed by the Day 1 milk bottle dominance tests, and remained stable throughout the period of the regroups (4 weeks) as assessed by subsequent competitive dominance tests (with which the Day 1 drinking order correlates highly for every regroup). The dominance hierarchy in each group was as predicted from the relative ranks in the group of 13, with the exception of regroups 8 and 9, when animal number 3, male, assumed the dominant position.

The effects of group formation and changes over time have been studied previously (Bernstein & Mason, 1963; Hawkes, 1970; Bernstein et al., 1974), and indicate that during the first few hours after group formation aggressive levels are high and affiliative interactions rare. As time progresses, so aggression and submissive behaviour decreases in frequency and other forms of social interaction (e.g., social grooming and huddling) increase. It should be noted that in the aforementioned studies, the animals comprising the newly formed groups were complete strangers until the point of group formation. In the present study all the animals had been living together for several years prior to the dominance manipulation, and in the majority of regroups, the dominance order conformed to the relative ranks of the animals in their stable group of 13. It might therefore be expected that aggressive, submissive and affiliative levels remain stable over the period of each regroup - the animals did not, in general, form different hierarchies, but retained their dominance positions relative to the other animals in the stable group. At best, it can be hypothesised that affiliative and disturbance behaviour levels might be temporarily altered by the regroup situations, and vary over time, as the animals are no longer living in their usual group of 13 animals, with its stable dominance hierarchy, patterns of affiliative relationships etc. It was important to establish whether there were any significant time effects on the behaviour of the animals in their regroup dominance positions as the weekly behavioural data is often used as repeated measures in many of the following analyses.

To test whether there are any significant changes in the behaviour of the animals in each regroup over the 4 week period for which each existed Friedman 2 way Anova's were computed. There were 3 separate analyses; analysis (1) tested for weeks effects, using data from all regroups (mean amount of fear, explore etc. summed over all animals in each regroup per week) except number 8b (with only 1 data point). Analyses (2) and (3) tested whether there were any effects of time in the first week of regroup establishment; it was hypothesized that the effects of regroup formation might be greatest in week 1. Separate analyses were run on 2 of the regroups, using animals x days 1 to 5. The two groups chosen were regroup 1 and regroup 8, the former chosen at random, the latter because in this regroup there was a dominance reversal which ran contrary to the order in the stable group of 13; it was reasoned that behaviour in the first few days in this regroup may parallel more closely than other more stable groups the behaviour in newly established groups of 'strangers' as reported by previous authors, as a new dominance hierarchy was being established, rather than one assumed from previous relative ranks. The results from these 3 analyses are given in Table 18.

As can be seen from the results of analysis (1), there are no weeks effects on any of the behaviours, suggesting the stability of the regroupings, with no decreases in, for example, amount of aggressive behaviour, or increases in affiliative behaviour. Analyses (2) and (3) show that for neither regroup 1 or regroup 8 are there days effects on behaviour in the first week of regroup formation. The results therefore do not support previous findings of changes over time in the behaviour of a newly established group of animals. This can perhaps best be explained by the fact that, contrary to other studies, the animals were well known to each other, and rather than establish new hierarchies (apart from regroups 8 and 9), maintained dominance positions relative to the other animals as in the stable group of 13 animals. By 'defaulting' to previous relative ranks, aggressive/submissive levels remain low and stable over time.

Table 18 Results of Friedman 2 way Anovas on effects of time

Behaviour	Analysis								
	(1) Regroups x weeks (9) (4)			(2) Regroup 1 x days (Week 1, days 1-5)			(3) Regroup 8 x days (Week 1, days 1-5)		
	χ^2	d.f.	p	χ^2	d.f.	p	χ^2	d.f.	p
Fear	0.15	3	n.s.	1.56	4	n.s.	1.86	3*	n.s.
Explore	1.08	3	n.s.	2.80	4	n.s.	3.36	4	n.s.
Play	0.30	3	n.s.	too infrequent			too infrequent		
Aggression	1.17	3	n.s.	0.54	4	n.s.	0.72	3*	n.s.
Affiliation total	4.44	3	n.s.	7.20	4	n.s.	2.88	4	n.s.
Sex	too infrequent			too infrequent			too infrequent		
Self	3.24	3	n.s.	9.28	4	n.s.	2.32	4	n.s.
Self aggression	5.76	3	n.s.	7.64	4	n.s.	2.34	3*	n.s.
Visual monitor	1.08	3	n.s.	1.28	4	n.s.	1.12	4	n.s.
Locomotion	3.48	3	n.s.	3.68	4	n.s.	2.52	4	n.s.
Behavioural change rate	3.0	3	n.s.	9.32	4	n.s.	0.92	4	n.s.

*analysis only possible on 4 days, since the s.d. on Day 1 was zero

5.4.3. Are there any significant differences between the regroups with respect to overall levels of fear, aggression etc.?

It may not be the case that the various regroups are directly comparable in terms of level of fear, affiliation etc. expressed in the regroup. If an individual's behaviour is a function of the particular situation (here, regroup), then we must determine the characteristics of the situation before we can conclude anything about an individual's personality. For example, we may find a high level of fear behaviour in one regroup as a result of there being a highly aggressive dominant in that regroup. In another regroup, the same animals may not show such high levels of fear behaviour, because the dominant of the regroup is less aggressive than in the former case.

To determine whether there were any differences between the various regroups in overall levels of fear, aggression etc. separate Friedman 2 way Anova's were run, using RD5 (5 dominance positions) x regroups (n=9, omits regroup 8b) for each behaviour (means over the 4 weeks per animal in each dominance position in each regroup). For some regroups there were missing data points for certain dominance positions: on the assumption of the null hypothesis 'no differences between groups' these points were substituted by the mean of the available data points for that dominance position, so as to maximise similarity between groups, rather than substitution by the mean of all other available data points for that group, which would maximise any apparent dissimilarity between the regroups. The results from these analyses are given in Table 19. Overall regroup means in Appendix 5.

From Table 19 it can be seen that there are no differences between the regroups except with respect to amount of affiliative behaviour , for which the regroups show significant differences. Can this difference be related to the composition of the regroups in terms of how dominant regroup members are in the stable group of 13?

Table 20 reports Kendall correlation coefficients between average dominance position in the group of 13 (D13) of each regroup and average amount of fear, explore etc. There are significant correlations between average D13 position and total affiliation (tau=-0.56, n=9, p=0.037) and total sex (tau=0.78, n=9, p=0.006), indicating that the regroups composed of more dominant animals in the group of 13 showed significantly higher mean levels of affiliation and significantly lower mean levels of sex than did regroups composed of more subordinate animals in the group of 13.

The difference in affiliation levels between the groups can be explained by a carry-over effect from the stable group of 13, where there is a significant correlation between dominance and 'sociability', the more dominant animals being the more affiliative animals, such that in the regroups composed of more dominant animals there is more affiliative behaviour.

Table 19 Results of Friedman 2 way Anovas, RD5 x regroups

Behaviour	χ^2	d. f.	p
Fear	6.49	8	n. s.
Explore	14.41	8	n. s.
Play	4.94	5*	n. s.
Aggression	12.93	8	n. s.
Affiliation total	19.43	8	0.013
Sex	1.14	3*	n. s.
Self	8.97	8	n. s.
Average D13	39.37	8	0.001

* indicates analysis only possible between some regroups

Table 20

Kendall correlation coefficients between average dominance rank in the group of 13 (D13) for each regroup x behaviour

2 tailed tests

Behaviour	Tau	n	P
Fear	0.39	9	n. s.
Explore	0.28	9	n. s.
Play	0.26	9	n. s.
Aggression	0.22	9	n. s.
Affiliation total	-0.56	9	0.037
Sex	0.78	9	0.006
Self	0.39	9	n. s.

5.4.4. How comparable are the regroups with respect to the correlations between dominance rank and behaviour?

To discover whether there were any differences between the regroups with respect to the correlations between behaviour and regroup dominance position individual Kendall correlation coefficients were computed for each regroup (omitting regroup 8b with only 1 data point) between RD5 (dominance position in the regroup) and free social behaviours. This sort of correlation will be referred to as 'relative correlation', where we are studying the correlation within regroups between dominance position and behaviour (i.e., the correlation relative to other animals in other dominance positions) rather than 'absolute correlation' which we will use to refer to the correlation within one individual animal between the various dominance positions he experiences and his behaviour in each of those positions; this notion of absolute correlation will be dealt with in Chapter 6). The results of the relative correlations are given in Table 21. With such a small number of data points (maximum=5, minimum (e.g., regroup 6b) = 3) it is difficult to achieve significance on a Kendall correlation. Nevertheless, the direction of each correlation coefficient can be combined into one analysis and a sign test computed to see if there is a significant trend for the correlations over all regroups for a given correlation between RD5 and behaviour to be positive or negative. The results of these sign tests are also in Table 21. If the results of the sign tests are significant then it shows that there is a significant trend over all regroups for

Table 21

Kendall correlation coefficients between RD5 and behaviour for each regroup

Regroup number	n	Behaviour Fear	Explore	Play	Aggression	Affiliation total	Sex
1	5	0.80*	-0.20	n.c.	-0.80*	-0.80*	n.c.
2	5	0.20	0.20	-0.12	-1.00*	0	n.c.
3	5	0.40	-0.20	-0.10	-0.80*	-0.40	n.c.
4	5	0	-0.20	-0.31	-0.74	-0.20	n.c.
5	5	0.74	-0.74	n.c.	0.53	0.10	n.c.
6b	3	0.33	-1.00	-1.00	-0.33	1.00	-1.00
7	5	0.40	0.40	n.c.	-0.60	-0.40	-0.63
8	3	0.33	-1.00	-0.33	-1.00	-0.33	-0.82
9	5	1.00*	1.00*	0.18	0	-0.33	0.18
Sign tests:							
x/n		0/8	3/9	1/6	1/8	2/8	1/4
sig. level		0.004	n.s.	n.s.	0.035	n.s.	n.s.

Regroup number	Self	Locomotion	displace	stereotypy	self aggression	behavioural change
1	0.60	0.4	-0.8*	0.6	-0.2	-0.6
2	-0.20	0.6	-1.0*	0.4	-0.2	-0.2
3	0.20	-0.2	-0.6	-0.2	0.2	0
4	0.40	-0.2	-0.7	-0.4	0.4	0.4
5	0.11	-0.6	-0.3	-0.8*	0.4	0
6b	1.00	-0.3	-0.3	-1.0	0.3	0.3
7	0.20	0.8*	-0.8*	0.5	-0.4	-0.8*
8	1.00	-1.0	-1.0	1.0	-0.3	-0.3
9	-0.33	0.7	-0.2	0.3	-0.7	1.0*
sign tests						
x/n	2/9	4/9	0/9	4/9	4/9	3/7
sig. level	n.s.	n.s.	p=0.002	n.s.	n.s.	n.s.

2 tailed tests   *p=<0.05   **p=<0.01
n.c. = coefficient not computable

the correlation coefficient between dominance rank and a given behaviour to be positive (or negative). If the results are not significant, then this shows that there is no universal trend over all regroups for a correlation (positive or negative) between dominance rank and behaviour.

It can be seen that for fear behaviour, there is a significant trend over all regroups for the correlation coefficients to be positive (mean tau = 0.47), although they were not significant for every individual regroup. Figure 9 is a graph showing the relationship between dominance position and amount of fear behaviour in 6 regroups. It can be seen that there is a trend for the more subordinate animals over all regroups to show higher levels of fear (x=0, n=8, p=0.004). Similarly for total aggressive behaviour and amount of displacement behaviour there is a significant trend over all regroups for the correlation coefficients to be negative (mean tau=-0.53), that is, for more dominant animals over all regroups to show higher levels of aggression (x=1, n=8, p=0.035) and more displacement behaviour(x=0, n=9, p=0.002). This is in keeping with the findings of Maslow (1936b) who reports, at least in pairings of unfamiliar rhesus monkeys, that aggressive behaviour is a characteristic of dominant animals, cringing and flight a characteristic of subordinates. It is contrary to the results using a stable and familiar group of animals as in P1 of this study, which found no relationship between aggression and dominance rank, although fear behaviours were not measured in P1. Figures 10 and 11 are graphs showing the relationship

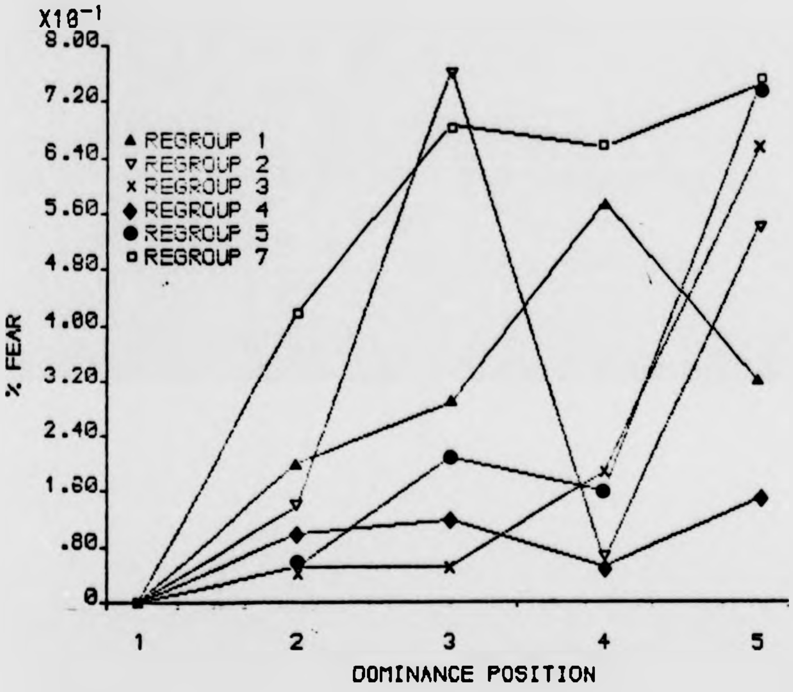


Figure 9 The relationship between amount of fear behaviour and dominance position within 6 regroups

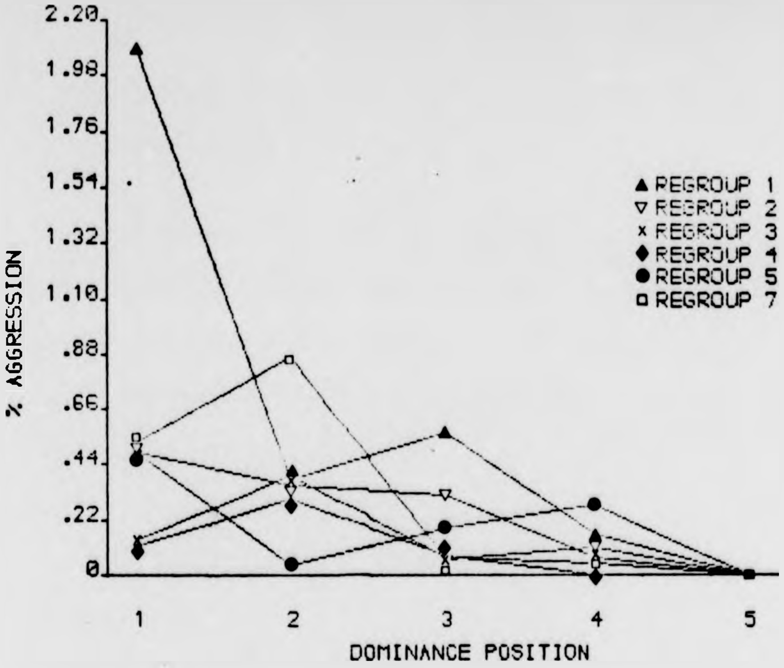


Figure 10 The relationship between amount of aggressive behaviour and dominance position within 6 regroups

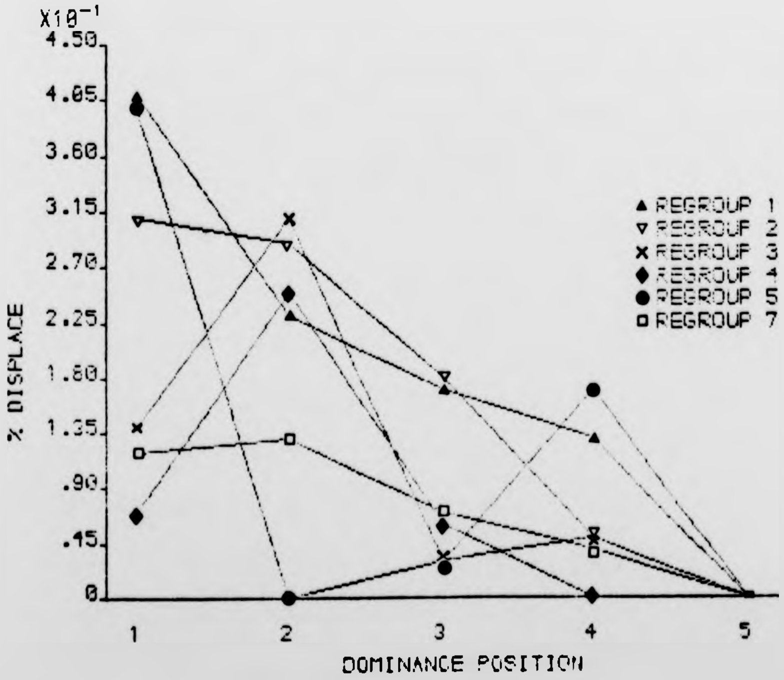


Figure 11 The relationship between amount of displacing behaviour and dominance position within 6 regroups

between dominance position and amount of aggressive and displacement behaviour for 6 regroups.

The correlations between dominance position and other behaviours (explore, play, affiliation, sex, self, locomotion, stereotypy, self-aggression, behavioural change rate) do not show any consistency over the different regroups - in some cases the correlation coefficients are positive, in others negative. Across the individual regroups, different trends (positive or negative correlation coefficients) may reflect regroup composition and the individual characteristics in the animals in those regroups, which will be discussed later.

5.5. <u>How successful was the manipulation of dominance positions in P2?</u>

In terms of expected and observed dominance positions within each regroup the manipulation appeared to have been successful, with most animals achieving and maintaining their dominance positions as predicted from their ranks relative to other animals in the stable group. As shown in Table 13, there are very few cases of dominance reversals. Animal number 8 dropped in rank in the group of 13 between the end of regroup 7 and the start of regroup 4, but her rank remained stable relative to the other animals thereafter. As might have been expected (Chamove & Bowman, 1976), animal number 3, a male, rose to the position of dominant in 3 out of the 4 regroups he was in. In regroup 7 animal number 3 remained at rank 4 - possibly the presence of animal number 13 (who was 4 ranks above him in the stable group of 13) prevented him dominating animal numbers 2 and 4 as he did in subsequent regroups. Instances of dominance reversals, either permanent or artifactual of the particular regroups resulted in the final data not being so complete as was initially desired; there were only 3 animals instead of 5 who occupied all 5 dominance ranks in the regroup phase, and 41 of a desired 45 data points. Decisions about subsequent regroup compositions after dominance reversals were made on the basis of maximising the number of available data points for final analysis.

In so far as maximising these data points, the manipulation can be regarded as successful. Another way of looking at the success of the manipulation is in terms of how well manipulating dominance position resulted in the emergence of the usually reported correlates of dominance/subordinance, viz. the correlation of dominance position with visual monitoring levels, aggression/submission levels etc. But it can be argued that any stability of these levels over manipulated dominance position does not reflect a failure to replicate previous correlates of dominance rank (and in any case, there is wide disagreement between previous findings) and thus a failure of the manipulation in these terms, but rather such stability demonstrates stable personality characteristics of the animals, which are unaffected by changes in the animals' dominance ranks. The manipulation did achieve successful dominance <u>position</u> manipulation in the majority of cases. As has been mentioned there were differences between newly established groups of 'strangers' and the animals used in this experiment, the regroups in this study being composed of well-acquainted animals, and the dominance hierarchies in the regroups generally 'defaulting' to relative ranks in the stable group. There has been no work done on manipulating dominance rank within a stable group, but it may well be that had the animals in the current study experienced varying dominance positions among groups of strangers then one might have seen evidence to support previous findings regarding the effects of group formation. It is arguable how different the social milieu was for the animals in the present study; rarely did they establish a new dominance hierarchy but simply interacted with a small subset from the usual group of 13 animals.

Evidence for the stability of the regroups comes from the analyses showing there were no significant changes in the aggressive/affiliative etc. levels of the animals in the regroups over the 4 weeks for which each existed or over the 5 days of week 1 (section 5.4.2). Further evidence for the stability comes from studying the relationship over regroups between dominance rank and behaviours previously thought to be dominance linked. The trend over all regroups for more dominant animals to exhibit more aggressive behaviour has been reported (and supports the review by Syme, 1974) as has that for more subordinate animals to show more fear behaviour (supporting Maslow, 1936b; Rowell, 1966). However, Rowell (1966) stresses that it is the submissive behaviour of the subordinate animal which is the best indicator of the establishment of dyadic dominance rank and not the aggressive behaviour of the dominant.

Table 22 reports the % fear and % aggression shown between pairs of adjacent animals in 9 regroups - the % fear shown by the subordinate of the pair to the dominant and the % aggression shown by the dominant to the subordinate. The result of a t test, comparing the amount of fear/aggression within dyads, also reported in Table 22 is not significant and there is thus no evidence to support Rowell's idea that it is submissive behaviour on the part of the subordinate animal that is the best indicator of an established dyadic dominance relationship; in some dyads there was more aggression shown by the dominant to the subordinate than fear by the subordinate to the dominant - in other dyads the reverse was true.

Table 23 reports of the results of Kendall correlation coefficients for each regroup between dominance position and various other behaviours which have been considered to be dominance linked - visual monitoring, present for groom and receive affiliation. Also reported are the results of sign tests carried out on the positivity or negativity of these coefficients over all regroups. From Table 23 it can be seen that there is no significant trend over all regroups for more subordinate animals to exhibit higher levels of visual monitoring behaviour, contrary to the findings of Chance (1967) and Keverne et al. (1978), and contrary to the findings of P1 of this study, where the 2 measures of visual monitoring levels loaded highly on the 'dominance' factors in both factor analyses, indicating that more subordinate animals did more. Crawford (1942) reports that subordinate animals were never

Table 22 Percentage of fear and aggression shown between adjacent pairs of animals in the regroup phase

Regroup number	Animal numbers dom/sub		% aggression from dominant to subordinate	% fear from subordinate to dominant
1	15	17	0.67	0.75
	17	5	0.28	0.61
	5	11	1.06	0.77
	11	10	0.65	0.11
2	17	5	0.65	0.34
	5	11	0.78	1.34
	11	10	0.66	0
	10	13	0	0.25
3	5	11	0.21	0.06
	11	10	0.08	0.19
	10	13	0	0.19
	13	8	0	1.64
4	11	10	0	0
	10	13	0	0.16
	13	8	0	0
	8	2	0	0.24
5	10	13	0.72	0.08
	13	8	0	0
	8	2	0.08	0.30
	2	4	0.79	0.69
6b	8	2	0.44	1.41
	2	4	0.91	0
7	13	2	0.56	1.48
	2	4	0.13	0.47
	4	3	0.26	0.12
	3	25	0	0.10
8	25	27	0.15	0.31
9	4	25	0	0
	25	27	0.06	0.42
	27	6	0	1.82

t test, comparing amount of aggression shown by dominant of the pair to subordinate with amount of fear shown by subordinate to dominant (paired test), $t = 0.45$, $p>0.05$

Table 23 **Kendall correlation coefficients RD5 x behaviour**

1 tailed tests *p=<0.05 **p=<0.01
n.c. = coefficient not computable

Regroup number	n	Behaviour Visual monitor	Present for groom	Receive affiliation
1	5	0	0.12	-0.20
2	5	0	-0.32	0.40
3	5	-0.40	n.c.	-0.20
4	5	-0.40	-0.53	0
5	5	-0.74	0.32	0.32
6b	3	-1.00	0	0.33
7	5	0.60	-0.11	0
8	3	-1.00	n.c.	-1.00
9	4	0.67	0.18	-0.67
sign tests:				
x/n		2/7	3/6	3/7
significance level		n.s.	n.s.	n.s.

seen to present for grooming, whilst 'we never saw a dominant do this and be refused'. The data from the present study does not support this finding - there is no significant trend over all regroups for the more dominant animals to present for grooming more than the subordinates. However, Crawford's study was with pairs rather than groups of animals, and is contrary to the finding of Bernstein & Mason (1963) who found no consistent relationship between grooming and social status, with the roles of groomer/groomee showing no consistent link to the relative dominance of the two animals.

P1 of the current study had indicated a significant correlation between dominance and the amount of affiliation received. (The correlation between 'receive groom' (Fbegm) and dominance rank was -0.44, that between 'receive huddle' (Fbehud) -0.72, n=13, p<0.05, see Table 5). In P2 however there was no consistent trend over all regroups for dominant animals to receive more affiliative behaviour, and thus no support for the greater attractiveness of dominant animals over subordinates in the regroups. Neither was there any evidence that the more subordinate animal of a dyad groomed his superior more than vice-versa; Table 24 shows the % grooming within adjacent pairs of animals in 9 regroups, and the result of a t test comparing the % grooming by the subordinate of the dominant with that of the dominant of the subordinate in each adjacent pair, which is not significant. Thus there is no evidence of a clearly established dyadic grooming relationship (contrary to Simpson's 1973 finding in chimpanzees).

Table 24 Percentage grooming between adjacent pairs of animals in the regroup phase

Regroup number	Animal numbers dom/sub		% grooming from dominant to subordinate	% grooming from subordinate to dominant
1	15	17	25.7	44.2
	17	5	27.4	9.1
	5	11	15.6	34.0
	11	10	13.3	0.9
2	17	5	7.1	1.5
	5	11	10.8	10.5
	11	10	25.6	2.4
	10	13	0.2	3.0
3	5	11	24.5	34.7
	11	10	51.5	2.5
	10	13	0.4	49.0
	13	8	5.5	0
4	11	10	14.3	3.7
	10	13	1.2	46.6
	13	8	2.6	0
	8	2	3.6	0
5	10	13	4.5	26.6
	13	8	15.8	0
	8	2	0	0
	2	4	5.5	23.7
6b	8	2	0	0
	2	4	30.5	17.1
7	13	2	8.0	3.2
	2	4	2.2	6.8
	4	3	17.1	0
	3	25	0	0
8	25	27	5.4	3.2
9	4	25	15.6	3.5
	25	27	8.7	40.7
	27	6	0	0

t test, comparing amount of grooming shown by dominant of the pair to subordinate with amount of grooming shown by subordinate to dominant (paired test), $t = 0.22$, $p > 0.05$

It appears as if manipulating dominance position within a stable group of 13 animals does not produce results to support previous findings of the relationship between dominance position and certain behaviours (visual monitoring, affiliation patterns). Some behaviours, such as levels of fear, aggression do seem to be dominance linked, at least in the manipulation phase.

The results from P1 indicated no significant correlation between dominance position and aggression (Table 9, correlation of Abe-ve, Jbe-ve and J1be-ve with D13 are not significant, although negative, indicating a slight trend for dominant animals to be more aggressive). It may be that aggression (and perhaps fear, although this was not measured in P1) in the manipulation phase is the result of that manipulation; in the regroups, the dominant animals assert their newly-found positions by aggression, with a corresponding effect of submissive and fearful behaviour on the part of the subordinates. Maslow (1936b) constructed a linear hierarchy of rhesus monkeys, based on their behaviour in pairs. On placing these individuals together in one large group, he stated that 'new behaviour emerged that was unpredictable from the data on pairings, since certain behaviours are the function of the size of the group' (p. 197). This was certainly the case in the present study; the formation of regroups resulted in a significant correlation between dominance rank and aggressive levels, a relationship not found in the stable group of 13 animals. This demonstrates the importance of the social situation in which an animal finds himself and the effect of the situation on the expression of certain behaviours.

It appears that the manipulation phase, whilst altering absolute dominance (in that an animal experienced up to 5 different positions in groups of 5) did not for the most part alter behavioural correlates of dominance, as reported by previous experimenters. Within each regroup there was a certain amount of assertiveness in the form of aggressive/dominance behaviour, which did correlate with dominance position, and a corresponding expression of fear/subordinate behaviour, correlating with subordinance.

Of course, it may be that stability of behaviour over changing dominance position reflects stable personality characteristics of the individual animals. After all, dominance <u>position</u> did change, even if behaviours previously considered to be dominance <u>linked</u> did not. We will return to the notion of personality in Chapter 7.

Chapter 6 THE USE OF DOMINANCE AS AN EXPLANATORY VARIABLE

6.1 Does dominance rank correlate with behaviours within individual animals?

Chapter 5 evaluated the various methods of dominance assessment and studied the relationship between dominance rank and behaviour within groups of animals. Correlations between RD5 and behaviour within and over all regroups will indicate the presence or absence of the relative correlation within regroups between RD5 and behaviour. For example, in the relative correlation analyses there is evidence for a relative correlation between RD5 and fear behaviour over all regroups, indicating that relative to other animals in the regroups the subordinate animals show higher levels of fear. In the same analyses there is evidence that relative to more subordinate regroup members, the dominant animals show more displacement behaviour and more aggression (total). Whether such correlations hold within animals (as opposed to within groups of animals) is another question. Does an animal display more fear behaviour and less aggression when subordinate than when dominant? We will call this 'within-animal' correlation 'absolute' correlation. It is evident that the presence of relative correlation between RD5 and a given behaviour does not entail the presence of absolute correlation. An animal may show more fear behaviour when subordinate relative to other more dominant regroup members but this high level of fear may be situation dependent (perhaps as the result of a highly aggressive, more dominant animal in that regroup), and therefore there may be no correlation within that individual animal between fear behaviour and subordinance over all RD5 positions.

In order to determine the absolute correlation within individual animals between changing dominance position and behaviour, individual Kendall correlation coefficients were computed between RD5 and each behaviour for each of the 11 animals who experienced at least 2 regroup dominance positions. These are reported in Table 25.

From Table 25 it can be seen that there are few correlations between RD5 and behaviour for individual animals which reach significance ($p<0.05$) perhaps partly due to the small n involved in most of the coefficients. However, the direction, +ve or -ve , of the coefficients can be combined to determine whether there is a significant trend over all animals for them to show more, or less of a given behaviour over changing dominance position. Table 25 also reports the results of sign tests which show that such a trend is only significant for fear behaviour; over all animals there is a trend for an absolute correlation between RD5 and amount of fear behaviour, all animals when more subordinate showing more fear than when dominant ($x=0$, $n=10$, $p<0.001$). Figure 12 is a graph of the relationship between amount of fear and RD5 for 8 animals (those who occupied at least 3 regroup dominance positions). It will be remembered (see Table 21) that fear behaviour also shows a relative correlation with RD5, that is, compared to other regroup members, subordinates show more fear behaviour. In contrast, aggressive behaviour shows an absolute correlation with RD5 within and across regroups, but

Table 25 Kendall correlation coefficients between rd5 and behaviour for each individual animal

*p=<0.05

Behaviour		Fear	Explore	Play	Aggression	Affiliation			Sex	Self
						init	rece	total		
Animal	n									
17	2	1.0	1.0	n.c.	1.0	1.0	1.0	1.0	n.c.	-1.0
5	3	1.0	1.0	n.c.	1.0	-0.3	0.3	-0.3	n.c.	0.3
11	4	0.3	0.7	-0.2	0	0.7	0	-0.3	n.c.	0
10	5	0.2	-0.2	-0.3	-0.8*	-0.6	0.2	-0.2	n.c.	0.6
13	5	0.8*	0.2	0.3	-0.6	0	0	-0.8*	-0.6	-0.2
8	4	0.3	-1.0*	n.c.	-0.9	-0.7	0	-0.3	n.c.	0.7
2	5	0	-0.2	n.c.	-1.0*	0.8*	0.2	0.2	n.c.	0.2
4	4	0.3	0	n.c.	-0.2	0	0.7	0	n.c.	-0.3
3	2	1.0	-1.0	-1.0	-1.0	1.0	-1.0	1.0	-1.0	-1.0
25	3	1.0	0.3	-1.0	-1.0	-1.0	-1.0	-1.0	-0.8	1.0
27	2	1.0	1.0	-1.0	-1.0	-1.0	-1.0	-1.0	n.c.	1.0
sign tests x/n		0/10	4/10	1/6	2/10	4/9	3/8	3/8	0/3	4/10
significance level		0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Behaviour	visual monitor	locomotion	displace	stereotypy	self aggression	behavioural change	present for groom
animal number							
17	-1.0	-1.0	1.0	1.0	-1.0	1.0	n.c.
5	1.0	1.0	0.3	1.0	0.3	-1.0	0.3
11	0.7	0.7	0	0.3	0.7	0.7	-0.2
10	-0.4	0	-0.8*	0.2	-0.4	0.4	-0.3
13	0.2	0.4	-0.5	0.6	0.2	-0.4	-0.6
8	-0.7	-0.7	-0.9*	-0.7	0.3	0.7	n.c.
2	0	-0.4	-0.6	-0.2	0	0.4	-0.2
4	-0.3	0	-0.2	0	-0.7	-0.3	n.c.
3	-1.0	-1.0	-1.0	1.0	-1.0	1.0	1.0
25	1.0	1.0	-1.0	1.0	-0.3	-0.3	-0.8
27	1.0	1.0	n.c.	-1.0	-1.0	1.0	-1.0
sign tests x/n	5/10	4/9	2/9	3/10	4/10	5/11	2/8
significance level	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

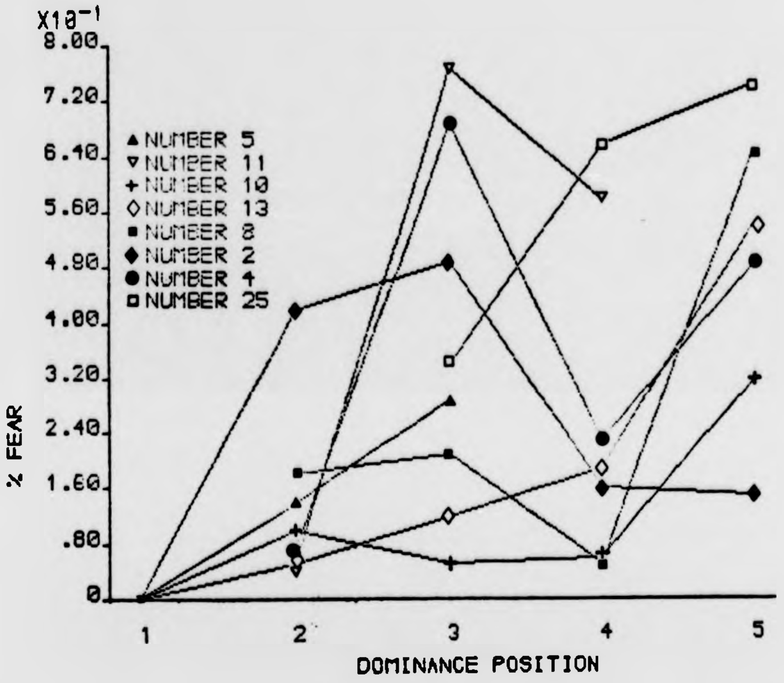


Figure 12 The relationship between amount of fear behaviour and dominance position within 8 animals

no relative correlation within and across animals ($x=2$, $n=10$, $p>0.05$). Thus it may be said that while animals change the amount of aggression they show according to their dominance position in a particular regroup relative to other animals in the group, relative to their own levels of aggression in the dominance positions they experience there is no correlation with dominance position.

Of course, since dominance rank is a relative term, there is no reason why we might expect to find evidence of absolute correlation between dominance rank and behaviour within individual animals. As an animal rises in dominance position there is no justification for expecting that his aggressive levels will rise in a similar fashion; all that is important for the maintenance of his particular dominance rank within a particular group is that he is relatively more aggressive than his subordinates.

6.2 Do dominance ranks have any explanatory use?

While most researchers agree that dominance/subordinance may prove useful concepts in explaining dyadic interaction patterns, there is doubt as to the usefulness of dominance ranks within a group of animals - whether assigning numbers (ranks) to animals can aid the description of social behaviour. Bernstein (1981) deals at length with this point; 'Until we can show that there is some communality among animals ranked number 7 in different groups numerical rankings remain an abstraction of questionable utility...We have little evidence that any specific rank causes an individual to behave in a specific fashion, or that knowledge of numerical ranks allows us to accurately predict the behaviour of specific individuals' (p. 428).

Previous analyses (Section 5.4.4) have shown that there is a degree of communality between animals of the same ranks in different groups; dominant animals are more aggressive than subordinates, and subordinate animals are more fearful than dominant animals. Bernstein appears to confuse the issue of the usefulness of ranks by overlooking 2 points; firstly, the idea of communality between the behaviour of animals occupying identical ranks in different groups ignores the individual differences which may play a part in each animal's behaviour (this will be discussed in Chapter 7). Secondly, while we may not be able to accurately predict the behaviour of specific individuals (e.g., such that we can predict that a dominant will be aggressive 50% of the time, or a number 2 ranked animal 25% of the time) since dominance is a relative term we can only expect to predict <u>relative</u> behaviour (e.g., that a dominant may be relatively more aggressive than a more subordinate animal). This distinction is evident from the data in the present study. As will be shown in Chapter 7, there is no communality among dominant animals in their regroups with respect to aggressive behaviour - some animals, as dominants, are significantly more aggressive than others. Yet relative to the other animals in the regroups the dominant animals are always more aggressive than the subordinates (sign test on correlation coefficients between dominance rank and aggression over 8 groups: $x=1$, $n=8$, $p=0.035$). While we may be unable to predict the absolute levels of aggression that an animal will show in a given dominance position, we can at least predict aggression levels relative to other animals in the same group. To expect animals in identical dominance positions across different groups to show exactly X% aggression or Y% affiliation is too simplistic. There is no a priori reason why different dominant animals in different groups should be X% aggressive, as long as they are aggressive enough to maintain their position of dominance in situations where it is challenged.

It has been demonstrated that there are communalities in behaviour between animals of the same rank in different regroups, if only relative to other group members (i.e., with respect to aggression, fear). Perhaps other communalities exist that are not linearly related to dominance rank. It is possible to test for significant differences between animals of different dominance positions over groups. Friedman Anovas were computed to test for behavioural differences between animals in the 5 regroup dominance positions over 6 regroups, numbers 1,2,3,4,5,7 (for which data was collected on all 5 animals in each regroup). Thus the analysis compares all rd1's over the 6 regroups with the rd2's,rd3's,rd4's and rd5's in those regroups. Ideally the population of animals comprising each dominance position should be identical, as any significant differences in behaviour between dominance positions may be due to population (sampling) differences. This would result in us overestimating the significance of the treatment (dominance position) effects. However, this overestimation may be partly counter-balanced by the fact that several animals occur in several dominance positions (e.g., animal numbers 10 and 13 occur in all 5 dominance ranks); if significant differences do emerge then it might be reasoned that treatment effects (dominance position) are powerful enough to override stable personality characteristics (we might expect, if animal number 13 is a fearful animal by nature, for her to be ranked the most fearful animal in every group regardless of her dominance rank in those groups). This test can therefore be viewed as a test of the relative stability of behaviour over animals in the 6 regroups with regard to dominance position, not with regard to particular animals (as in Chapter 7, where individual Friedman Anovas are worked for each animal over changing dominance position). The results are given in Table 26, and means in Appendix 6.

It can be seen that there are significant differences between the behaviour of animals occupying different dominance positions in the 6 groups for the amount of fear behaviour, aggression, self-directed behaviour and displacements expressed by the animals occupying those positions. The amount of fear behaviour in each group increases with increasing subordinance (in the order rd5, rd3, rd4, rd2, rd1, according to rank sums) while the amount of aggression and displacing decreases (in the order rd1, rd2, rd3, rd4, according to rank sums). Rd5 animals in the regroups show the most self behaviour, then rd1 animals, rd3, rd4, with rd2 animals showing the least (based on rank sums). Figure 13 is a graph of the relationship between amount of self behaviour for 8 animals. The analysis for total affiliation just fails

Table 26 **Do animals of different dominance position within groups behave significantly differently?**

Friedmans Anovas, dominance position (n = 5) x groups (n = 6)

*p<0.05

Behaviour	χ^2	d. f.
Fear	9.8*	3
Explore	3.8	4
Aggression	10.4*	3
Affiliation		
total	8.9	4
initiate	4.9	4
receive	7.6	4
Self	10.8*	4
Self-aggression	2.3	4
Behavioural change	2.0	4
Stereotypy	1.2	4
Displace	10.4*	3
Locomotion	4.1	4
Visual monitor	2.1	4

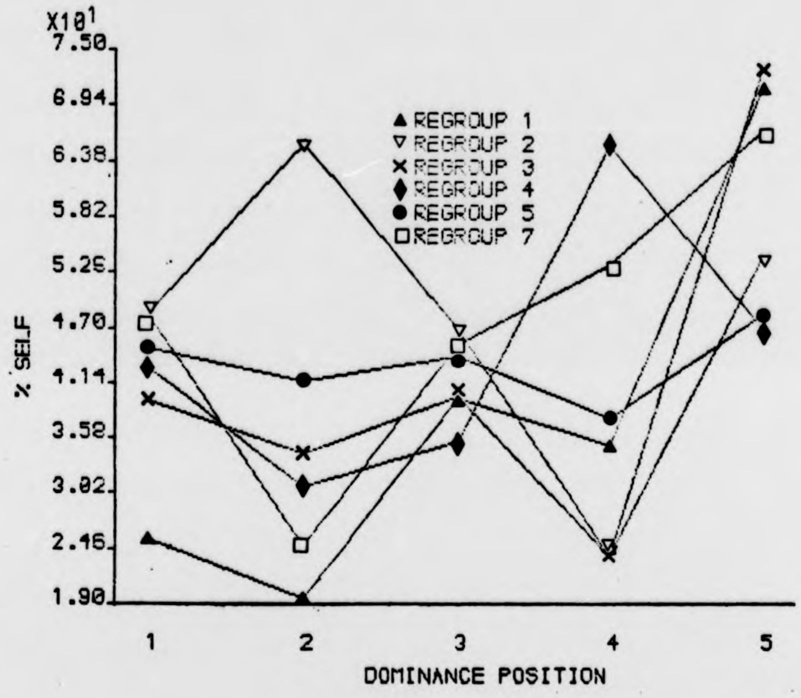


Figure 13 The relationship between amount of self behaviour and dominance rank within 6 regroups

to reach significance, although rd2/rd3 animals show equally high levels, followed by the rd1/rd4 animals, with animals occupying rd5 positions within regroups showing the least amount of affiliation. There are no significant differences between the behaviour of animals in different dominance positions within regroups with respect to amount of exploratory behaviour, self-aggression, behavioural change, stereotypy, locomotion, visual monitoring, affiliation initiate and affiliation receive, suggesting that these these behaviours are not dominance-related. However, Bernstein's (1981) criticism that 'it has not been demonstrated that the particular behavioural propensities of animals in their group are a function of their rank in their group' is not true, at least with respect to some behaviours. Relative to other animals the amounts of fear, aggression, self and displacing shown by animal number 13 is different from the levels expressed by other animals in the same regroups in every dominance position she occupies.

6.3 Are dominance ranks important for the interaction between animals in particular groups?

While dominance ranks may prove useful to human observers in aiding the description of primate behaviour is there any evidence that dominance ranks have any meaning to animals within a dominance hierarchy? Are animals capable of making anything other than the gross discrimination of 'who's above' and 'who's below' them? Section 5.4.4. showed that, at least relative to other animals in a group a dominant is more aggressive and a subordinate more fearful than animals of other ranks. Do animals respond differentially to other animals according to the dominance rank of those animals? - or as Seyfarth (1981) aptly questions 'Do group-living animals rank each other?'. In an earlier paper (Seyfarth, 1976) on free-ranging ursinus baboons (P. cynocephalus ursinus) it would certainly appear that animals are indeed capable of 'ranking' each other, at least with respect to grooming solicitations amongst females; individuals showed a clear preference for grooming more dominant animals and the rank hierarchy of their preferred groomees was consistent with the dominance ranks that Seyfarth had drawn up on the basis of approach-retreat interactions. 'Thus by responding in this way, females revealed that they had gone beyond the simple discrimination of 'dominant to me' versus 'subordinate to me' and created a true rank hierarchy of individuals' (Seyfarth, 1981, p.447). Stammbach (1978) found that the greater the difference in rank between 2 female hamadryas baboons (P. hamadryas) the greater the proportion of grooming done by the lower ranking female of the higher ranking. Similar data indicating that monkeys are capable of ranking each other can be found in Gouzoules (1974) with respect to the amount of sexual harrassment received by stumptailed macaques (more dominant females receive more) and in Cheney (1978) with respect to play in ursinus baboons (where the attractiveness of an infant as a play partner was positively correlated with his mother's dominance rank).

Using Friedmans Anova it is possible to test whether animals respond significantly differently to other animals in other dominance positions in the same regroups. This was done with respect to several interaction patterns; amount of presentation to another animal, amount of fear, visual monitoring, grooming, aggression and displacing directed towards that animal, for all rd1 animals, all rd2, rd3, rd4 and rd5 animals (n.b., some analyses not possible - e.g., rd4 animals only aggressed rd5 animals, and rd5 animals aggressed no animals). The rationale behind the selection of these particular behaviours was that the dominance hierarchy of the group might be revealed in the amount of interaction between the various dyads of animals. A dominant animal may be the most aggressive and assertive, (i.e., in the form of number of displacements of a particular animal), towards the second most dominant animal in his group, as the rd2 animal is the closest to him in rank and may offer the most serious threat to his dominant status. Similarly, a subordinate animal may show the greatest fear of, the greatest visual monitoring of and present the most to the most dominant animal in the group (since, as has been demonstrated, the dominant is relatively the most aggressive animal in the group). An rd3 animal may preferentially groom the most dominant animal above all others in the group (Seyfarth, 1976). Again, the criticisms of the present analyses are the same as in the analyses performed testing for relative consistency within groups. Note that in the current analysis the population of animals comprising each dominance rank within each group for each animal is different; when dominant, the number 2 animal in animal number 15's group was number 17; when number 17 was dominant, the number 2 animal in her group was animal number 5. If differences emerge, they could be due to population differences, rather than to treatment effects (the dominance ranks occupied by the 'target' animals). This is counterbalanced by the fact that some animals occur as 'target' animals in several dominance positions; if, say animal number 13, is particularly 'attractive' regardless of her dominance rank, then this would tend to reduce the likelihood of obtaining significant differences between the amount of affiliation directed to animals of particular dominance ranks. Results in Table 27, means in Appendix 7.

The results show that, at least for some behaviours when occupying some dominance positions, animals do indeed behave significantly differently to other animals. When in position rd2, animals direct significantly different amounts of visual monitoring to animals in position rd1 (most), rd3 (next most), rd4 (next) and rd5 (least). Figure 14 is a graph illustrating the relationship between amount of visual monitoring that rd2 animals direct to other animals of different ranks. Similarly when occupying position rd3, there are significant differences between the amount of visual monitoring animals do of other animals in positions rd1, rd2, rd4, rd5 (most to least). Figure 15 illustrates the relationship between the amount of visual monitoring that rd3 animals direct to other animals of different rank. The differences in visual monitoring levels of other animals in the group when an animal is in position rd1, rd4 or rd5 are not significant. Yet when in position rd2

Table 27 **Do animals behave significantly differently to animals of differing rank?**

Friedmans Anovas. 'target' animal's dominance position (n = 4) x your dominance position

*p<0.05 **p<0.01 n.c. = not computable

(i) all dominant (rd1) animals. n = 8. Behaviour to rd2, rd3, rd4 and rd5 animals

Behaviour	x2	d.f.
Fear of	n.c.	
Present to	n.c.	
Visual monitor	5.55	3
Groom	10.65**	3
Aggress	0.56	3
Displace	3.90	3

(ii) all rd2 animals. n = 8. Behaviour to rd1, rd3, rd4 and rd5 animals

Behaviour	x2	d.f.
Fear of	n.c. (only show fear to rd1)	
Present to	n.c. (only present to rd1)	
Visual monitor	12.15**	3
Groom	11.50**	3
Aggress	0.44	2
Displace	0.25	2

(iii) all rd3 animals. n = 8. Behaviour to rd1, rd2, rd4 and rd5 animals in their respective regroups.

Behaviour	x2	d.f.
Fear of	0.00	1
Present to	0.50	1
Visual monitor	13.90**	3
Groom	1.76	3
Aggress	0.00	1
Displace	1.10	1

(iv) all rd4 animals. n = 9. Behaviour to rd1, rd2, rd3 and rd5 animals in their respective groups.

Behaviour	x2	d.f.
Fear of	0.06	2
Present to	0.66	2
Visual monitor	1.67	3
Groom	2.23	3
Aggress	n.c. (d.f. n-1=0)	
Displace	n.c. (d.f. n-1=0)	

(v) all rd5 animals. n = 8. behaviour to rd1, rd2, rd3 and rd4 animals

Behaviour	x2	d.f.
Fear of	0.86	3
Present to	1.31	2 (no presenting to rd2 animals)
Visual monitor	4.65	3
Groom	3.64	3
Aggress	n.c.	
Displace	n.c.	

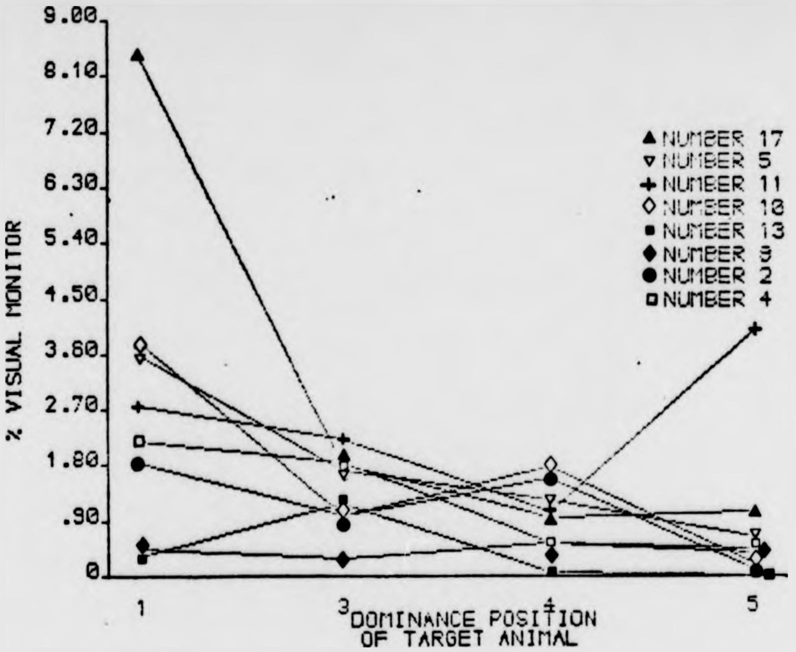


Figure 14 The amount of visual monitoring by Rd2 animals of animals in other dominance positions in the same regroups

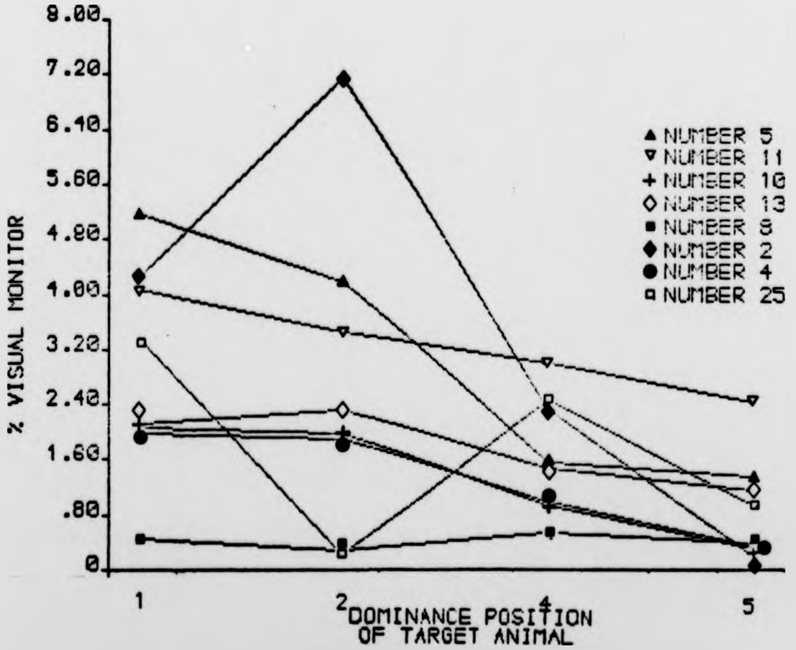


Figure 15 The amount of visual monitoring by Rd3 animals of animals in other dominance positions in the same regroups

or rd3 an animal will visually monitor other animals to a level commensurate with the latters' rank. Keverne et. al (1978) report that the animals receiving most visual monitoring in groups of talapoin monkeys are not necessarily the most aggressive animals but are high ranking. Previous analysis (section 5.5) found no significant correlation between dominance rank and amount of visual monitoring; evidently it is the direction and not the total of visual monitoring which may be a better indicator of an underlying dominance hierarchy (at least be observing the visual monitoring behaviour of animals in positions rd2 and rd3).

There is also evidence from the data on grooming behaviour that animals 'rank' each other. The rd1 animals show significant differences between the amount of grooming they direct to rd2, rd5, rd4 and rd3 animals (most to least, see Figure 16), and rd2 animals differentiate between rd3, rd1, rd4 and rd5 animals (most to least, see Figure 17). The trends do not conform to Seyfarths (1977) 'attractiveness' hypothesis as neatly as that of the visual monitoring data to Keverne et al's (1978) findings. Rd1 animals groom rd5 animals more than rd4 and rd3 animals (although being the most 'attractive' themselves may be the reason why the attractiveness hypothesis fails here). Rd2 animals groom rd3 animals more than rd1 animals; on the attractiveness hypothesis one would predict the reverse to be the case.

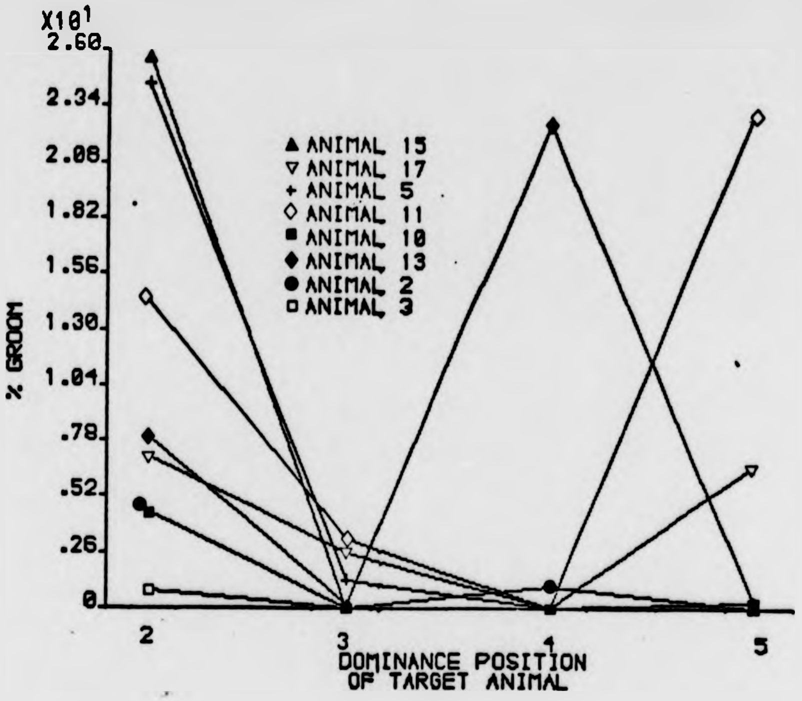


Figure 16 The amount of grooming done by Rd1 animals of animals in other dominance positions in the same regroups

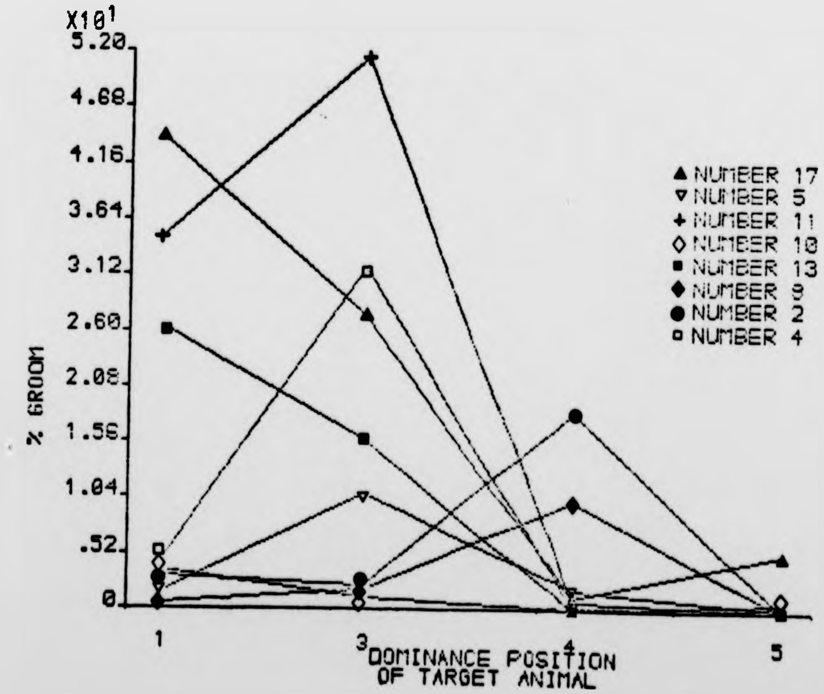


Figure 17 The amount of grooming done by Rd2 animals of animals in other dominance positions in the same regroups

There is no evidence in the present study that animals responded differentially to others in their groups with respect to the amount of fear, presentation, aggression and displacements directed to animals in specific dominance ranks.

Even if we cannot explain why animals, at least in some dominance positions, with respect to some behaviours, respond significantly differently to other animals depending on the latter's rank, the dismissal by Bernstein (1981) that 'dominance rankings may reflect our ability to count rather than any important variable in social organisation' (p. 419) seems unwarranted. It does appear to be the case that animals 'rank' each other, although such rankings may not be evident throughout all social interaction patterns and for all dominance positions, but, given that dominance is only one of a number of factors influencing interactions (see Section 1.7) there is no reason to expect dominance to be a universally influential phenomena.

Chapter 7 THE EVIDENCE FOR PERSONALITY DIMENSIONS

7.1 Are there significant differences between the animals when occupying the same dominance positions?

One way of studying individual differences between the animals is to compare the behaviour of different animals when occupying identical dominance positions. If dominance rank is an important variable affecting an individual's behaviour then we cannot infer anything about the personality of animals from observing each animal in one particular dominance position (as was done in P1), But if we can observe all animals in the same dominance positions we can then hold constant one variable (dominance rank) which influences behaviour and investigate another variable which may have an important effect on behaviour - personality. We can then identify individual differences in the behaviour of animals when occupying identical dominance ranks (e.g., the levels of aggression of dominant animals, or the levels of fear of subordinate animals).

To determine individual differences in behaviour in identical dominance positions Friedman 2-way Anova's were computed for various behaviours for each dominance position in P2, animal's x weeks (i.e., each animal's weekly score on a particular behaviour). Means (over all 4 weeks per animal for each regroup dominance position he occupied) are given in Appendix 3, results of the Friedman Anova's in Table 28. Due to the nature of the data, different populations of animals comprise each dominance position (see Table 14), although there is a considerable degree of overlap.

Table 28 Results of Friedman Anovas, animals x weeks for each regroup dominance position

n.c. = not computable   *p=<0.05   **p=<0.01
~ = analysis only possible on a subset of animals

Behaviour	Regroup dominance position 1		2		3		4		5	
	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.
Fear	n.c.		6.56	7	11.10	7	17.15*	8	5.13	7
Explore	16.25*	7	6.50	7	11.92	7	17.07*	8	14.17*	7
Aggression	23.06**	7	8.17	6~	13.31	7	7.42	7~	n.c.	
Affiliation (total)	19.67**	7	15.92*	7	8.25	7	14.73	8	18.52**	7
Affiliation (initiate)	11.08	7	15.67*	7	5.19	7	22.15**	8	19.44**	7
Affiliation (receive)	18.15*	7	14.67*	7	14.17*	7	16.22*	8	20.77**	7
Self	5.83	7	22.33**	7	3.75	7	17.46*	8	10.83	7
Visual monitor	20.08**	7	6.92	7	8.83	7	18.93*	8	16.67*	7
Locomotion	15.50*	7	12.08	7	15.42*	7	16.00*	8	18.00*	7
Displace	15.65*	7	2.39	7	7.12	7	6.25	8	n.c.	
Stereotypy	9.75	5~	12.58	7	12.89*	5~	16.87*	7~	20.67**	7
Self-aggression	12.25	7	19.67**	7	18.06*	7	14.72	8	21.60**	7
Behavioural change rate	7.22	7	8.75	7	13.08	7	22.67**	8	14.83*	7

From Table 28 it can be seen that there are significant differences between the animals for some behaviours for some dominance ranks, but that the only behaviour showing consistent differences between the animals at every dominance position is 'affiliation receive', that is, at all regroup dominance positions there were significant differences between the amount of affiliation each animal received in comparison to other animals who experienced that same dominance position, reflecting individual differences in the attractiveness of the animals. Figure 18 is a graph showing the amount of affiliation received by 8 animals over the various dominance positions each animal experienced. Significant differences are also apparent between the amount of fear behaviour shown by the animals, but only between those animals who occupied position rd4. There are also significant differences between the amount of exploratory behaviour shown by the animals who occupied positions rd1, rd4 and rd5 (see Figure 19), aggressive behaviour in position rd1, affiliation (total) in rd1, rd2, rd5; affiliation (initiate) in positions rd2, rd4, rd5; self behaviour in rd2, rd4. There are also significant differences between animals in various dominance positions for the following sub-behaviours; visual monitoring behaviour in positions rd1, rd4, rd5; locomotion in rd1, rd3, rd4, rd5; displace in rd1; stereotypy in rd3, rd4, rd5; self-aggression in positions rd2, rd3, rd5; behavioural change rate in positions rd4, rd5 (see Figure 20).

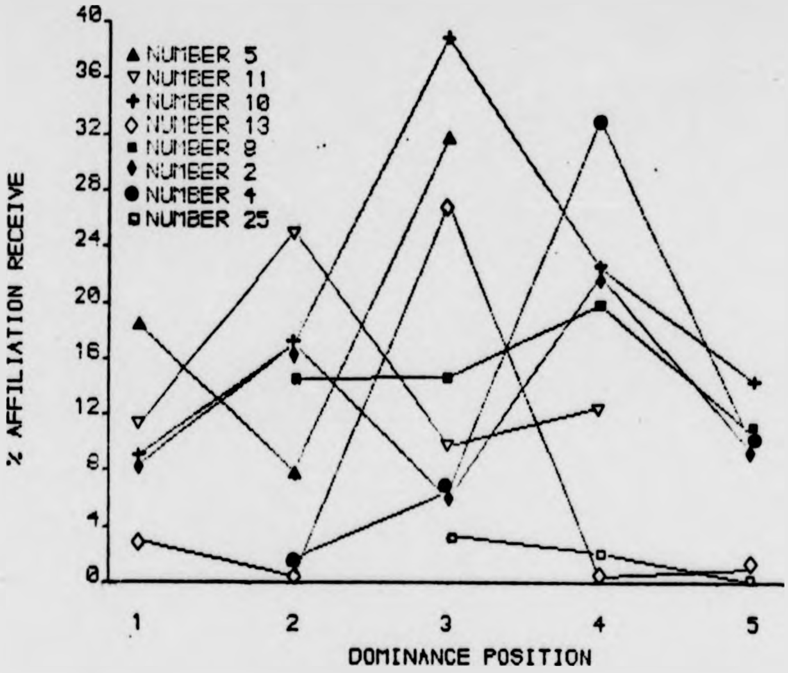


Figure 18 Amount of affiliation received by 8 animals over changing dominance position

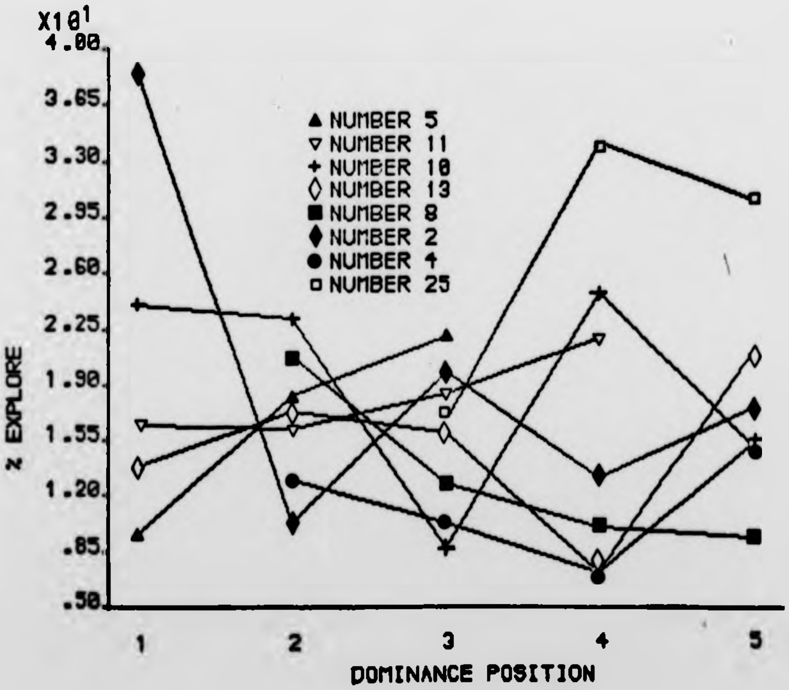


Figure 19 Amount of exploratory behaviour by 8 animals over changing dominance position

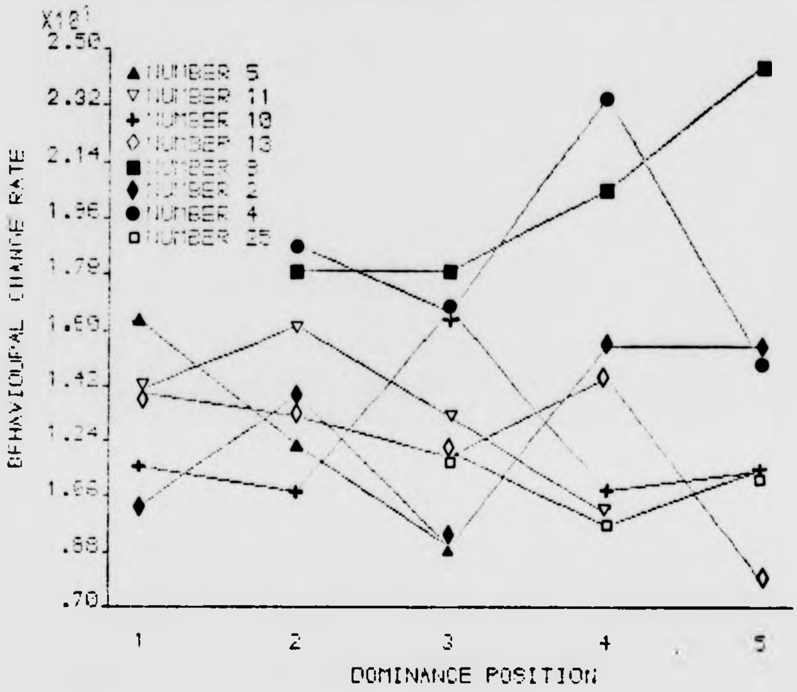


Figure 20 Behavioural change rate for 8 animals over changing dominance position

Why is it that there are significant differences between animals occupying the same dominance positions for some behaviours only? It may be that those dominance positions which failed to show differentiation between the animals for a given behaviour were occupied by animals who were homogeneous in their levels of that behaviour in that particular dominance position, or more likely, that that particular dominance position did not differentiate between the animals with respect to those behaviours. For example, the finding of no significant difference between the levels of fear expressed by the animals who occupied rd5 positions may be due to the fact that all the animals who occupied this position during P2 were equally fearful, or that there are differences between the fearfulness of these animals but this dominance position (i.e., this situation) failed to tap these differences, all animals in this position behaving equally fearfully. Behaviours may differ in their vulnerability to situational influences; Moos (1969) found that for smoking behaviour, 41.9% of the variance was due to persons, 7.1% to the setting, whilst for talking 68.3% was due to the situation, and only 10.5 to persons. 'The percentage of variance accounted for by different sources of variance varied greatly depending on the particular behavior being studied ' (p.409). In other words, some behaviours are more susceptible to environmental influences than others, and there may be differences between how much influence different environments have on behaviour. An example of such a behaviour is aggression; the amount of limitation on aggressive levels increases with increasing subordinance. Thus in a position of dominance an animal's level of aggression is not limited by other animals and his level of aggression is more likely to be a function of his personality; indeed, present analyses revealed significant individual differences between the behaviour of dominant animals with respect to aggression levels. In other positions aggressive levels are more constrained. This can most clearly be seen in dominance position rd5, where no aggression was ever shown; however, some animals who experienced rd5 positions also experienced other dominance positions where they did show aggression. Behaviour is often a product of the animal's perception of a certain situation (e.g., the amount of fear he shows when subordinate), and the level of expression of a particular behaviour can be constrained or facilitated by that situation (e.g., aggression when subordinate vs. dominant).

Mischel (1977) considers the question when are situations most likely to exert powerful effects (on behaviour) and, conversely, when are person variables likely to be most influential?. He states that 'psychological situations are powerful to the degree that they lead everyone to construe the particular events in the same way' (p.347). Mischel offers the example of the stimulus of a red traffic light - 'it exerts powerful effects on the behaviour of most motorists because they all know what it means, are motivated to obey it, and are capable of stopping when they see it. Therefore it would be easier to predict drivers' behaviour at traffic lights from knowing the colour of the light than from making inferences about the 'conformity', 'cautiousness' or other traits of the drivers' (p.347)(unless it's 3 o'clock in the morning). Conversly, Mischel holds that 'situations are weak to the degree that they are not uniformly encoded, do not generate uniform expectancies concerning the desired behaviour'. (For example, a card from the Thematic Apperception Test, with instructions to create a story based on the picture - here the type of story reported depends more on the person who is the story-teller rather than on the card.) 'To the degree that people are exposed to powerful treatments (in this study, dominance positions) the role of individual differences among them are minimal. Conversely, when treatments are weak, ambiguous or trivial, individual differences...should have the most significant effects' (p.347).

As previously noted, behaviours differ in their susceptibility to situation influences, and as Mischel notes, 'complex social settings... vary in the degree to which they prescribe and limit the range of expected and acceptable behaviour for persons in particular roles and settings, and hence permit the expression of individual differences'. For the 13 behaviours considered in the present analyses, there were significant differences between animals occupying rd5 positions for 81.8% of behaviours, for rd4 positions 69.2% of behaviours, 58.3% for rd1 positions, 38.5% for rd2 positions and 30.8% for rd3 positions (see Table 29).

Table 29 Percentage behaviours showing significant differences between animals for each regroup dominance position

Regroup dominance position	Number behaviours revealing differences	% behaviours revealing differences	Sign test	
			x	p
	n			
1	7 / 12	58.33	5	n. s.
2	5 / 13	38.46	5	n. s
3	4 / 13	30.76	4	n. s.
4	9 / 13	69.23	4	n. s.
5	9 / 11	81.81	2	0.033

From Table 29 it can be seen that dominance position rd5 offered the most opportunity for individual differences to emerge. Sign tests were also computed for each regroup dominance position to answer the question 'are there more behaviours which reveal significant differences between the animals in this position than there are behaviours which do not significantly differentiate the animals?' Rd5 was the only dominance position to show significance on this analysis, ($x=2$, $n=11$, $p<0.033$). Thus there are significantly more behaviours that differentiate animals in position rd5 than behaviours which do not differentiate. That there are more behaviours which show significant individual differences between the animals who occupied the position rd5 than for any other regroup dominance position is somewhat surprising; if our concept of dominance incorporates the notion of 'limitation of behaviour' and that subordinate animals are subject to the greatest amounts of limitation on their behaviour then we might expect the role of individual differences to be minimal in the behaviour of subordinate animals. This is clearly not the case; the evidence for individual differences was greater in the behaviour of subordinate animals than in the behaviour of the animals when occupying any other dominance positions.

The nature of each dominance position is perhaps reflected in the way in which there are significant differences between the animals for some behaviours but not for other behaviours; there are no differences between the rd5 animals with respect to fearful behaviour, although it may be remembered that both the regroup data (Table 21) and individual data (Table 25) show a significantly positive correlation between regroup dominance position and fear behaviour (subordinate = more). It may therefore be concluded that when in position rd5, animals show the greatest levels of fear behaviour, but that there are no significant differences between the animals with respect to amount of fear they show when occupying the most subordinate position in a regroup (rd5), the 'situation' proving powerful in eliciting high fear levels, for all animals. Conversely, rd5 animals show significant differences in their levels of self-aggression, and if self-aggressive behaviour reflects frustration level (Gluck & Sackett, 1974), then some animals find that being in the position rd5 more frustrating than do other animals in the same position. Thus, while the situation rd5 was powerful to the extent that it elicited similar levels of fear behaviour, it was ambiguous to the extent that different animals perceived it as being more or less frustrating.

Conversely, the situation rd1 was powerful in eliciting similar levels of self-aggression in all rd1 animals (rd1 perceived as uniformly frustrating for all animals) but ambiguous to the extent that there were significant differences between aggression levels in rd1 animals, some acting more aggressively than others. Thus if self-aggression is to be regarded as a personality trait, it may only be in certain situations (e.g., rd2, rd3, rd5) that it can be measured with a view to differentiating between individuals, as these situations are analogous to an ambiguous T.A.T.

card, where individual differences can become apparent. There are no significant differences between the levels of self-aggression expressed by animals when occupying positions rd1 and rd4; it may be concluded therefore that these dominance positions are regarded as uniformly frustrating (or not frustrating) situations. Similarly, if aggression is a personality trait, then we can only discern individual differences in aggression by studying animals in positions of dominance (rd1); positions rd2, rd3, rd4 constrain aggressive levels to a uniform extent, whilst position rd5 inhibits the occurrence of aggression altogether.

Appendix 8 gives the results of Kendall Correlation coefficients between behaviours for each regroup dominance position (i.e., 5 matrices). The individual pattern of correlations for each dominance position provides further evidence of the uniqueness of each situation; animals who were highly affiliative as dominants were less exploratory than were less affiliative animals in a position of dominance ($tau=-0.71, p<0.05$), but this relationship between affiliative and exploratory behaviour did not hold for any other regroup dominance positions. Similarly, animals who were highly aggressive in position rd3 were also more exploratory than less aggressive animals in position rd3 ($tau=0.69, p<0.05$), but again, this relationship between aggression and exploratory behaviour did not hold for any other regroup dominance position.

The importance of the situation and the particular behaviour under study must be considered when one is attempting to discover personality traits. If significant individual differences do not emerge, then this may be due to powerful situation effects, rather than that particular behaviour not being reflective of some personality trait, and individual differences in the levels of that behaviour may emerge in a different test situation. Of course, it might be argued that if a particular behaviour is reflective of a particular personality trait then differentiation between subjects should be possible in all situations; this is too strong an argument, as behaviour is evidently modified by the social setting, and individuals adapt their behaviour to the particular situation (e.g., by showing aggression when dominant, but never showing aggression when subordinate).

7.2 How can we explain the significant differences between animals in the same dominance positions?

The question that will now be considered is how might we explain the differences between animals when occupying the same dominance positions? Can such differences be related to factors which are not personality dependent, such as age, sex, rearing condition, or to previous dominance position in the stable group of 13? Only those behaviours for which there are significant differences between animals in the same dominance position will be considered with respect to age, sex, rearing condition and previous dominance position differences. These variables may well be related to many behaviours, but here, for economy, I shall only consider those behaviours which, for a given dominance position, significantly differentiate between the animals who occupied that position.

(1) Age

Kendall correlation coefficients were computed between age and behaviour to assess whether individual differences between animals in identical dominance positions were related to age differences. These coefficents are reported in Table 30.

(2) Sex

Mann-Whitney 'U' tests were computed to assess whether individual differences between animals in identical dominance positions were related to sex differences. This is only possible for position rd1, which was occupied by 8 animals in total, 6 females and 2 males. Results of these analyses are given in Table 31.

(3) Rearing condition

Kruskal-Wallis analyses were computed to assess whether individual differences between animals in identical dominance positions were related to differences in rearing condition. Results from these analyses are given in Table 32.

(4) Previous dominance position in the stable group of 13 animals

Kendall correlation coefficients were computed between previous dominance position in the stable group of 13 animals and those behaviours on which the animals showed significant differences for each dominance position to assess whether previous dominance position in a stable group could account

Table 30 Kendall correlation coefficients between behaviours on which animals show significant differences in a given dominance position and age

2 tailed tests *p=<0.05 **p=<0.01
n.c. = coefficient not computable

Behaviour	Dominance position				
	1 n=8 tau	2 n=8 tau	3 n=8 tau	4 n=9 tau	5 n=8 tau
Fear	n.c.	no diffs	no diffs	0.43	no diffs
Explore	-0.36	no diffs	no diffs	0.20	0.14
Aggression	0.14	no diffs	no diffs	no diffs	n.c.
Affiliation total	0.21	0.47	no diffs	no diffs	-0.50
Affiliation initiate	no diffs	0.33	no diffs	0.14	-0.29
Affiliation receive	-0.21	-0.11	0.04	-0.59*	-0.21
Self	no diffs	-0.18	no diffs	0.14	no diffs
Visual monitor	-0.29	no diffs	no diffs	0.14	0.29
Locomotion	-0.36	no diffs	-0.25	0.03	0.21
Displace	0.07	no diffs	no diffs	no diffs	n.c.
Stereotypy	no diffs	no diffs	-0.44	0.08	0.14
Self-agg	no diffs	-0.11	-0.18	no diffs	-0.07
Behaviour change	no diffs	no diffs	no diffs	-0.56*	-0.36

Table 31 Mann-Whitney 'U' tests on position rd1 only. Sex differences in behaviours for which rd1 animals show significant differences

Behaviour	Mann-Whitney 'U' value	p	
Explore	9	0.083	
Aggression	8	0.510	
Affiliation (total)	8	0.510	
Affiliation (receive)	12	0.045*	Rank sum males=15, n=2,
Visual monitor	8	0.510	females=21, n=6
Locomotion	7	0.739	
Displace	6	1.00	

Table 32 Kruskal-Wallis test statistics from analyses of rearing condition differences for behaviours on which animals show significant differences in a given dominance position

*p=<0.05 **p=<0.01
n.c. = not computable

Behaviour	Dominance position				
	1 d.f. = 3	2 d.f. = 3	3 d.f. = 3	4 d.f. = 3	5 d.f. = 3
Fear	n.c.	no diffs	no diffs	4.36	no diffs
Explore	5.25	no diffs	no diffs	3.49	0.14
Aggression	2.81	no diffs	no diffs	no diffs	n.c.
Affiliation (total)	2.50	4.06	no diffs	no diffs	6.17
Affiliation (initiate)	no diffs	5.39	no diffs	4.56	5.50
Affiliation (receive)	0.81	0.25	5.25	3.58	2.00
Self	no diffs	4.25	no diffs	4.38	no diffs
Visual monitor	5.25	no diffs	no diffs	1.60	2.00
Locomotion	5.25	no diffs	2.81	2.58	3.00
Displace	1.55	no diffs	no diffs	no diffs	no diffs
Stereotypy	no diffs	no diffs	2.90	3.29	4.17
Self-agg	no diffs	0.06	3.89	no diffs	1.00
Behaviour change	no diffs	no diffs	no diffs	6.24	3.33

Table 33 Kendall correlation coefficients between behaviours on which animals show significant differences in a given dominance position and previous dominance position in the stable group of 13 animals

2 tailed tests *p=<0.05 **p=<0.01
n.c. = coefficient not computable

Behaviour	Dominance position				
	1 n=8 tau	2 n=8 tau	3 n=8 tau	4 n=9 tau	5 n=8 tau
Fear	n.c.	no diffs	no diffs	0.11	no diffs
Explore	0.43	no diffs	no diffs	0.11	0.57*
Aggression	-0.07	no diffs	no diffs	no diffs	n.c.
Affiliation (total)	-0.43	-0.36	no diffs	no diffs	0.50
Affiliation (initiate)	no diffs	-0.21	no diffs	-0.28	-0.29
Affiliation (receive)	-0.14	-0.07	-0.64*	-0.17	-0.50
Self	no diffs	0.21	no diffs	0.22	no diffs
Visual monitor	0.50	no diffs	no diffs	0.06	0.43
Locomotion	0.43	no diffs	-0.14	-0.17	0.64*
Displace	-0.21	no diffs	no diffs	no diffs	n.c.
Stereotypy	no diffs	no diffs	-0.40	-0.11	0.00
Self-agg	no diffs	-0.21	0.00	no diffs	0.21
Behaviour change	no diffs	no diffs	no diffs	-0.11	-0.21

for any of the observed differences in behaviour between animals of identical rank in the regroup phase. These coefficients are given in Table 33.

As can be seen from Tables 30 to 33 factors such as age, sex, rearing condition and previous dominance position in a stable group have limited success in accounting for the significant differences observed in the behaviour of animals when occupying identical dominance positions. Table 30 shows that in position rd4 there are significant correlations between age and affiliation receive (tau=-0.59, n=9, p=<0.05), and between age and behavioural change rate (tau=-0.56, n=9, p=<0.05), indicating that younger animals receive less affiliation and have a higher behavioural change rate than older animals when in position rd4. There has been no work done on age differences in dominance behaviour, although Tokuda & Jensen (1969) report a significant correlation between age and dominance position (older animals are more dominant, although this was probably confounded with weight), and Bernstein & Mason (1962, 1970) studied differential responses of monkeys according to age, but in isolation situations of fear or frustration, rather than in social settings.

Sex differences were only computable for position rd1. There was a significant difference between the amount of affiliation received in position rd1 which was related to sex - males received more affiliation when rd1 than did females (Mann-Whitney 'U' = 12, p=0.045). This may be due to the perceived greater attractiveness of males as dominants than females. There was no evidence that the significant difference between the behaviour of dominant animals with respect to the amount of affiliation initiated was related to sex differences, in contrast to the findings of Sparks (1967) and Rhine (1973) who report that females do significantly more grooming than do males. A study by Keverne et al. (1968) indicated that males do significantly more visual monitoring than females, at least in mixed sex groups. There was no evidence in the present study that significant differences between rd1 animals with respect to visual monitoring could be explained by sex differences, although such a comparison may not be warranted, as the females were always dominant in single-sexed groups, the males in mixed-sex groups. There is thus no direct comparison between the sexes with respect to visual monitoring in mixed-sex groups, at least in this study.

Angermeier et al. (1968) report that establishment of male dominance is characterised mainly by the aggressive initiative of the dominant animal, whilst female dominance is established primarily by avoidance behaviour on the part of the subordinate (see also Walker-Leonard, 1980). However, Angermeier et al.'s study used pairs rather than groups of animals, and Walker-Leonard's study used triads. The present study, using groups, does not indicate any sex differences in aggressive behaviour (sex differences in fear behaviour not computable). Of course, the lack of any sex differences in aggressiveness in the behaviour of dominant animals in the present study may be as a result of the nature of the manipulation of dominance, where animals rarely contested dominance ranks but defaulted to relative ranks as in the stable group. Had new dominance orders been established perhaps sex differences in dominance establishment as reported by Angermeier et al. may have been apparent.

In the present study there was no evidence that rearing condition could account for any of the observed significant differences between the behaviour of animals occupying the same dominance position. Sackett (1965) reports rearing condition differences in aggressive levels, with motherless-peer reared animals showing the highest levels, then feral-mother reared, 1 year wire-cage reared (with visual and tactile contact with others), 6 month isolates and finally 1 year isolates who show the least aggression. However Sackett's study involved pairing the animals with a unfamiliar tranquillised stimulus animal and therefore the results are not directly comparable to the present study and the present analysis on rearing differences in behaviour in a group of familiar animals in a free social setting.

The only evidence of a correlation between previous dominance position in the stable group of 13 and behaviour in regroup dominance position is that for position rd3, where there is a significant correlation between previous dominance and amount of affiliation received (tau=-0.64, n=8, p<0.05), and for position rd5, where there is a significant correlation between previous dominance and amount of exploratory behaviour (tau=0.57, n=8, p<0.05), and between previous dominance rank and amount of locomotion (tau=0.64, n=8, p<0.05). Thus when in position rd3 animals that were previously more dominant in the group of 13 received significantly more affiliation than did animals who were previously more subordinate in the group of 13. When in position rd5 animals that were previously more subordinate in the group of 13 were more exploratory (showed higher levels of locomotory behaviour) than did animals who were previously more dominant in the group of 13. There has been little work done on the influence of previous dominance position on behaviour in subsequent dominance positions in primates, although Angermeier et al. (1967b) report that the only factor influencing dominance position in newly formed triads of animals from different rearing conditions was dominance position in previous groupings, specifically the number of previous aggressive encounters that an animal had won as opposed to lost.

It appears that factors such as age, sex, rearing condition and previous dominance position have limited success in explaining the significant differences found between animals in identical dominance positions in the manipulation phase. The influence of these factors varies according to the particular regroup dominance position; sex differences (which could only be evaluated in position rd1) were only apparent for 1 behaviour, age was only related to 2 behaviours in rd4, previous dominance was only related to 1 behaviour in rd3 and 2 in rd5, and rearing condition was unrelated to any of the significant differences found between the animals when occupying identical dominance positions. The degree of the relationship between such factors (sex, age etc.) and behaviour is a function of the particular situation (dominance position). These factors cannot of themselves explain all the differences found in the behaviour of the animals over various dominance positions.

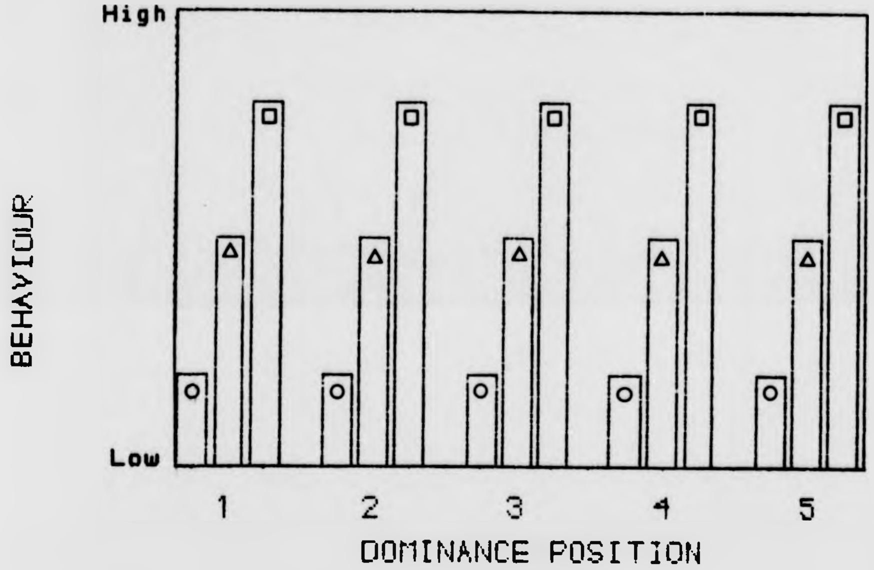
7.3 Does the behaviour of the animals show absolute consistency over changing dominance position?*

Sections 7.3 and 7.4 aim to evaluate the usefulness of the trait/state theories and the social behaviour theories of personality. This will be done by analysing for the consistency or inconsistency of behaviour within subjects over changing dominance position. How many behaviours show consistency (which would lend support to the trait/state theories of personality) and how many behaviours show inconsistency (i.e., are situationally variable, which would support a social behaviour theory of personality)?

Magnusson & Endler (9177) distinguish 3 sorts of consistency of behaviour; absolute, relative and coherent. Section 7.3 will deal with absolute consistency, section 7.4 with relative consistency, while the question of coherence will be discussed in Chapter 9.

Absolute consistency means that the level of an individual's particular behaviour remains consistent over varying situations (here, dominance positions). Figure 21 (adapted from Argyle & Little, 1972) illustrates the concept of absolute consistency. Friedman 2-way Anova's were computed for each individual animal, for several behaviours, using 4 weeks of data for each dominance position as repeated measures. The results of these analyses are given in

* see qualifications on Page 367



<u>Figure 21</u> (adapted from Argyle & Little, 1972). The notion of 'absolute consistency' in behaviour - levels of behaviour remain consistent over changing dominance position

Table 34.

Ideally one might wish for absolute consistency within all animals over changing dominance position for a given behaviour if that behaviour is to be said to reflect absolute consistency. However, as previously discussed, different behaviours are subject to varying amounts of situation (here, dominance position) effects, according to the influence or ambiguity that a given situation exerts on that behaviour. In addition, there may be individual differences in reaction to changing dominance position, some animals being affected by changes in dominance position more than others, with consequent effects on their behaviour. Sign tests were computed for each behaviour to answer the question 'are there more animals showing absolute consistency on this behaviour than there are animals not showing absolute consistency?', the results of which are given in Table 34 (incomputable for play and sex as they occurred too infrequently).

The behaviours which show absolute consistency (i.e., show significance on a sign test, $p<0.05$) for most animals over their respective changing dominance positions are; fear, explore, aggression, affiliation receive, visual monitor, self-aggression, behavioural change and displace. For these behaviours, there were no significant effects of changing dominance position when the animals are considered as a population. There are, however, individual differences in the effects of changing dominance position; animal number 5 showed unstable levels of fear, locomotion and behavioural change rate over the various dominance positions she

Table 34 Results of Friedman 2-way Anovas, testing for absolute consistency for each individual animal, dominance position x weeks

*p=<0.05 **p=<0.01

Animal number	d.f.			Behaviour										
		Fear	Explore	Aggression	Affil total	Affil initi	Affil receiv	Self tot	Self agg	Visual monit	Behaviour change	Stereotypy	Locomotion	Displace
17	1	2.3	1.0	1.0	4.0*	4.0*	4.0*	4.0*	0	0	0	0.3	1.0	1.0
5	2	6.0*	3.5	4.5	4.5	2.0	4.5	4.5	3.5	4.5	6.5*	0.9	6.0*	2.6
11	3	6.1	3.3	2.9	2.1	2.7	3.3	4.8	6.6	2.1	3.3	3.6	1.2	3.3
10	4	7.4	5.4	5.6(3)	7.0	5.0	8.4	11.0*	8.1	3.0	2.2	8.2	5.0	8.0*
13	4	8.2	5.0	7.3(3)	8.6	6.2	4.9	10.0*	5.6	5.0	12.2*	9.1(3)*	5.6	0.9(2)
8	3	2.7	0.9	1.0(1)	4.5	9.3*	2.1	3.9	3.9	3.9	3.0	2.4(2)	3.9	2.3(1)
2	4	5.7	7.4	6.0(3)	9.0	11.4*	7.2	4.6	5.4	4.6	7.4	9.8*	12.3*	3.7(3)
4	3	3.8	4.9	0.3(1)	3.9	4.0	3.3	3.9	3.0	3.9	1.5	0.9(2)	3.9	n.c.
3	1	0.0	1.0	0	4.0*	0.0	0.0	0.0	2.3	1.0	1.0	n.c.	4.0*	0.3
25	2	1.5	6.5*	2.3(1)	4.9	4.9	2.4	4.5	3.1	6.5*	1.5	0.3(1)	0.5	2.3(1)
27	1	0.0	1.0	n.c.	4.0*	4.0*	1.0	0.0	4.0*	1.0	0.0	4.0*	4.0*	n.c.
Sign tests														
x/n		1/11	1/11	0/10	3/11	4/11	1/11	3/11	1/11	1/11	2/11	3/10	4/11	1/9
significance level		0.006	0.006	0.001	n.s.	n.s.	0.006	n.s.	0.006	0.006	0.033	n.s.	n.s.	0.020

(1) d.f. for this analysis = 1
(2) d.f. for this analysis = 2
(3) d.f. for this analysis = 3

experienced; number 17 showed unstable levels of affiliation (total initiate and receive) and self behaviour; number 27 showed unstable levels of affiliation (total, initiate), locomotion, self-aggression and stereotypy. These individual instabilities may reflect individual reactions to changes in dominance position, which are reflected in the lack of absolute consistency for certain animals for certain behaviours and are evidence for person x situation (dominance position) interaction (this point will be discussed in Chapter 9). Some animals show much less absolute consistency over changing dominance position than others. Table 35 reports the percentage per animal of behaviours showing absolute consistency over changing dominance position. Sign tests were computed for each animal to answer the question 'are there more behaviours which do not show absolute consistency than there are which do show absolute consistency?', the results of which are also in Table 35.

As can be seen in Table 35, animal number 27 showed absolute consistency over changing dominance position in only 54.5% of behaviours considered here, whereas animal number 11 showed absolute consistency in 100% of behaviours, and her behaviour can therefore be considered to have been hardly affected by changes in dominance position (low situation effects). Why is it that some animals show much greater absolute consistency in behaviour over changing dominance position than others? Can such consistency be related to any other characteristic of that animal?

Table 35

Sign tests per individual animal, on number of behaviours showing absolute consistency v. number of behaviours not showing absolute consistency over changing dominance position

1 tailed tests x = number behaviours for that animal not showing absolute consistency over changing dominance position

Animal number	x	n	p	% consistent behaviours	consistency ranking (1=low consistency)
17	4	13	0.133 (n.s.)	69.2	2
5	3	13	0.046	76.9	4
11	0	13	0.001	100.0	10.5
10	2	13	0.011	84.6	7.5
13	3	13	0.046	76.9	4
8	1	13	0.002	92.3	9
2	3	13	0.046	76.9	4
4	0	12	0.001	100.0	10.5
3	2	12	0.019	83.3	6
25	2	13	0.011	84.6	7.5
27	5	11	0.291 (n.s.)	54.5	1

Table 36

Kendall correlation coefficients between 'consistency ranking' from Table 35 and relative ranks derived from Phase 2.

(excludes animal numbers 15, 6)
2 tailed tests

Consistency rank and relative rank on:	tau	n	p
Fear	0.04	11	0.874 (n.s.)
Explore	0.35	11	0.152 (n.s.)
Aggression	0.46	11	0.057 (n.s.)
Affiliation (total)	-0.06	11	0.812 (n.s.)
" (initiate)	0.27	11	0.267 (n.s.)
" (receive)	0.34	11	0.343 (n.s.)
Self	-0.23	11	0.340 (n.s.)
Self-aggression	0.51	11	0.017
Visual monitor	0.23	11	0.342 (n.s.)
Behavioural change rate	-0.52	11	0.032
Stereotypy	0.01	11	0.751 (n.s.)
Locomotion	0.04	11	0.874 (n.s.)
Displace	0.04	11	0.874 (n.s.)

Table 36 lists Kendall correlation coefficients between 'consistency ranking' (from Table 35) and relative rankings from P2 for several behaviours, in an attempt to relate the amount of absolute consistency in behaviour shown by each animal over varying dominance position to other characteristics of the animals. The relative ranking order was determined by taking the total number of animals each animal showed higher levels of a given behaviour in a given dominance position and computing a percentage over all dominance positions he experienced. For example, animal number 15 was the most aggressive of all rd1 animals, therefore he showed higher aggressive levels than 7 out of a total of 7 animals, = 100%. Animal number 2 showed higher aggressive levels than 25 out of a total of 29 animals who shared the same dominance ranks as herself = 86.2%. These rankings are given in Appendix 9.

From Table 36 it can be seen that the only significant correlations are between consistency ranking and relative ranking on self-aggression (tau=0.51, n=11, p<0.017), and between consistency ranking and relative ranking on behavioural change rate (tau=-0.52, n=11, p<0.032). Thus animals who show the most absolute consistency in behaviours over changing dominance position are relatively more self-aggressive and have a higher rate of behavioural change than do animals who show less consistency in behaviour over changing dominance position.

If we regard the consistency ranking as a measure of how much each individual's behaviour was influenced by changes in dominance position then those animals whose behaviour was most affected by changes in dominance position are also the most self-aggressive animals and have higher rates of behavioural change.

7.4 Does the behaviour of the animals show relative consistency over changing dominance position?

Section 7.3 considered the question of absolute consistency of behaviour within individual animals over changing dominance position. Relative consistency considers whether the rank order of group of individuals with respect to a specified behaviour is the same across all situations. Thus while the absolute levels of a behaviour over situations may vary for different animals relative consistency holds that the rankings of the animals on that behaviour remain stable relative to each other; individual A may display 50% aggression in situation X, 25% in situation Y, but A will always display more aggression than individual B in every situation. Figure 22 (adapted from Argyle & Little, 1972) illustrates the concept of relative consistency.

As Lay (1977) points out, relative consistency (referring to the correlation between rankings of animals on behaviour over situations) is often used interchangeably with the notion of absolute consistency (referring to the presence or absence of variability within individuals in behaviour over situations) (e.g.,Bem & Allen, 1974). The absence of absolute consistency in behaviour is not damaging to a trait theory of

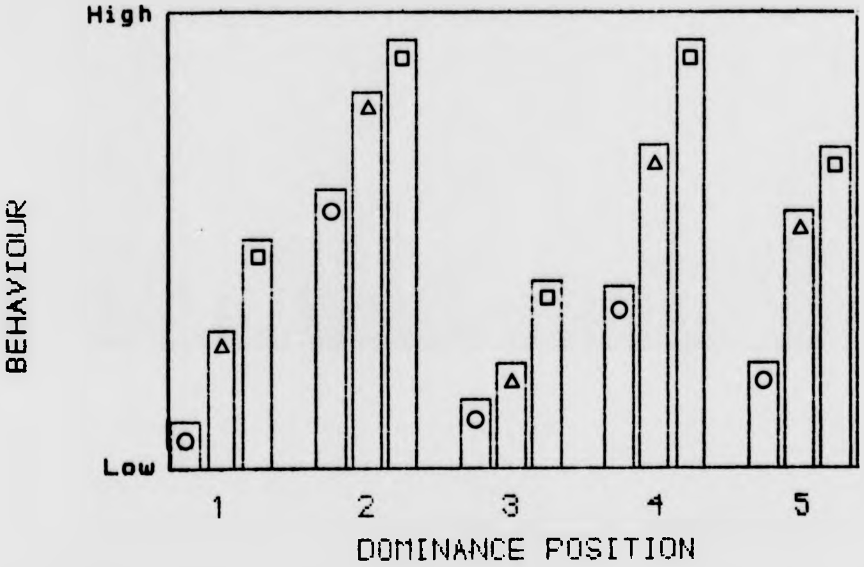


Figure 22 (adapted from Argyle & Little, 1972). The notion of 'relative consistency' in behaviour - the ranks of the individuals on amount of behaviour remain consistent over changing dominance position, even though absolute levels of behaviour vary

personality; as Eysenck & Eysenck (1980) note, 'it would be unreasonable to deny the possibility that specific behavioural inconsistency may coexist with a more conspicuous consistency at the mediating level' (p. 193). The trait measurement model does not deny the effects of the situation on behaviour, but these effects are supposed to be general and to influence the level of behaviour but not affect the rank orders of individuals with respect to the behaviour being measured. Hence the trait model assumes relative consistency without necessarily assuming absolute consistency.

To determine relative consistency Friedmans Anova's were computed for 13 behaviours for all 13 animals over the 5 dominance positions. A modified analysis[2] enabled the use of data from all 13 animals, yielding a 13 x 5 data matrix, with several missing data points (Benard & Van Elteren, 1953). These analyses give a test statistic which approximates to chi-squared and also a Kendall Coefficient of Concordance (W) between relative rankings in each dominance position for all animals for every behaviour. Results of these analyses in Table 37.

The significance of the χ^2 from these analyses can be evaluated using standard χ^2 tables, but caution is needed in interpretation. Firstly, the approximation is only good for fairly large degrees of freedom (Benard & Van Elteren, 1953).

Footnote 2:

I am grateful to Robin Campbell for writing this program.

Table 37 Results from Friedman Anovas testing for relative consistency

W = x2/m(n-1)
*p<0.10 **p<0.05

Behaviour	χ^2 value	d.f.	W
Fear	18.4*	11	0.63
Explore	14.7	12	0.41
Aggression	16.0	11	0.56
Affiliation			
total	17.0	12	0.47
initiate	20.5*	12	0.57
receive	19.9*	12	0.56
Self	11.5	12	0.32
Self-aggression	23.6**	12	0.66
Visual monitor	20.2*	12	0.56
Behavioural change rate	20.2*	12	0.56
Stereotypy	22.3**	12	0.62
Locomotion	17.8	12	0.49
Displace	14.7	11	0.51

Secondly, the distribution of the test statistic derived from these analyses cannot be assumed to be the same as that under conditions where there are no missing data points. Appendix 10 illustrates this point. A complete 13 x 5 data matrix with no missing data points and with hypothetical 'best fit' data (where relative ranks are stable across all dominance positions) yields a χ^2 of 60.0, p<0.00001 and a W of 1.0 with 12 degrees of freedom (Appendix 10, example A). An incomplete 13 x 5 matrix (example Bi), as occurs in the present data with several missing data points, but with comparable hypothetical 'best fit' data yields a χ^2 of only 35.7, p<0.001 (from standard tables) and a W of 1.00 with 12 degrees of freedom. Thus under these conditions, the maximum χ^2 value obtainable is 35.7 not 60. Similarly, an incomplete 12 x 4 matrix (as occurs in the case of fear and aggressive behaviour) with hypothetical 'best fit' data yields an χ^2 of 28.9, p<0.05 (from standard tables) and a W of 1.0 (Appendix 10, example Bii). Evaluating the significance of the approximation to χ^2 deriving from these analyses by using standard χ^2 tables may not be justified as the distribution of the test statistic under the present conditions of missing data may be different from the test statistic under conditions of no missing data (Prentice, pers. comm.). By performing a large number of analyses using a 13 x 5 (or 12 x 4) data matrix of random rankings with missing data points corresponding to those in the present analyses it would be possible to discover the distribution of the test statistic deriving from data of this kind. It would then be possible to infer the critical values corresponding to various significance levels. While this would be the ideal method of evaluating the present results it would be a lengthy task. In the absence of knowing the true distribution of χ^2 under the present conditions of missing data it is reasonable to assume that the significance of the test statistic deriving from each analysis is underestimated, and accordingly I shall accept as significant any χ^2 values which are significant at $p<0.1$.

The behaviours which show significant χ^2 values ($p<0.1$) on standard tables are self-aggression and stereotypy, affiliation initiate and receive, visual monitor and behavioural change rate and fear behaviour.

Tentatively it may be concluded that the behaviours showing relative consistency across different dominance positions are; fear, self-aggression, stereotypy, affiliation initiate, affiliation receive, visual monitor, behavioural change rate and aggression (all with $W > 0.55$). It may be that more behaviours would show significant χ^2 approximations if the distribution of the test statistic under these conditions were known. At least for the behaviours mentioned above we can conclude that the relative rankings of the animals with respect to self – aggression etc. over different dominance positions remain stable.

7.5 Evaluation of the trait/state model and the situationism model of personality

Table 38 summarises the results of the various analyses from Chapters 4-7. Each behaviour was analysed in a number of different ways with various questions in mind. This section

Table 38 Summary of analyses on each behaviour from Chapters 4, 5, 6, 7.

✓ = behaviour shows this particular result

* see qualifications on Page 367

Analysis	Correlates with dominance position			Shows differences		Differences within dominance position related to:	Shows consistency	
	in P1	in P2 within regroups	in P2 within animals	within regroups (between dominance positions)	within each dominance position (between animals)		Absolute *	Relative
(section) Behaviour	4.4	5.4.4.	6.1	6.2	7.1	7.2	7.3	7.4
Fear	n.m.	✓	✓	✓	✓rd4		✓	✓
Explore	✓				✓rd1, 4, 5	rd5 - D13	✓	
Aggression	✓	✓		✓	✓rd1		✓	
Affiliation								
total	✓				✓rd1, 2, 5			
initiate	✓				✓rd2, 4, 5			✓
receive	✓				✓rd1, 2, 3, 4, 5	rd1-sex, rd3-D13, rd4-age	✓	✓
Self	✓			✓	✓rd2, 4			
Visual								
monitor	✓				✓rd1, 4, 5		✓	✓
Locomotion	✓				✓rd1, 3, 4, 5	rd5 - D13		
Displace	n.m.	✓		✓	✓rd1		✓	
Stereotypy					✓rd3, 4, 5			✓
Self-aggression					✓rd2, 3, 5		✓	✓
Behavioural change rate	n.m.				✓rd4, 5	rd4 - age	✓	✓

attempts to incorporate all the results into a meaningful framework within which both the trait/state model and the situationist model of personality can be evaluated.

It is evident from these analyses that behaviour can be studied in a number of different ways, depending on what question is being asked. Firstly, behaviour can be studied within and across individuals, in terms of whether over situations that behaviour is stable or unstable. In addition, behaviour within individuals may be correlated with dominance position, to determine whether there is a linear relationship between dominance position and behaviour (absolute correlation).

Behaviour can also be studied within and across groups of animals. We can consider whether the rank order of animals on a given behaviour remains stable over changing dominance position (relative consistency) or whether behaviour within groups of animals is related to dominance position, either linearly (relatiive correlation) or non-linearly (section 6.2).

Thirdly, by studying individuals in the same dominance position we can discover whether there are individual differences in the behaviour of animals in similar situations, which may be related to other characteristics such as age, sex etc.

A trait/state model of personality assumes relative consistency in behaviour of individuals over situations and for individual differences between subjects in behaviour within situations. Situationism assumes that there is no absolute consistency in behaviour, that behaviour is situationally variable, and that there are no significant individual differences in behaviour within situations.

From Table 38 it can be seen that <u>fear behaviour</u> while unrelated to dominance position in the stable group of 13 animals in P1 is correlated with dominance position in P2 both within and across individuals (absolute correlation) and within and across regroups (relative correlation). There are no significant differences in fear levels across different dominance positions within animals (absolute consistency), and the relative rank ordering of animals on fear behaviour is consistent from one dominance position to the next (relative consistency). Thus we can predict that levels of fear will be greater in more subordinate animals in a group and will be greater for all animals when subordinate than when dominant. Although fear behaviour will increase with subordinancy there will be no significant fluctuations in the level of its expression for each animal (=absolute consistency) and we can to some extent predict how fearful each animal will be in a given dominance position, and we will be able to predict the relative rankings of animals on levels of fear when occupying identical dominance positions. We will only find significant differences between animals in fear behaviour if we study the animals in position rd4; differences in fear behaviour of the animals in other dominance positions are not significant. The absence of any correlation between dominance position and fear behaviour in P1 and the presence of such a correlation in P2 indicates that the correlation between dominance rank and fear behaviour is a product of the manipulation and does not occur in more stable and larger groups. We can conclude that fear behaviour is a product of both situation and personality; all animals will display more when in a subordinate situation, both relative to other regroup members and relative to other dominance positions they themselves occupy, although the absolute level of fear will depend on the particular animal and we may only discern significant individual differences in one dominance position (rd4).

Exploratory behaviour correlates with dominance position in the stable group (in P1) but not with dominance position in the regroups in P2 (either within and across individual animals or within and across regroups). There are no significant fluctuations in levels of exploratory behaviour for each animal across changing dominance position (=absolute consistency), although minor fluctuations in exploratory levels prevent us from predicting relative ranks on exploratory behaviour within dominance positions (i.e., exploratory behaviour does not show relative consistency). In addition, we can only discover individual differences in exploratory levels by studying animals in dominance positions 1, 4 and 5. We can conclude that exploratory behaviour is a 'situation free' behaviour, whose level of expression is dependent on stable personality dimensions.

Aggressive behaviour is not correlated with dominance position in a stable group (in P1) but is correlated with dominance position within and across regroups in P2 (but not within and across animals). Thus relative to other animals in a regroup a dominant will be more aggressive, a subordinate the least, although on an individual basis, an animal will be no more aggressive when dominant than when subordinate. Aggression also shows absolute consistency but not relative consistency, and we can only discern significant individual differences in aggressive levels by studying animals when in a position of dominance. We can predict both the relative and absolute levels of aggression that an animal will display in every dominance position. Aggression is a joint function of the personality of an animal and the dominance position he occupies, although it correlates with dominance position only in P2 as a result of the manipulation of regroups and is unrelated to dominance in a larger group.

The analysis of affiliative behaviour was in 3 separate parts; affiliation total (receive + initiate + initiator unknown), affiliation receive and affiliation initiate. Affiliation (both receive and initiate) was found to be correlated with dominance position in P1 in a stable group situation, but there was no correlation between affiliation (total, receive or initiate) and dominance in P2. Neither affiliation total nor affiliation initiate shows absolute consistency within animals over changing dominance position, although affiliation receive shows absolute consistency. Affiliation initiate and receive show relative consistency, but only at $p<0.1$. There are apparent significant differences in affiliation total between animals in positions rd1, rd2, and rd5; significant differences in affiliation initiate in rd2, rd4 and rd5 and significant differences between amount of affiliation received between animals in all regroup dominance positions. The amount of affiliation received by rd1 animals was related to sex (males receive more), the amount received by rd4 animals was related to age (younger animals receive less), and the amount that rd3 animals received was related to their previous dominance position in the group of 13 (D13)(previously more dominant animals receive more). We can conclude that affiliative behaviour is not related to dominance, at least in small groups as in P2, and neither is there any evidence that it is reflective of a stable personality trait, although there is some evidence that the amount of affiliation an animal receives is consistent over changing dominance position, some animals receiving consistently more than others in every position.

Self behaviour correlated with dominance position in P1, but did not correlate with dominance position in P2. Neither did self directed behaviour show absolute or relative consistency over changing dominance position. There was evidence for a non-linear relation between dominance position and amount of self or solitary behaviour in P2; the analysis which tested for differences between amount of self behaviour between animals of different dominance ranks over 6 regroups (section 6.2) found that animals in position rd5 show the highest levels, then rd1 animals, rd3, with rd4 and rd2 animals showing the lowest levels (χ^2=10.8, d.f.=4, $p<0.05$). It was possible to discern individual differences in the amount of self-directed behaviour expressed by the animals but only when occupying rd2 and rd4 positions. We may conclude that self behaviour is situation dependent and that there is no evidence that self behaviour can be considered to be a stable (in either relative or absolute terms) personality trait.

Of the various sub-behaviours which were analysed, the only one which was found to be related to dominance rank in P2 was amount of displacement behaviour, which was linearly related to dominance position, but only within and across regroups and not within and across individual animals. Thus dominant animals in each regroup did more displacing than more subordinate animals. There was also evidence that displacement behaviour was reflective of a stable personality trait; animals show absolute consistency over changing dominance position in amount of displacements (this is quite compatible with a within group correlation of displacement behaviour with dominance position, as a test for absolute consistency is a less exact test than that for correlation). However, only animals occupying rd1 were found to differ significantly in their amount of displacement behaviour, indicating individual differences in the assertiveness of dominant animals.

Visual monitoring behaviour was not related to dominance position in P2, either within and across regroups or within and across individuals, although it did correlate with dominance position in P1. Visual monitoring behaviour also showed absolute consistency within animals over changing dominance position and relative consistency (p<0.1), and there were significant differences between the animals' levels of visual monitoring in positions rd1,rd4 and rd5. Visual monitoring behaviour can thus be considered to be reflective of a stable personality trait, related to dominance position only in a large, stable group.

Locomotion correlated with dominance position in P1, but did not correlate with dominance position in P2. Neither did locomotion show consistency, either relative or absolute, although there were significant differences in amount of locomotion in rd1,rd2,rd4 and rd5 animals. Locomotion cannot be considered to be reflective of a stable personality trait, and is situation dependent for each animal.

Stereotypy and self-aggression did not correlate with dominance position, either in P1 or P2. Stereotypy showed relative, but not absolute consistency over changing dominance position, and there were significant differences between the animals when occupying positions rd3,rd4 and rd5. Self-aggression was consistent in both absolute and relative terms, and there were significant differences between the animals when occupying positions rd2,rd3 and rd5. Thus, stereotypy and self-aggression are situation-free characteristics of the animals, and we can predict the relative ranks of the animals in each dominance position, although we can only predict absolute levels for self-aggression.

Behavioural change rate was not related to dominance position in P2 (and not measured in P1), and showed absolute consistency and relative consistency ($p<0.1$). There were significant differences between behavioural change rates for animals when occupying positions rd4 and rd5 and the differences in position rd4 can be related to age (younger animals show a higher rate of behavioural change). Behavioural change rate is thus reflective of a situation-free personality trait.

Part of the problem in interpretation of the data from the present study is that the various analyses use data from different sets of individuals, regroups etc., and thus cannot be easily combined into one concluding statement. The analyses often combine the results from analyses on individual animals into one, testing for general effects of changes in dominance position. Yet, despite such limitations from the summary of analyses for each behaviour it can be seen that neither a trait/state theory of personality nor a situational specificity theory of behaviour can account for the behaviour of all the animals over changing dominance position. Only exploratory behaviour, amount of affiliation received, self-aggression, behavioural change rate and stereotypy appear to be consistent (either in relative terms, absolute terms or both) patterns of behaviour, showing no significant situation effects, although even with respect to these behaviours, it is relative ranks of the animals in each dominance position, although we can only predict absolute levels for self-aggression.

Behavioural change rate was not related to dominance position in P2 (and not measured in P1), and showed absolute consistency and relative consistency ($p<0.1$). There were significant differences between behavioural change rates for animals when occupying positions rd4 and rd5 and the differences in position rd4 can be related to age (younger animals show a higher rate of behavioural change). Behavioural change rate is thus reflective of a situation-free personality trait.

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As the results from the above analyses are often combined over all animals by means of a sign test, while we can discuss general effects over all animals of changing dominance position, or general effects regarding the presence or absence of consistency such effects may not be applicable to individual animals. Yet if we need a different theory for each individual animal which will allow us to explain and predict his behaviour over changing situations then such general theories such as have been used by trait/state theorists are effectively redundant, and theories of situational specificity which search for general effects of situations on the behaviour of individuals and argue that an individual's behaviour is largely a function of the situation fare no better. Behaviour is evidently a function of the complex interaction between the individual and the situation. The problem is how does such an interaction take place and how can we come to understand and predict the behaviour of any one individual within a particular situation? This will be discussed in Chapter 9.

Chapter 8. RESULTS FROM THE PERSISTENCE TESTS, ISOLATION TESTS AND STIMULUS ANIMAL TESTS

8.1 Is behaviour in the persistence and isolation tests related to dominance rank?

During Phase 2 each animal was tested in the persistence and isolation tests in each of the various dominance positions he experienced. This was to assess whether changes in dominance position resulted in changes in behaviour specific to these test situations, or whether such behaviour might reflect stable personality differences in the animals, as shown by stability of behaviour in these tests over changing dominance position. P1 had suggested that the behaviour of the animals in persistence and isolation tests was not correlated with dominance rank; the data from P2 allows us to investigate whether such behaviour is related in a non-linear way to dominance position. The results of section 6.2 demonstrated that the animals of different dominance ranks within a regroup show significant differences in the amount of self-directed behaviour in a free-social situation, but that self behaviour is not linearly related to dominance rank - the relationship appears to be quadratic; animals in position rd5 displayed the most self behaviour, followed by animals in position rd1, rd3, rd4 with animals in positions rd5 showing the least self behaviour. Is it possible that similar non-linear differences exist between the behaviour of animals in different dominance ranks in non-social situations? As in section 6.2 Friedman Anovas were computed to test for behavioural differences in persistence and isolation tests between animals in the 5 regroup dominance positions over 6 regroups (numbers 1,2,3,4,5 and 7). Thus the analyses compare the behaviour of all rd1's over the 6 regroups with the rd2's, rd3's, rd4's and rd5's in those regroups. The results of these analyses are reported in Table 39 (persistence tests) and Table 40 (isolation tests), and it can be seen that there are no significant differences in the behaviour of animals in different dominance positions within regroups with respect to any of the behaviours measured in the persistence and isolation tests. It is perhaps interesting to note that the analysis for self-aggression in the isolation test just fails to reach significance (χ^2=9.2, p=0.055, d.f.=4); rd1's display the most self-aggression, followed by rd2's, rd5's, rd3's and rd4's. The correlation between dominance rank in the stable group (P1) and self-aggression in isolation was also just non-significant (tau=-0.30, n=13, 2-tailed test). There does appear to be a tendency for more dominant animals to be more self-aggressive in isolation.

Stamm (1961) reports differences in the behaviour of dominant and subordinate animals in reaction to isolation, the more dominant animals showing greater behavioural disturbance, and Richards (1974) reports that, in problem-solving tasks, dominant rhesus monkeys show greater persistence. This was not true in the present study where there were no significant correlations between dominance rank and behaviour in persistence or isolation tests in either P1 or P2. It may be that persistence in problem-solving is not the same as

Table 39 Do animals of different dominance position within groups behave significantly differently in persistence tests?

Friedmans Anovas, dominance position (n = 5) x groups (n = 6).

*p<0.05

Behaviour		χ^2	d.f.
Look through divider	(%)	5.2	4
	(f)	5.6	4
arm through divider	(%)	1.2	4
	(f)	2.0	4
push divider	(%)	0.9	4
	(f)	1.0	4
locomotion	(%)	2.3	4
	(f)	4.9	4
dominance environment		not computable - too infrequent	
self-aggression		4.7	4
stereotypy		4.0	4
other		7.5	4

Table 40 Do animals of different dominance position within groups behave significantly differently in isolation tests?

Friedmans Anovas, dominance position (n = 5) x groups (n = 6).

*p<0.05

Behaviour		χ^2	d.f.	
dominance environment		not computable - too infrequent		
visual explore environment		2.1	4	
stereotypy		0.6	4	
play		1.2	4	
contact explore environment	(%)	3.9	4	
	(f)	3.6	4	
self-aggression		9.2	4	p=0.055
locomotion	(%)	4.9	4	
	(f)	6.6	4	
whimper	(%)	0.6	4	
	(f)	0.7	4	
scream	(% and f)	not computable - too infrequent		
self groom		6.4	4	
self huddle		5.0	4	
masturbate		not computable - too infrequent		

persistence in a potentially unsolvable task, or that the persistence test in the present study was not so much a test of persistence, but a test of reaction to frustration. Of course, there is doubt as to how reliable the persistence and isolation tests were; few behaviours show significant and high test-retest correlation coefficients (see Table 4).

8.2 How consistent is the behaviour of the animals in the persistence and isolation tests?

The results of the present study found no relationship between dominance rank and the behaviour of animals in isolation and persistence tests; can we assume that such behaviour is a function of the personality of the animals? While it is not possible to test for the presence or absence of absolute consistency in the behaviour of animals in the persistence and isolation tests over changing dominance position (since there are no repeated measures within each position) it is possible to test for relative consistency, that is, whether the rank order of the animals with respect to certain behaviours in the isolation and persistence tests are stable across situations (i.e., changing dominance positions).

The relative consistency of behaviour in the persistence and isolation tests was assessed, using the same method as described in section 7.4, which assessed relative consistency in the free-social behaviour of the animals, using a modified Friedman Anova test which allows for missing data points. The results of these analyses are given in Table 41 (persistence tests) and Table 42 (isolation tests).

Table 41 Results from Friedman's Anova's, testing for relative consistency of behaviour in persistence tests

*p<0.05 **p<0.01

Behaviour		χ^2	d.f.	W
look through divider	(%)	13.5	12	0.38
	(f)	21.1*	12	0.59
arm through divider	(%)	21.6*	12	0.60
	(f)	30.2**	12	0.84
push divider	(%)	21.4*	12	0.59
	(f)	18.8	12	0.52
locomotion	(%)	21.3*	12	0.59
	(f)	21.0	12	0.58 (just n.s.)
dominance environment		not computable - too infrequent		
self-aggression		25.8*	12	0.72
stereotypy		21.5*	12	0.60
other		23.4*	12	0.65

Table 42 Results from Friedman's Anova's, testing for relative consistency of behaviour in isolation

*p<0.05 **p<0.01

Behaviour	χ^2	d.f.	W
dominance to environment	not computable - too infrequent		
visual explore environment	13.1	12	0.36
stereotypy	28.6**	12	0.79
play	17.7	12	0.49
contact explore environment	13.5	12	0.38
self-aggression	13.3	12	0.37
locomotion	17.5	12	0.49
whimper (%)	17.3	12	0.48
whimper (f)	18.3	12	0.51
scream(%)	9.5	12	0.26
scream(f)	9.5	12	0.26
self groom	18.9*	12	0.52
self huddle	19.0*	12	0.53
masturbate	not computable - too infrequent		

(A) Persistence tests.

From Table 41 it can be seen that all but 3 of the 12 behaviours recorded in the persistence tests show significant χ^2 values ($p<0.1$) and thus can be regarded as showing high relative consistency over changing dominance position; for example, look through divider gap (frequency), arm through gap (both frequency and percentage time), push divider (percentage only), locomotion (percentage), self-aggression, stereotypy, and 'other' behaviour all show significant χ^2 values ($p<0.1$) and have high Kendall coefficients of concordance (>0.58). It is surprising that so many of the behaviours in the persistence tests show relative consistency; as previously discussed, the χ^2 approximation under conditions such as in the present study with many missing data points is likely to be different from that of a normal χ^2 distribution, on which standard tables are based. However, it may be remembered that the only behaviours showing test-retest reliability ($p<0.05$) in P1 (Table 10) were frequency of looking through divider gap, and percentage time and frequency of inserting arm through divider gap. We are therefore only justified in concluding that these behaviours (frequency of looking through the divider gap and frequency and percentage time spent inserting arm through gap) show relative consistency, as other behaviours in the persistence tests show poor test-retest reliability. Thus the relative rankings of the animals on behaviours such as frequency of looking through the divider gap and inserting arm through gap (% and frequency) are consistent over changing dominance position.

(B) Isolation tests.

From Table 42 it can be seen that 3 behaviours in the isolation tests shows significant relative consistency (p<0.1); stereotypy, self groom and self huddle. The relative rankings of the animals on other behaviours measured in isolation are not consistent over changing dominance position. It may be remembered (Table 4) that test-retest correlation coefficients were only significant (p<0.05) for the following behaviours; masturbate, locomotion (duration and frequency), explore visual and whimper. The reliability of the other isolation measures is therefore suspect, and we may not be justified in accepting that stereotypic, self grooming or self huddling behaviour in isolation shows significant relative consistency, since test-retest reliability is low.

Behaviour in persistence tests appears to show much more relative consistency than does behaviour in isolation. Why might this be? Fiske & Rice (1955) discuss 3 types of variability in behaviour, one of which, 'type 2' variability holds that when an individual is presented with the same situation at 2 points in time the initital exposure to that situation affects the 2nd exposure. Thus it may be that the animals, having been exposed to a situation of isolation before were much less disturbed on the 2nd (and 3rd etc.) occasions. Behaviour in the persistence tests show much greater relative consistency over changing dominance position, although test-retest reliabilities were low. However, the analyses for relative consistency may be provide a better measure of the reliability of the persistence (and isolation) tests than the test-retest coefficients from P1. The test-retest coefficients were based on the correlation of behaviour between only 2 tests; as Epstein (1979) notes, the error of measurement is often grossly overlooked, and if behaviour is examined over a greater number of samples then consistency is more likely to emerge, as the error of measurement is reduced. We may be more justified in accepting the results of the analyses for relative consistency in deciding on how reliable the isolation and persistence tests are than relying on test-retest correlation coefficients based on the correlation between behaviours in only 2 tests. However, I shall accept as reliable only those behaviour which show both significant test-retest reliability from P1 and relative consistency over changing dominance position in P2, i.e., time spent looking at the test orange piece and frequency and time spent trying to grasp the orange piece in the persistence tests.

8.3 Can behaviour in a persistence test be related to age, sex or rearing condition?

The results from the analyses of relative consistency in behaviour in the persistence tests indicated that there are certain animals who show much higher levels of both looking at the test orange segment and attempting to grasp it in a persistence task. Can such persistence be related to other factors, such as age, sex or rearing condition, or is persistence a personality trait which is independent of factors as age, sex etc.?

(1) Age differences in persistence.

Kendall correlation coefficients were computed between age and relative ranks on the 3 behaviours in the persistence tests which showed relative consistency (frequency of looking through the divider gap, frequency and percentage time spent attempting to grasp the orange piece). The relative ranks were computed in the same way as those for relative ranks on free-social behaviour in section 7.3, and are reported in Appendix 11 and the Kendall correlation coefficients are reported in Table 43.

(2) Sex differences in persistence.

To assess whether frequency of looking through the divider gap and frequency and percentage time spent attempting to grasp the orange in the persistence tests were related to sex differences, Mann-Whitney 'U' tests were computed using relative ranks as used in (1) above, the results of which are reported in table 44.

(3) Rearing condition differences in persistence.

Similarly, to assess rearing condition differences, Kruskal-Wallis analyses were computed for the same behaviours. Results in Table 45.

As can be seen from Tables 43 to 45, there are no age, sex or rearing condition differences in those behaviours which show stable relative rankings in the persistence tests. We can therefore regard persistence as a personality trait (in as much as the relative rankings of the animals with respect to

Table 43 Kendall correlation coefficients between age and relative ranks on behaviours showing relative consistency in the persistence tests.

2 tailed tests

*p<0.05

Behaviour	tau	n	p
look through (f)	-0.30	13	0.16
arm through (%)	-0.21	13	0.33
arm through (f)	-0.04	13	0.86

Table 44 Results of Mann-Whitney 'U' tests on sex differences in behaviour in persistence tests. Based on relative ranks derived from Phase 2.

Behaviour	'U'	p
Look through divider gap (f)	17	0.67
Arm through divider gap (%)	20	0.40
Arm through divider gap (f)	17	0.67

Table 45 Results of Kruskal-Wallis analyses on rearing condition differences in behaviour in persistence tests. Based on relative rankings derived from Phase 2.

Behaviour	H	d.f	p
Look through divider gap (f)	5.78	4	0.21
Arm through divider gap (%)	3.53	4	0.47
Arm through divider gap (f)	7.44	4	0.11

persistence behaviour remain consistent over changing dominance position) which is not related to age, sex or rearing condition differences.

8.4 Is behaviour in a persistence test related to aspects of social behaviour?

If persistence as a stable personality characteristic is not related to age, sex or rearing condition, is it related to any other aspects of the animals' behaviour, i.e., behaviour in a free-social setting? To answer this question the relative ranks of the animals on those 3 measures showing stable relative rankings and significant test-retest reliability in the persistence tests were correlated with relative rankings derived from P2 on 13 measures of social behaviour, for example, with relative rankings on amount of fear behaviour, aggression, affiliation, stereotypy etc., (from Appendix 9). The results of these Kendall Correlations are given in Table 46.

As can be seen from Table 46 the relative rankings of the animals on some behaviours in a free-social setting correlate significantly ($p<0.05$) with relative rankings on those behaviours in the persistence test which show significant test-retest reliability and relative consistency. Animals who in a persistence test frequently glance at the object out of reach are also more exploratory relative to other animals, less affiliative and show high levels of visual monitoring and high behavioural change rates in a social setting. Animals who show high levels of attempting to grasp the test object in

Table 46 Kendall correlation coefficients between relative rankings on behaviours in persistence tests and rankings on free social behaviour. (From Phase 2, over all regroup dominance positions each animal experienced).

2 tailed tests *p=<0.05 **p=<0.01

Behaviour	n	Persistence test Looktho'(f)	arm through (%)	arm through(f)
Free social behaviour:				
how disturbed	11	0.15	-0.11	-0.04
fear	12(1)	0.40	-0.06	-0.02
explore	13	0.58*	0.10	0.17
aggression	12(2)	0	0.06	0.06
Affiliation				
total	13	-0.60*	-0.27	-0.31
intiate	13	-0.40	-0.28	-0.35
receive	13	-0.31	-0.01	0.04
self	13	0.36	0.43*	0.29
self-aggress	13	-0.17	-0.36	-0.04
visual monitor	13	0.59**	0.26	0.16
behavioural change rate	13	-0.47*	0.12	-0.10
stereotypy	13	0.11	0	0.45*
locomotion	13	0.32	0.10	0.19

(1) excludes animal number 15
(2) excludes animal number 6

a persistence test also engage in relatively more solitary behaviour; animals who show a high frequency of attempts to grasp the test object also show more stereotypic behaviour in a free-social situation than do other animals.

Thus there are 3 behaviours in persistence tests which exhibit stable relative rank orders for the animals over changing dominance position and which correlate with various behaviours in a social setting.

In conclusion, behaviour in a persistence test is not related to dominance position, but is reflective of a stable personality trait, and this trait is also related to aspects of social behaviour. Behaviour in isolation is also unrelated to dominance position, but it is felt that the isolation test is unreliable, although this may be due to the high error of measurement inherent in any evaluation of reliability when correlating behaviours over a small sample of tests.

8.5 Can behaviour in stimulus animal tests be related to dominance rank, sex or rearing condition?

(A) Introduction of dominant stimulus animal (DSA). Appendix 12 lists number of 15 second periods each animal in each regroup was seen to engage in a particular behaviour during DSA tests. There were also noticeable differences between the regroups on the introduction of the stimulus animals and these are summarised below. For the sake of clarity, the identity of each animal is designated by the animal's number, followed by his dominance rank in that particular regroup, such that, e.g., 13-2 indicates animal number 13 in position rd2.

Regroup 1. The DSA was not, in fact, dominant in this regroup. On initial introduction to animal number 15-1 DSA immediately presented to him. With the removal of the divider separating the two males from the females of regroup 1 the females supported 15-1 rather than DSA (as also happened in regroup 8). There was a lot of excitement screams, and maintenance of intra-group dominance relations (presenting, support in agonistic interactions versus DSA etc.) and intra-group affiliation. 15-1 exhibited frequent dominance behaviour, in the form of yawns, bouncing and teeth-grinding. 10-5 was equally as aggressive to DSA as 15-1 - she frequently aggressed DSA either on her own, or with or in support of 15-1.

Regroup 2. All regroup members (female) submitted by presenting to DSA on his introduction. DSA mated to ejaculation with 5-2 5 times, and was harrassed on every occasion by 11-3, 3 times by 17-1 and twice by 10-4. 13-5 never harrassed. 17-1 followed DSA more than any other animal in this regroup. 13-5 in general avoided DSA, only presenting, withdrawing or lipsmacking when approached by him.

Regroup 3. (All female). DSA was dominant to all group members who submitted by presenting. There were 3 matings, 2 with 11-2, 1 with 10-3, 5-1 harrassing all of them, 11-2 harrassing 1, 10-3 and 8-5 harrassing 2. 13-4 never harrassed. There were few approaches by regroup members to DSA, and no interactions (affiliative or agonistic) between regroup members.

Regroup 4. (All female). 11-1, 10-2, 2-5 immediately approached and presented to DSA on his introduction. 13-3 and 8-4 presented also on later occasions. DSA mated 5 times, 3 times with 11-1, twice with 10-2. 11-1 harrassed both matings with 10-2, 10-2 harrassed twice, 13-3 once, 2-5 3 times and 8-4 4 times. It was noticeable that 11-1 harrassed for a longer period than did any other animal. There was some aggression between regroup members, particularly 13-3 to 2-5. 11-1 was initially the most disturbed by the introduction of DSA, pacing up and down and maintaining close proximity to DSA.

Regroup 5. (All female). All group members submitted to DSA, although 10-1 was the last to do so. 8-3 was noticeably attentive to DSA - possibly she was in oestrus; she kept a close distance to DSA, affiliation (sex?) rattling to him whilst he mated with other animals, following him and presenting to him. DSA mated 10 times with 4-5, 10-1 and 8-3 harrassing 5 times, 2-4 4 times, 13-2 once. 2-4 is the closest friend of 4-5, the animal who was mated, and was classed as the main harrasser (i.e., harrassed for the longest period of all harrassing animals) on 3 out of the 4 occasions she harrassed. 8-3 was also seen to self-aggress several times after presenting to DSA who would sexually inspect her, but not mount. Interactions between group members were infrequent.

<u>Figure 23</u> Dominant stimulus animal mating with animal number 8 in regroup 6b

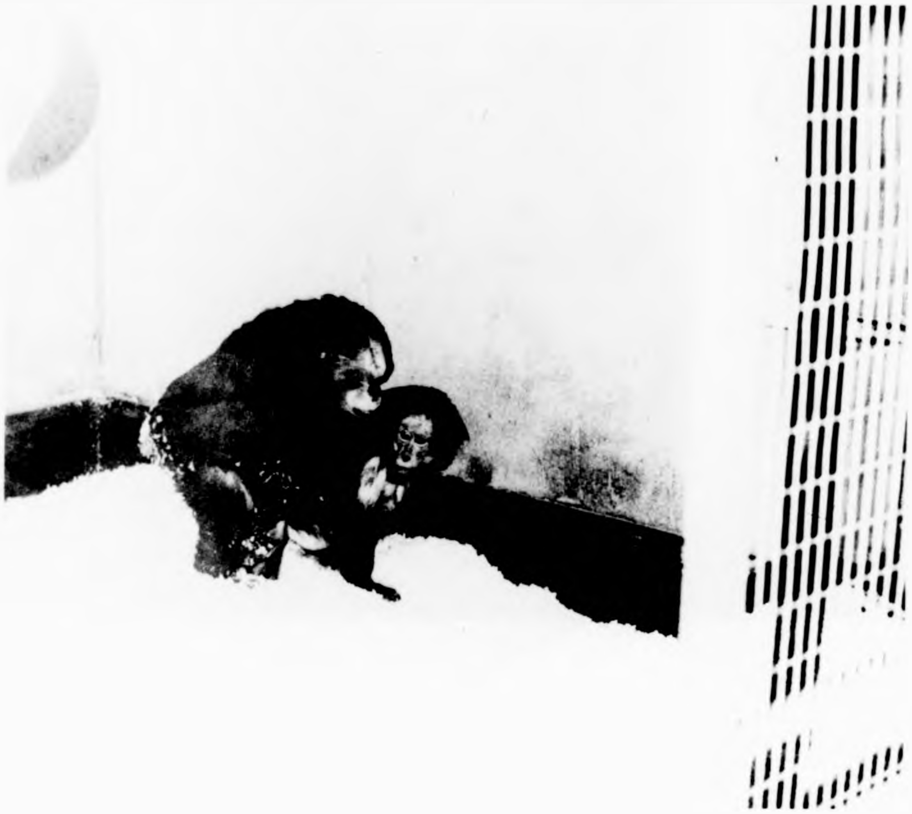


Figure 23 Dominant stimulus animal mating with animal number 8 in regroup 6b

Regroup 6b. (All female). 13-1 presented and followed DSA more frequently than any other regroup member. There were 7 matings, 2 with 13-1, 1 with 8-2 (see Figure 23) and 4 matings with 2-3. 8-2 harrassed on 3 occasions, 4-4 on 1 occasion. 8-2 was also seen to self-aggress after an aborted mating with DSA. There was a certain amount of intra-group affiliation, notably from 13-1 to 2-3 in the form of female sex, aggression and affiliation.

Regroup 7. The introduction of DSA to regroup 7 resulted in some complex interactions. 3-4 (male) immediately aggressed DSA and was supported by 2-2 and 4-3. 13-1 aggressed 3-4, perhaps in appeasement to DSA to whom she lipsmacked and presented. 13-1 and 2-2 maintained high levels of affiliation with each other and later aggressed 3-4 together. The relationship between 13-1 and 3-4 remained equivocal, with 3-4 continuing to aggress 13-1 and DSA, 13-1 responding with aggression back to 3-4 and submitting to DSA. Then 2-2 submitted to DSA, and was mated by him twice and began to aggress 3-4 along with 13-1 and 4-3. DSA later joined in the aggression against 3-4. 25-5 kept a distance but did harrass one mating.

Regroup 8. The introduction of the male DSA to regroup 8 posed problems for 3-1 (male). 3-1 initially aggressed DSA but was not supported in this by the females of the regroup who submitted to DSA. Thereafter 3-1 maintained a distance from DSA, withdrawing if he approached. Later 3-1 was aggressed by 2-2 and 4-3 who were supported by DSA. 25-4 and 27-5 avoided all animals, withdrawing and submitting to DSA on approach. DSA mated 4 times with 4-3 and was harrased 3 times by 2-2, twice by 25-4 and once by 27-5.

Regroup 8b. 2-1 seemed disturbed by the introduction of DSA. She readily submitted to him and was mated 3 times, after which she would withdraw screaming and self-aggressing. Affiliative interactions amongst regroup members were infrequent, although there was alot of aggression, particularly from 25-3 and 27-4 to 6-5.

Regroup 9. Apart from an initial and brief aggressive episode and in contrast to the other occasions on which he encountered DSA 3-1 made no attempt to dominate DSA in this regroup, submitting to him and showing excited affiliation patterns (screaming, mouth-to-mouth etc.) and masturbating. 4-2, 25-3, 27-4 similarly submitted to DSA and all aggressed 6-5, noteably 25-3 who was often the instigator of aggressive bouts against 6-5.

Summary

The effects of the introduction of DSA differ according to regroup composition, both in terms of the individual characteristics of the animals in each regroup and the sex of those animals. In all the single-sex female groups the male DSA was unequivocably dominant, frequently mating the females. In groups including male animals the situation was more complex, sometimes with the females supporting the familiar regroup male (as in regroup 1), sometimes supporting DSA (as in regroup 8). In regroup 1 the introduction of DSA caused excitement and high intra-group affiliative levels. In contrast, interactions between members in other regroups were infrequent, although intra-group aggression was common in regroups composed of more subordinate animals (in the group of 13), and was particularly marked in animal number 25 (rd3 in regroup 8b, rd4 in regroup 8).

There were marked differences in the reactions of each animal to the introduction of the DSA, in terms of fear, aggressive levels etc. Are such differences related to (1) regroup dominance position or (2) sex differences or (3) rearing condition differences?

(1) Regroup dominance position and behaviour during DSA test.

Friedman Anovas were computed between regroup dominance position (using data from all 10 regroups) and the following behaviours during DSA tests; total number of 15 second periods each animal (a) interacted with DSA (either in aggression, affiliation or fear), (b) harrassed a mating by DSA, (c) showed fear to DSA, (d) was involved in aggressive encounters with DSA, (e) was involved in intra-group dominance maintenance behaviour (e.g., aggression/dominance behaviour or fear), (f) was involved in intra-group affiliative behaviour, (g) self-aggressed. The results are given in Table 47.

There are no significant differences between animals when in the 5 regroup dominance positions with respect to; amount of harrassment of matings by DSA, number of aggressive encounters with DSA, amount of intra-group dominance maintenance, amount of intra-group affiliation, amount of

Table 47 **Results of Friedman Anovas, regroup dominance position x behaviour in DSA test (number of groups = 10)**

*p=<0.05 **p=<0.01

Behaviour		Rank sum				χ^2	d.f.
	rd1	rd2	rd3	rd4	rd5		
Interacted + DSA	38	40	29	26	17	14.0**	4
Harrassed matings	31	30	30.5	32	26.5	0.7	4
Show fear to DSA	30.5	42	29	29	19.5	10.3*	4
Aggressive encounter + DSA	37.5	32	28.5	26.5	25.5	3.8	4
Dominance maintenance	35.5	27.5	26.5	32	28.5	2.2	4
Intra-group affiliation	28.5	27	23	n.i.	21.5	2.0	3[+]
Self-aggress	31.5	33	27	27.5	31	1.1	4

[+] (rd4 omitted, since s.d.=0)

self-aggression during DSA test. However there were significant differences between animals in different dominance positions over the 10 regroups with respect to the total amount of interaction with the DSA and the amount of fear shown to DSA (χ^2=14.0 and 10.3, p<0.01 and p<0.05 respectively, d.f.=4); animals in position rd2 show the greatest amount of both total interaction and fear to DSA, then rd1's, rd'3s, rd4's and rd5's show the least total interaction with DSA and the least fear of DSA. The finding that it is rd2 animals who show the greatest amount of interaction with DSA and the most fear of the DSA is perhaps surprising, since it might be expected that the dominant animal of the regroup would interact most, protecting other regroup members from an intruder, putting himself in between DSA and the rest of the group (Bernstein, 1964). Here, it may be that DSA was nearly always dominant, and rarely was his dominance challenged.

(2) Sex differences in behaviour during DSA test.

Mann-Whitney 'U' tests were computed to assess whether there were any sex differences in behaviours during DSA tests, for the same behaviours as in the analyses on regroup dominance position differences. These differences are only calculable for position rd1 and the results are reported in Table 48.

There are no significant differences in position rd1 between the sexes for the following behaviours during the DSA tests; amount of interaction with DSA, amount of harrassment

Table 48 Mann-Whitney 'U' tests on sex differences in DSA tests
Position rd1 only n=8

2 tailed tests

Behaviour	Mann-Whitney 'U'	p	
Interacted + DSA	6	1.00	
Harrassed matings	1	0.09	
show fear to DSA	0	0.046	males n=2, rank sum=3 females n=6, rank sum=33
Aggressive encounter + DSA	12	0.039	males n=2, rank sum=15 females n=6, rank sum=21
Dominance maintenance	9	0.21	
Intra-group affiliation	3	0.25	
self-aggress	4	0.38	

Table 49 Kruskal-Wallis analyses on rearing differences in behaviour
during DSA tests, for each regroup dominance position

*p=<0.05 **p=<0.01

Behaviour	Regroup dominance position				
	1 d.f.=3	2 d.f.=3	3 d.f.=3	4 d.f.=3	5 d.f.=3
Interacted + DSA	2.33	1.58	3.07	4.77	5.44
Harrassed matings	3.67	3.81	2.08	1.66	2.16
show fear to DSA	0.06	3.58	1.08	0.10	4.14
aggressive encounter + DSA	1.81	2.09	1.20	3.50	3.00
dominance maintenance	1.19	2.52	2.95	3.57	1.50
intra-group affiliation	2.48	2.95	3.00	n.c.	3.00
self-aggress	4.11	1.39	3.00	2.00	5.13

of matings by DSA, amount of intra-group dominance maintainance behaviour, amount of intra-group affiliative behaviour, and amount of self-aggression. There are significant differences for; amount of fear shown to DSA (U=0, p=0.045), with female rd1 animals showing significantly more than male rd1 animals, and for number of aggressive encounters with DSA (U=12, p=0.039), rd1 males involved in significantly more aggressive encounters with DSA than rd1 females. Thus in the face of a dominant stimulus animal, dominant males will be more aggressive, and show less fear than will dominant females. Bernstein (1964) reports that dominant males will place themselves in between a dominant intruder and group members, although he does not provide comparable data for dominant female animals. Mitchell (1979) reports that dominant female macaques respond to external challenge by resorting to non-contact forms of aggression, whilst males are more likely to become involved in contact aggression, resulting in serious wounding. Certainly none of the dominant females in the present study overtly challenged the DSA, unlike the dominant males, and in other dominance positions although females did sometimes aggress DSA (e.g., in regroups 1 and 7) this was only ever in support of a male regroup member, and female aggression to DSA never occurred in the single-sexed groups. This is contrary to a finding by Neville (1968) who reports in a free-ranging troop of rhesus macaques which lacked any adult males that the oldest 2 females of the troop would chase off adult males that tried to join their troop.

(3) Rearing condition differences in behaviour during DSA tests.

Kruskal-Wallis analyses were computed for each regroup dominance position to assess rearing differences in behaviours during DSA tests, for the same behaviours as in the analyses on regroup dominance position differences and sex differences. These are reported in Table 49. There are no rearing condition differences in behaviour during DSA tests in any of the regroup dominance positions. There has been no work to date on rearing condition differences in reaction to dominant stimulus animals, although Sackett (1965) reports differences between animals from various rearing conditions in reaction to subordinate stimulus animals.

In summary, individual reactions to the introduction of DSA can be related in part to sex differences and in part to regroup dominance position. However it is not the case that the dominant animal of the regroup is always the main aggressor of the intruder, and neither does he show any differential reaction with respect to maintenance of group cohesion (e.g., intra-group affiliation).

(B) Introduction of subordinate stimulus animal (SSA).

Appendix 13 lists the number of 15 second periods each animal in each regroup was seen to engage in a particular behaviour during SSA tests. Unfortunately, in the middle of the testing period of P2 circumstances beyond experimental control necessitated using a different subordinate stimulus animal for the remaining groups than had been used for previous regroups. The usefulness of this test was then reduced as the regroup animals exhibited different responses to this new SSA (an 11 month old female infant) than to the previous SSA (who was a 4 year old female juvenile). Nevertheless, constant was the fact that the SSA was unfamiliar and younger and smaller than any of the regroup animals, and both SSA's were female.

Regroup 1. SSA=animal number 77. All regroup members in general avoided SSA, either actively withdrawing from her or ignoring her presence. Some animals, noteably 5-3, 11-4, 10-5 even seemed to be afraid of her, responding to her approaches with lipsmacking or presenting. 15-1 did mildly aggress SSA (brow threats) on occasion after she approached him, or would respond to her approach with self-aggression. 15-1 also exhibited dominance behaviour in the form of yawns and dominance bounces in her presence. SSA submitted to all group members by presenting. It was noticeable that all animals, except 15-1 seemed to behave very calmly, avoiding sudden movement and behaving cautiously with respect to SSA.

Regroup 2. SSA=animal number 77. Again, all animals avoided SSA, withdrawing or avoiding her, or lipsmacking and presenting on her approach. SSA even took a raisin from the experimenter in front of 17-1!

Regroup 3. SSA=animal number 46. SSA in general maintained a distance from all regroup members, and aroused a certain amount of curiousity from them. 5-1 in particular would often follow her and initiate grooming. On one occasion

8-5 mildly threatened SSA.

Regroup 4. SSA=animal number 46. After some initial mild threats by 13-3 and 2-5 to SSA there was very little interest in SSA, but the more subordinate members of the regroup did appear to watch her more closely than others.

Regroup 5. SSA=animal number 46. Again the introduction of SSA to regroup 4 did not result in many changes in the behaviour of the regroup animals. 10-1 and 4-5 did occasionally follow SSA and on 2 occasions 2-4 mildly threatened SSA.

Regroup 6b. SSA=animal number 77. Interactions with SSA were infrequent and only of an affiliative nature. 8-2, 2-3 and 4-4 avoided SSA (see Figure 24).

Regroup 7. SSA=animal number 46. 25-5 was quite aggressive to SSA, either threatening her or actively chasing and grabbing her. On one occasion 13-1 who was very affiliative to SSA actually protected SSA by chasing 25-5 away. 2-2 was similarly aggressive to SSA, although less so than 25-5. 4-3 and 3-4 largely ignored SSA.

Regroup 8. SSA=animal number 46. Animal 25-4 (rd5 in regroup 7) was again the most aggressive towards SSA. 3-1 and 27-5 were also aggressive, although this was primarily low key (brow threats). 27-5 was initially not aggressive to SSA, approaching her cautiously, lipsmacking but later joined in the aggressive episodes instigated by 25-4.

8-5 mildly threatened SSA.

Regroup 4. SSA=animal number 46. After some initial mild threats by 13-3 and 2-5 to SSA there was very little interest in SSA, but the more subordinate members of the regroup did appear to watch her more closely than others.

Regroup 5. SSA=animal number 46. Again the introduction of SSA to regroup 4 did not result in many changes in the behaviour of the regroup animals. 10-1 and 4-5 did occasionally follow SSA and on 2 occasions 2-4 mildly threatened SSA.

Regroup 6b. SSA=animal number 77. Interactions with SSA were infrequent and only of an affiliative nature. 8-2, 2-3 and 4-4 avoided SSA (see Figure 24).

Regroup 7. SSA=animal number 46. 25-5 was quite aggressive to SSA, either threatening her or actively chasing and grabbing her. On one occasion 13-1 who was very affiliative to SSA actually protected SSA by chasing 25-5 away. 2-2 was similarly aggressive to SSA, although less so than 25-5. 4-3 and 3-4 largely ignored SSA.

Regroup 8. SSA=animal number 46. Animal 25-4 (rd5 in regroup 7) was again the most aggressive towards SSA. 3-1 and 27-5 were also aggressive, although this was primarily low key (brow threats). 27-5 was initially not aggressive to SSA, approaching her cautiously, lipsmacking but later joined in the aggressive episodes instigated by 25-4.

Figure 24 Subordinate stimulus animal number 77 with animal number 8 in regroup 6b

Figure 24 Subordinate stimulus animal number 77 with animal number 8 in regroup 6b

Regroup 8b. SSA=animal number 77. As in other tests with the infant SSA all animals (apart from 6-5 who ignored her) exhibited cautious reactions to her, lipsmacking, presenting and withdrawing on approach. Even 25-3 (rd5 in regroup 7, rd4 in regroup 8) normally aggressive to the juvenile SSA acted calmly and neutrally to the infant SSA. 2-1 exhibited some dominance behaviour, yawning on occasion while SSA was presenting to her.

Regroup 9. SSA=animal number 46. 3-1 was the most aggressive to SSA, both at low levels (brow threats) and high levels (chasing and biting). 25-3 was also aggressive, although mainly at a low level. 4-2 was the most affiliative to SSA, grooming her frequently and was never aggressive. 27-4 approached SSA carefully, and also groomed her. 6-5 ignored SSA.

In summary, the success of the SSA tests in eliciting marked differences in the behaviour of the group members was limited by the ages and dispositions of the SSA's. The female infant SSA (animal number 77) was generally treated cautiously and often the animals (noteably the females) displayed fear reactions. This can be perhaps explained by the females displaying poor mothering behaviour, rejection and fear responses towards even their own infants. The juvenile female SSA did not elicit any fear reactions but behaved so subordinately, cringing, cowering and self-huddling that she was of little threat to the dominance status of any of the regroup members. It is perhaps noteable that the only rd1 animals to exhibit aggression or dominance behaviour towards

SSA were males, although animal number 2 (rd1 in regroup 8b) yawned on approach by SSA.

Again, individual differences are apparent; in regroups 7,8,9 one animal (number 25) was particularly aggressive, even though the cowering SSA really offered no serious threat to her dominance position. In contrast, animal number 27 (rd4 in regroups 8b and 9, rd5 in regroup 8) seemed to sense how upset SSA was, and approached her with care and was affiliative.

There were marked differences in reaction to the introduction of SSA, in terms of fear, aggressive levels etc. These will be considered in relation to (1) regroup dominance position, (2) sex differences and (3) rearing condition differences.

(1) Regroup dominance position and behaviour during SSA test.

Friedman Anovas were computed between regroup dominance position and the following behaviours during SSA tests; total number of 15 second periods each animal (a) interacted with SSA (either in aggression, affiliation etc.), (b) showed fear to SSA, (c) showed aggression to SSA, (d) was affiliative to SSA, (e) received fear from SSA, (f) was involved in intra-group dominance maintenance behaviour, (e.g., aggression/dominance behaviour or fear), (g) was involved in intra-group affiliative behaviour, (h) self-aggressed.
The results are given in Table 50.

Table 50 Results of Friedman Anovas, regroup dominance position x behaviour in SSA test (number of groups = 10)

*p=<0.05 **p=<0.01

Behaviour	Rank sum					χ^2	d.f.	
	rd1	rd2	rd3	rd4	rd5			
Interacted + SSA	43.5	26.5	25	23.5	31.5	10.6*	4	
showed fear to SSA	30	33.5	30.5	27.5	28.5	0.8	4	
Aggress SSA	30.5	26	27.5	31	35	1.9	4	
Affiliate + SSA	38	31	27.5	27	26.5	3.7	4	
Fear from SSA	42.5	23.5	28.5	24.5	31	9.3	4	(p=0.055)
Dominance maintenance	25	16	19	n.i.	n.i.	4.2	2[+]	
Intra-group affiliation	27	33.5	32.5	29	28	1.3	4	
self-aggress	32	32	28.5	29.5	28	0.6	4	

[+] rd4, rd5 never showed this

There are no significant differences between regroup dominance position for the following behaviours in the SSA test; amount of fear shown to SSA, amount of aggression shown to SSA, amount of affiliation shown to SSA, amount of intra-group dominance maintenance. behaviour, amount of intra-group affiliation, amount of self-aggression. There are significant differences for amount of total interaction with SSA (χ^2=10.6, d.f.=4, $p<0.05$) with rd1's showing the highest levels, then rd5, rd3, rd4, rd2. The differences between the amount of fear expressed by SSA to animals in each regroup dominance position just fails to reach significance (χ^2=9.3, d.f.=4, $p=0.055$), but it is worth mentioning that the SSA expresses most fear to rd1 animals. Obviously, combining data from the 2 SSA tests which used different stimulus animals may not be appropriate, as the reactions of the animals were very different toward each SSA.

(2) Sex differences in behaviour during SSA test.

Mann-Whitney 'U' tests were computed to assess whether there were any sex differences in behaviours during SSA tests, for the same behaviours as in the analyses on regroup dominance position differences. These differences are only calculable for rd1. The results are given in Table 51.

The only significant sex difference is between the sexes for amount of aggression shown to SSA ($U=12$, $p=0.008$) with males showing significantly more than females. Southwick & Siddiqi (1972) found that when an infant is introduced to a group of rhesus monkeys neither sex shows intolerance or

Table 51 Mann-Whitney 'U' tests on sex differences in SSA tests
Position rd1 only n=8

2 tailed tests

Behaviour	Mann-Whitney 'U'	p	
Interact + SSA	11	0.10	
Fear to SSA	6	1.00	
Aggress SSA	12	0.008	males n=2, rank sum=15
Affiliate to SSA	4	0.48	females n=6, rank sum=21
Fear from SSA	9	0.24	
Dominance maintenance	8	0.40	
Intra-group affiliation	9	0.08	
Self-aggress	9	0.08	

Table 52 Kruskal-Wallis analyses on rearing differences in behaviour
during SSA tests, for each regroup dominance position

*p=<0.05 **p=<0.01

Behaviour	Regroup dominance position				
	1 d.f.=3	2 d.f.=3	3 d.f.=3	4 d.f.=3	5 d.f.=3
Interacted + SSA	1.14	5.41	3.85	5.36	1.75
Showed fear of SSA	4.81	2.41	1.77	2.00	7.00
Showed aggression to SSA	2.33	3.00	4.67	3.05	2.00
Affiliative to SSA	1.75	6.12	3.94	6.37	3.89
Showed fear from SSA	5.16	5.25	1.93	5.75	2.37
Dominance maintenance	0.32	3.89	2.42	n.c.	n.c.
intra-group affiliation	3.00	5.19	2.41	2.00	3.00
self-aggress	3.00	1.39	3.00	2.00	3.00

aggression, although Mitchell (1979) reports sex differences in the reaction to an infant being threatened from outside the group; while both sexes assume a protective role females usually pick up the infant and retreat from danger, threatening the intruder, whereas adult males tend to place themselves between the intruder and the infant and attack or threaten.

(3) Rearing condition differences in behaviour during SSA tests.

Kruskal-Wallis analyses were computed for each regroup dominance position to assess rearing differences in behaviours during SSA tests, for the same behaviours as in the analyses on regroup dominance position differences and sex differences. These are reported in Table 52.

There are no rearing condition differences in behaviour during SSA tests in any of the regroup dominance positions. Sackett (1965) reports differences between animals from various rearing conditions in reaction to subordinate stimulus animals; motherless-mother reared infants were almost twice as aggressive as feral reared infants, and the degree of aggression towards a stimulus animal decreased as the amount of isolation experienced from birth increased, with animals who had experienced 1 year of isolation showing the least aggression.

In summary, the success of the SSA test was limited by the nature of the stimulus animals used, who either represented little threat to even the most subordinate members of the regroups or else, in the case of the infant stimulus animal actually elicited fearful reactions from the regroup members. However there were significant differences between the animals' reactions to the SSA, noteably the total amount of interaction with SSA, with the dominant animals of each regroup interacting with SSA the most, and the amount of aggression directed to the SSA, male dominant animals showing more aggression to SSA than female dominant animals.

Chapter 9. THE INFLUENCE OF FRIENDSHIP PATTERNS ON AFFILIATIVE BEHAVIOUR, THE PERSON X SITUATION ISSUE AND THE PROSPECTS FOR PERSONALITY RESEARCH

9.1 You need friends...

Two weeks after the end of Phase 2 data were collected on all animals living in the stable group of 13 animals. It was argued that after two weeks the group would have settled into a normal pattern of interaction, and the usual dominance hierarchy would have become established. A milk bottle dominance test, run with all animals shut out in the outside area confirmed this; the dominance order was 15, 17, 5, 11, 10, 13, 8, 2, 4, 3, 25, 27, 6. Over the next two weeks a hour of data was collected on each animal, using the DTU and behaviour categories similar to those used in P2, but with a more detailed 'direction' category, which used a different code for every animal. Every animal was tested every 2 days, with the same random order as used in P2 DTU testing for 10 minutes per day. From this data the pattern of affiliative interactions in the stable group was determined; it was felt that this would have some bearing on affiliative behaviour in the regroup phase, in terms of which animals each animal was grouped with and how 'friendly' these animals were. Table 53 presents a matrix of the affiliative relationships between the 13 animals in the stable group, and indicates that animals interact most with those animals most adjacent to themselves in the dominance hierarchy. To test whether this is a significant effect, a paired t test was computed which compared the percentage time each animal spent in affiliative

Table 53 Affiliative patterns in the stable group of 13 animals. Percentage affiliation over 2 weeks of data.

	Target animal												
	15	17	5	11	10	13	8	2	4	3	25	27	6
dominance rank	1	2	3	4	5	6	7	8	9	10	11	12	13
Initiating animal													
15	–	15	0	0	7	0	0	0	0	0	0	0	0
17	69	–	17	0	0	0	0	0	1	0	0	0	0
5	1	0	–	1	11	0	2	1	3	0	0	0	2
11	16	0	9	–	16	0	0	0	0	0	0	0	0
10	27	0	0	22	–	0	0	0	0	0	0	0	0
13	0	0	2	28	1	–	2	0	0	31	0	8	0
8	0	0	0	0	0	0	–	0	4	0	1	2	0
2	0	0	0	0	0	0	0	–	1	16	0	10	16
4	0	0	0	5	0	0	12	31	–	14	0	0	0
3	0	0	0	0	0	0	0	0	1	–	0	0	0
25	0	0	1	0	1	0	0	0	2	0	–	18	0
27	0	0	5	0	0	0	0	0	0	0	4	–	0
6	0	0	0	0	0	0	0	0	0	0	0	0	–

behaviour with immediately adjacent animals (either one rank above or below himself, divided by the number of adjacent animals) with the percentage time each animal spent in affiliative behaviour with non-adjacent animals (divided by the number of non-adjacent animals), regardless of who initiated the interaction. The result of this test is also given in Table 54.

Table 54 shows that there is a significant difference between the amount of affiliation between adjacent and non-adjacent animals; animals are significantly more affiliative with animals of adjacent dominance rank to themselves than to non-adjacent animals ($t=2.62$, $p<0.05$, d.f.=12). In 7 out of the 9 regroups in P2 animals occupying rd1 and rd5 positions did not have one of their normal adjacent partners (in the group of 13) to interact with, unlike those animals in positions rd2, rd3 and rd4. One would expect therefore, since they have lost one of their usual friends, that rd1 and rd5 animals would be less affiliative in these regroups than animals in the other regroup dominance positions. in Section 6.2 the Friedman analysis for differences in affiliation total between animals in different dominance positions in 6 regroups just failed to reach significance, but animals in positions rd2/rd3 showed the highest levels, then rd1/rd4 animals, with rd5 animals showing the least total affiliation.

Table 54 **Total percentage affiliative behaviour with adjacent and non-adjacent animals in Phase 3.**

	adjacent		non-adjacent	
Animal number	n	% affiliation	n	% affiliation
15	1	84.0	11	4.6
17	2	50.5	10	0.1
5	2	13.5	10	2.8
11	2	24.0	10	4.9
10	2	19.5	10	4.6
13	2	1.5	10	6.9
8	2	1.0	10	2.1
2	2	16.0	10	4.3
4	2	23.5	10	2.5
3	2	7.5	10	4.7
25	2	11.0	10	0.3
27	2	11.0	10	2.5
6	1	0	11	1.6

paired t test, $t=2.62$, $p<0.05$, d.f.$=12$.

Does the amount that animals interact with other animals in the stable group reflect how much they interact with the same animals in in the regroup phase? How stable are friendship patterns over changing group composition and do animals change their affiliative interactions according to which other animals are also in the regroups? A Kendall correlation coefficient was computed between the total percentage of time each animal in each regroup dominance position he experienced was affiliative to other animals in that regroup and his total percentage affiliation with those same animals in P3, over all data cases (n=41). This coefficient is reported in Table 55, and shows that there is a significant correlation between the amount of time animals spend in affiliative interaction with other animals in each regroup and the amount of time they interact affiliatively with the same 4 animals in the stable group of 13 (tau=0.31, n=41, $p<0.005$). Thus an animal in a regroup containing animals with which he does not interact in the stable group is likely to show lower levels of affiliation than when in a regroup composed of his friends, and this will be particularly marked in the case of rd1 and rd5 animals who have lost one of their usually adjacent friends. This shows the importance of the situation for affiliative behaviour; in Chapter 7 (Sections 7.3, 7.4, 7.5) it was shown that affiliation total achieved neither relative nor absolute consistency over changing dominance position; affiliation initiate showed relatively consistency but only at $p<0.1$ and not absolute consistency; affiliation receive showed absolute consistency and relative consistency only at $p<0.1$. There is

Table 55 Percentage affiliation with animals at each regroup dominance position for each animal in phases 2 and 3.

Animal number	Regroup number	Other animals in that same regroup				% affiliation in regroup (P2)	% affiliation in stable group (P3)
15	1	17	5	11	10	418	135
17	2	5	11	10	13	70	17
17	1	15	5	11	10	312	101
5	3	11	10	13	8	283	25
5	2	17	11	10	13	71	40
5	1	15	17	11	10	168	39
11	4	10	8	13	2	112	66
11	3	5	10	13	8	214	76
11	2	17	5	10	13	132	76
11	1	15	17	5	10	191	64
10	5	13	8	2	4	97	1
10	4	11	8	13	2	154	39
10	3	5	11	13	8	216	50
10	4	17	5	11	13	124	50
10	1	15	17	5	11	64	79
13	7	2	4	3	25	100	31
13	5	10	8	2	4	179	3
13	4	11	10	8	2	260	31
13	3	5	11	10	8	228	33
13	2	17	5	11	10	65	31
8	6b	13	2	4	25	78	19
8	5	10	13	2	4	205	18
8	4	11	10	13	2	65	2
8	3	5	11	10	13	64	4
2	8b	4	25	27	6	72	58
2	7	13	4	3	25	191	48
2	6b	13	8	4	25	81	32
2	5	10	13	8	4	184	32
2	4	11	10	8	13	136	0
4	9	3	25	27	6	43	15
4	7	13	2	3	25	160	47
4	6b	13	8	2	25	130	48
4	5	10	13	8	2	131	48
3	8	2	4	25	27	57	31
3	7	13	2	4	25	121	62
25	9	3	4	27	6	131	22
25	8	2	4	3	27	27	22
25	7	13	2	4	3	0	0
27	9	3	4	25	6	56	22
27	8	2	4	3	25	30	32
6	9	3	4	25	27	0	0

tau=0.31, n=41, $p<0.005$

certainly evidence for a strong situation effect on affiliative behaviour, and whether an animal's friends are regrouped with him has more of an effect on his affiliation levels than does his dominance rank.

9.2 What are the respective contributions of person, situation and person x situation variables to behaviour?

The debate concerning the respective contributions of person and situation variables to individual differences in behaviour has converged on an 'interactionist' position, that the person x situation interaction accounts for more of the observed variance in behaviour than either person or situation variables alone (Bowers, 1973; Argyle & Little, 1972; Endler, 1973). This has resulted in lively debate as to which is most important, individuals, situations or their interaction.

To investigate the relative contributions of person (here, animal), situation (here, dominance position) and animal x dominance position effects, 2 way Anovas were computed, using 3 different samples of animals in various dominance positions. The contributions of animals, dominance positions and animals x dominance positions were examined for the following behaviours; fear, explore, aggression, affiliation initiate, affiliation receive and self behaviour, using weeks per dominance position per animal as a repeated measures within subjects. The first set of analyses used data from 5 animals, numbers 10,13,8,2,4, for 4 dominance positions (rd2, rd3, rd4, rd5); the second set of analyses used data from 5 animals, numbers 5,11,10,13,2, for 3 dominance positions (rd1, rd2, rd3); the third set of analyses used data from 3 animals, numbers 10,13,2 in all 5 regroup dominance positions. The rationale behind the selection of these particular animals was the desire to maximise the number of available data points (= animals x dominance positions). The Anova model used was a mixed model, in which the 'F' ratio for column (here, dominance position) effects is computed by dividing the column mean square by the mean square for the interaction term, rather than by the error term (see Hays, 1974, p.556). Table 56 reports the results of these analyses, which are summarised in Table 57.

From Table 56 it can be seen that the significance of animal, dominance position and animal x dominance position effects vary both according to the particular behaviour in question and the particular sample of animals. Leaving aside the validity of partitioning variance in this Anova approach to personality assessment, it can be seen from the summary table that the effects of animal (person), dominance position (situation) and animal x dominance position interaction (person x situation) vary from one analysis to the next. Evidently studies can be 'arranged' so that the situation or the person or the interaction between the two accounts for the majority of the variance. 'Accordingly, it will never be possible to give definite answers in terms of relative variance contributions to the question of whether individual differences or situational factors or their interaction are more important in determining behaviour' (Olweus, 1977). According to Anastasi (1958), this way of framing the question

Table 56 Results from 2 way anovas to assess the importance of animal, dominance position and animal x dominance position effects on social behaviour.

*p=<0.05 **p=<0.01

Behaviour	Analysis 1		Analysis 2		Analysis 3	
Animal numbers	10, 13, 8, 2, 4		5, 11, 10, 13, 2		10, 13, 2	
Dominance positions	rd2, rd3, rd4, rd5		rd1, rd2, rd3		rd1, rd2, rd3, rd4, rd5	
Behaviour	F	d.f.	F	d.f.	F	d.f.
Fear:						
animal effect	1.23	4	3.69*	4	3.95*	2
rd effect	2.33	3	1.70	1(i)	0.53	3(i)
a x rd effect	1.48	12	2.48*	4	4.64*	6
Explore:						
animal effect	1.24	4	1.15	4	0.94	2
rd effect	0.50	3	0.26	2	0.78	4
a x rd effect	1.42	12	3.64**	8	2.84**	8
Aggression:						
animal effect	6.94**	4	5.22**	4	9.55**	2
rd effect	3.67	2(ii)	0.50	2	9.72*	3(ii)
a x rd effect	1.14	8	2.06	8	0.64	6
Affiliation:						
(a) initiate						
animal effect	9.36**	4	3.01*	4	12.54**	2
rd effect	0.79	3	0.45	2	1.31	4
a x rd effect	2.44*	12	1.18	8	1.87	8
(b) receive						
animal effect	2.27	4	1.80	4	4.94*	2
rd effect	1.53	3	2.63	2	1.67	4
a x rd effect	1.72	12	1.87	8	1.70	8
Self						
animal effect	4.54**	4	0.65	4	0.98	2
rd effect	1.88	3	0.17	2	2.81	4
a x rd effect	2.24*	12	1.90	8	1.49	8

note; (i) analysis does not include rd1 (s.d. = 0)
(ii) analysis does not include rd5 (s.d. = 0)

Table 57
Significant effects show by each of the 3 different analyses:

Behaviour		Analysis	
	1	2	3
Fear	no effects	animal effects a x rd interaction	animal effects a x rd interaction
Explore	no effects	a x rd interaction	a x rd interaction
Aggression	animal effects	animal effects	animal effects rd effects
Affiliation			
initiate	animal effects a x rd interaction	animal effects	animal effects
receive	no effects	no effects	animal effects
Self	animal effect a x rd interaction	no effects	no effects

is inappropriate, and a more fruitful approach is to be found in the question 'how do these variables interact?'.

9.3 Coherence in personality and the prospects for personality research

Neither a trait/state theory of personality nor a pure situationalist theory can explain all of an individual's behaviour. Chapter 7 showed the effects of both personality and situations on behaviour, although the contribution of each variable varied for different behaviours. Thus exploratory behaviour was situation-free and personality dependent; self behaviour was situationally dependent and showed neither absolute nor relative consistency; fear and aggressive behaviour were products of both situation and personality, subordinate animals showing more fear behaviour and less aggressive behaviour, although absolute levels of fear and aggression were personality dependent. If neither the trait/state nor the situational specificity theory of behaviour can account for the behaviour of individuals over changing dominance position then what might be an alternative strategy? Magnusson & Endler (1977) discuss a possible alternative - the concept of 'coherence' which refers to behaviour that is 'inherently lawful' and hence predictable without necessarily being consistent in either absolute or relative terms. 'Coherence means that the individual's pattern of stable and changing behaviour across situations of different kinds is characteristic of him or her and may be interpreted in a meaningful way within the interaction model' (Magnusson & Endler, 1977, p.7). Figure 25 (from Magnusson &

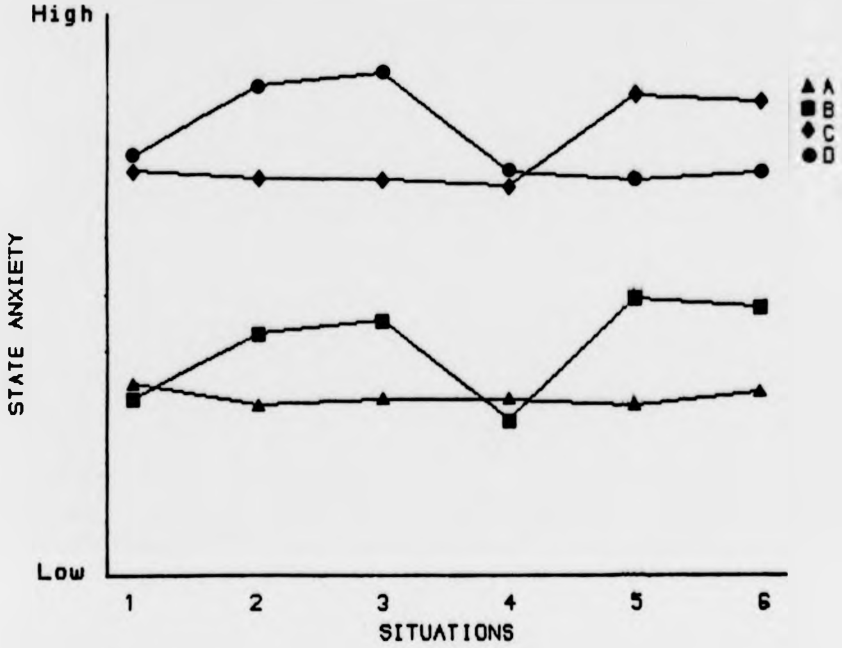


Figure 25 (from Magnusson & Endler, 1977) Anxiety profiles for 4 individuals over 6 situations

Endler, 1977) illustrates the state anxiety profiles for 4 individuals across 6 different situations; the 4 profiles can be assumed to be characteristic for the 4 individuals' ways of reacting to these different types of situations. Figure 25 also illustrates that (1) individuals can differ with regard to mean level of state anxiety across situations of different kinds (compare profiles for A and D); (2) that individuals with the same mean level of state anxiety across situations differ in a systematic and predictable way in their pattern of state anxiety reaction across different situations (compare profiles for C and D). According to Magnusson & Endler behaviour is consistent in the sense of coherence because an individual behaves in a way that can be predicted for each situation under the conditions that (1) the interpretation and meaning of the situation to the individual is known, (2) the individual's disposition to react in that kind of situation is known, and (3) there is a psychological theory providing the links between factors (1) and (2).

How might we best understand the link between personality and situational variables? Mischel (1973) believes that we must study cognitive social learning variables in order to understand the behaviour of an individual in a particular situation, such as the individual's competence in generating adaptive behaviours that will be of benefit to him in a situation, his individual encoding and categorisation of events, his expectancies of a situation, his subjective values of the outcome of the situation and his self-regulating systems and goals. By studying such variables Mischel believes that we can better understand why a person behaves in a particular way in a particular situation.

Figure 26 (from Forgas & Schulman, 1979) presents a diagram of the complex interaction between the individual person and the situation. It follows that if we are to understand the behaviour of an individual within a situation we must understand (1) the way in which the individual perceives the situation (in terms of his expectancies, constructs, goals etc.), (2) how the person influences the situation and (3) how the situation affects the individual (in terms of prescribing, limiting or sanctioning his behaviour). There are many studies which, using cognitive social learning theory, have shown considerable success at arriving at a better understanding of the complex interaction between person and situational variables (review by Mischel, 1973) yet such a theory cannot be easily applied to the study of animal personality; we cannot determine how an individual animal encodes situations, what his goals are, his expectancies and subjective values. As Mischel (1973) notes, rats and pigeons (and monkeys) cannot tell us their expectancies or goals. Thus while measurement of such variables in human personality research (using verbal reports) can considerably improve the understanding of behaviour, we cannot make such measurements in animal personality research and are forced to rely solely on the measurement of overt behaviour as our data. We are similarly limited in our ability to assess situations; several studies, using questionnaires, have sought to identify how different situations might be characterised (Bem & Funder,

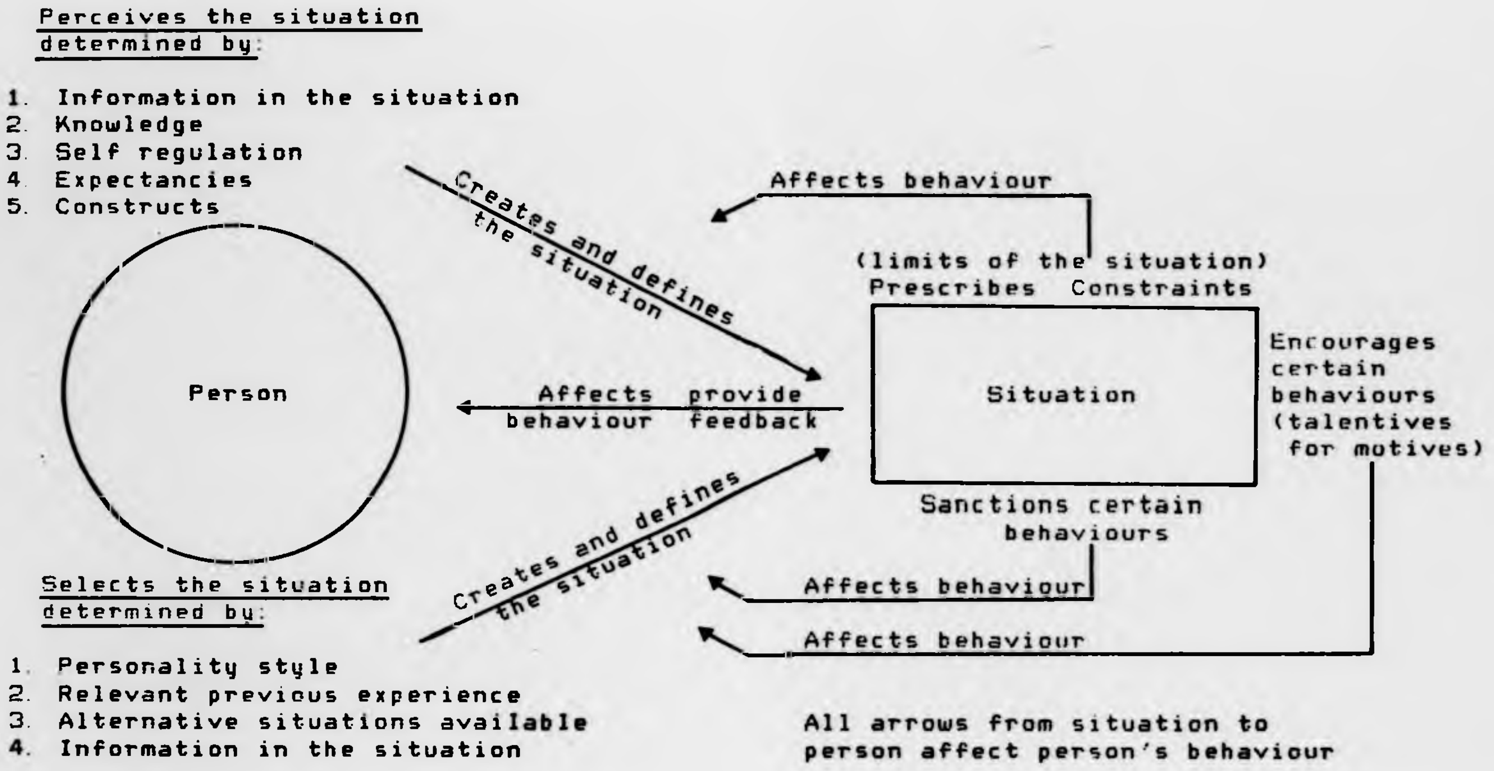


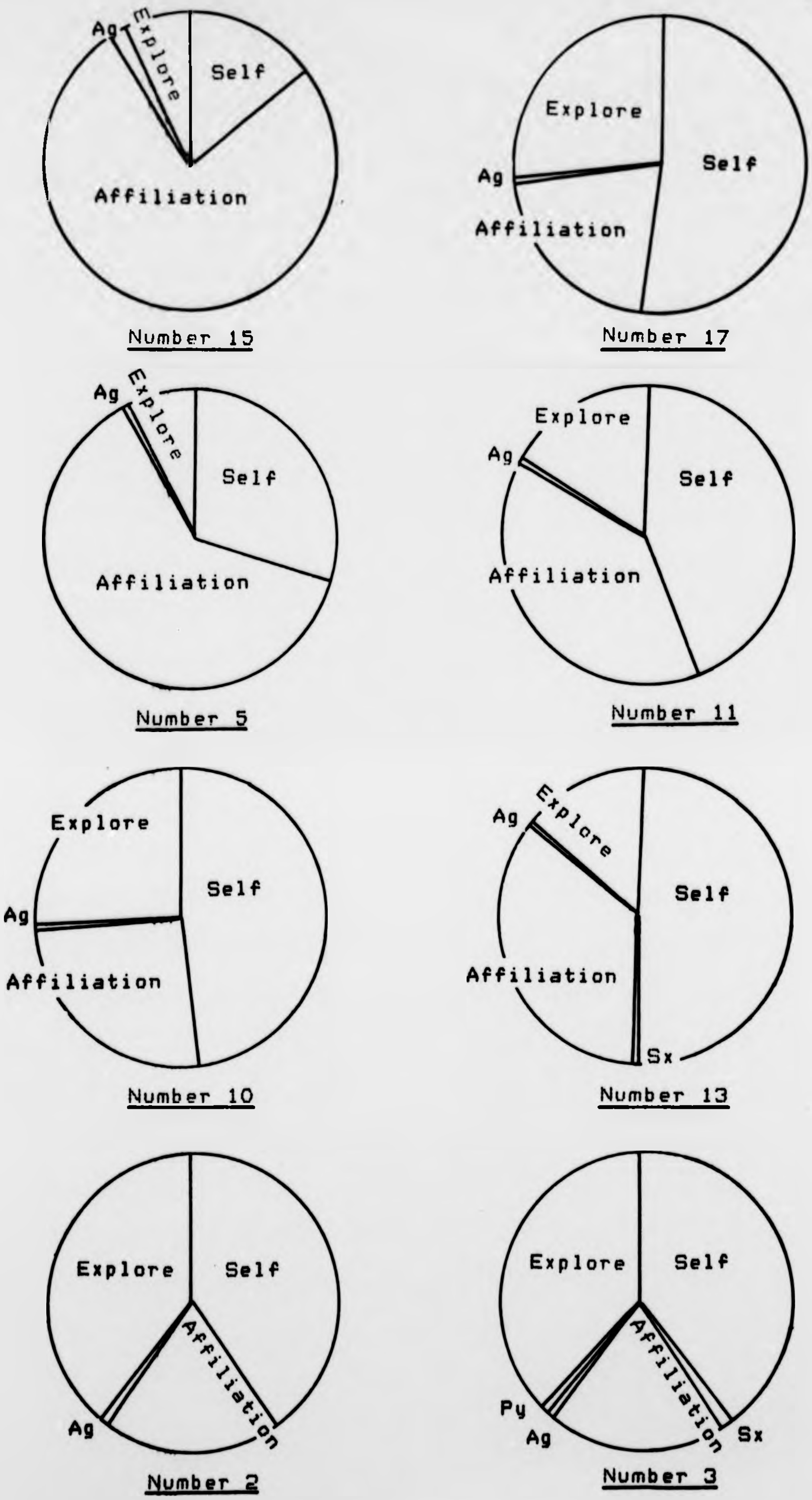
Figure 26 (from Forgas & Schulman, 1979) The complex interaction between person and environment. The situation provides incentives to behaviour or inhibits behaviour. Thus the situation is perceived as having positive and/or negative press. The person, in turn, creates and defines the situation through selective perception and attention. The interaction is bi-interactional with constant feed-back.

1978; Magnusson, 1971; Magnusson & Ekekhammar, 1973, 1978). Such is the fortune of the human personality theorist.

However universal we would like our theory of personality to be it is evident that there are no principles concerning the relationship between dominance (situation) and behaviour which are applicable to all animals. This is evident from studying individual cases; for example, despite the trend over all animals for a positive correlation between increasing subordinancy and amount of fear behaviour (Section 6.1) animal number 2 shows no such trend (the correlation between dominance position and her fear levels over changing dominance position =0, n=5). Thus we cannot apply the principle that increased subordinancy results in increased levels of fear for this particular animal. Similarly, despite evidence over all animals for absolute consistency over changing dominance positions in rate of behavioural change (Section 7.3) both animal numbers 5 and 13 show unstable levels (i.e., no consistency) of behavioural change rate over changing dominance position. Furthermore, for those behaviours which do not show absolute consistency over all animals (e.g., stereotypy) the relationship between dominance position and these behaviours is different for different animals; animal number 13 shows her highest levels of stereotypy when in position rd5, yet animal number 2 is the least stereotypic in position rd5 relative to other positions she occupies, and shows her highest levels of stereotypy in position rd3. Evidently the effects of changes in dominance position are different for different animals. For some animals (e.g., numbers 11, 4) the effects of changes in dominance position are minimal. Conversely, other animals (e.g., number 13) are more affected by situational changes. Campus (1974) concluded that the low correlations often found between behaviours across different situations result in part from the fact that some individuals are highly consistent in their behaviour cross-situationally while other individuals are not consistent at all, and that consistency itself could be considered to be a personality trait. Epstein (1979) found similar individual differences in consistency, with a few individuals showing highly stable behaviour over changing situations, others showing almost no stability in behaviour with most individuals showing moderate stability. Cummings (1939) found that the degree of variability shown by subjects correlated negatively with persistence and introversion and that highly variable individuals were rated by others as original, imaginative and talkative while low variability individuals were regarded as conventional, thorough and pugnacious. Campus (1974) reports that consistency in behaviour over different situations is positively correlated with extraversion (contrary to the finding of Cummings) but negatively correlated with anxiety, overt hostility (as Cummings found) and hostility turned inward (e.g., shame and self-punitiveness). The present study also found a relationship between degree of consistency in behaviour over changing dominance position and other behaviour; there was a negative correlation between degree of inconsistency and relative rankings on the amount of behavioural change (Table 36, tau=-0.52, n=11, p<0.032) and a positive correlation between degree of inconsistency and relative rankings on self-aggression (tau=0.51, n=11, p<0.017). Thus animals who display the most consistency in behaviour over changing dominance position have a lower rate of behavioural change than do less consistent animals and are also less self-aggressive (supporting the finding of Campus). Campus also reports that for the consistent person the characteristics of the person accounted for a major part of the behavioural variance, whereas for inconsistent people the important determinants of behaviour were the situations or the interaction between person and situational variables. Campus argues that since the inconsistent individual changes his definition of himself in accordance with his interpretation of the demands of the situation he may be regarded as situationally bound in the way that he perceives himself. On the other hand, it may be that individual behaviour is more similar across situations which are perceived and interpreted as similar by the individual than across situations which are perceived as less similar (Magnusson & Ekehammar, 1978). If we can measure how each individual perceives each situation then we can relate changes in individual behaviour from situation to situation to information about how the individual perceives these situations (Magnusson, 1971; Magnusson & Ekehammar, 1973, 1978).

Bem (1972) considers what sort of individuals might display trait-like consistency. He offers as an example the defensive person who monitors his behaviour in order to maintain a particular self-presentation and who may be unwilling to alter his behaviour according to the situation. Bem argues that this image-maintenance process may be important for dealing with individual differences in personality and suggests that further research in human personality might attempt to obtain from the individual those traits that are central for his self-concept (e.g., as Kelly's Role Construct Repertory Test does). Baldwin (1942) provides interesting evidence that the organisation of personality variables within an individual may differ from the pattern of personality variables derived from group studies. From a sequence of 20 daily ratings of each of 4 children an intra-individual factor analysis of each child was obtained. These intra-individual factors were compared with those obtained from a group factor analysis. While there was a certain degree of similarity between the factors obtained from 3 of the 4 individual factor analyses and those of the group factor analysis, the results of the factor analysis of the fourth child were markedly different. The first factor, 'temporal change' reflected the process of adjustment over time to the nursery school situation, and the group factor analysis revealed that this process was generally characterised by increases in affectionateness, curiousity, cheerfulness and decreases in social withdrawal and inactivity. However, for each individual child there were other variables related to this adjustment process which did not receive high loadings in the group analysis, reflecting each child's uniqueness. A second factor, 'conformity', also showed individual differences; the individual factor analysis of one child indicated that conformity was related to non-cruelty and non-quarrelsomeness; with another child, conformity was related to friendliness, sense of humour and non-resistance. Some children responded to various authorities (e.g., a child leader in the group, abstract nursery school standards, the teacher) in the same way, either with rebelliousness or conformity. Hence for these children, the similarity of response was evidence that for the child these situations were equivalent. Other children responded differently to the various authorities, by obeying the teacher and conforming to established rules but resisting the bossing of a peer. For these children, the 3 types of situations (authorities) were not equivalent. There were further individual differences evident in the children with respect to rebelliousness, which for one child was positively correlated with emotional expression (temper tantrums), for another child with social withdrawal and for another child with talking and arguing. Baldwin's study shows the idiosyncratic organisation of behaviour within an individual and thus provides encouragement for an ideographic approach to personality and questions the predictive utility of common, group-derived personality traits (Mischel, 1973).

Figure 27 illustrates individual differences in the behaviour of the 8 animals who experienced a position of dominance (rd1) in this study. There were significant differences between the 8 animals with respect to amount of exploratory, affiliative and aggressive behaviour expressed when dominant (Section 7.1). The individual behavioural profiles indicate that, as dominants, animal numbers 15 and 5



Number 15 Number 17

Number 5 Number 11

Number 10 Number 13

Number 2 Number 3

Figure 27 Behavioural profiles for 8 animals when dominant (rd1)

Ag=Aggression Py=Play Sx=Sex

were primarily affiliative, animals 17, 10 and 13 engaged primarily in solitary activities, animals 2 and 3 were primarily exploratory. Animal number 15 was the most aggressive, animal number 11 the least aggressive. There is evidence suggesting that the social structure of a group of monkeys may be affected by the personality of the animals within that group. Yamada (1971) noted differences between 5 groups of Japanese macaques with respect to tolerance levels in adult males and the rejectiveness of the females. In groups composed of animals with rejective characters and less tolerant males there was a greater distance between animals at feeding sites than in groups composed of less rejecting and more tolerant individuals. In addition, the composition of each group with respect to the aggressiveness of the high-ranking males and the rejectiveness of the females determined the success or failure of the peripheral males' attempts to penetrate the central part of the group (to gain access to food or oestrus females). Yamada concludes that while dominance rank is of great importance in the social order there is a lot of characteristic behaviour which is not related to rank, and that there are aspects of social structure which are determined by factors other than rank. The importance of the personality of alpha males in the maintenance of the home range of a troop has also been noted (Pirta & Singh, 1980), as has the effect of personality on aggressive levels, both inter- and intra-group (Hanby, 1980).

In the present study there was a significant difference between the 9 regroups with respect to amount of affiliative behaviour over the 4 weeks during which each regroup existed, and this was related to the composition of the regroups with respect to the dominance ranks of the animals in the stable group of 13 - regroups composed of previously more dominant animals showed higher levels of affiliation than did those composed of previously more subordinate animals. Although it was not possible to make statistical estimates of regroup differences in behaviour in the DSA or SSA tests it was evident that such differences did exist; regroup number 1, who showed the greatest amount of affiliation during free-social behaviour testing (see Appendix 5) also showed high levels of intra-group affiliative behaviour during DSA and SSA tests and high levels of intra-group dominance maintenance behaviour (see Appendices 12 and 13). In regroups showing lower levels of affiliation during free-social behaviour (e.g., regroup number 9), there were higher levels of aggression during free-social behaviour testing. During stimulus animal tests these 'low affiliative' regroups showed very little intra-group affiliative behaviour but high levels of intra-group dominance maintenance, mainly of an aggressive nature as opposed to the presenting, supporting other regroup members in agonistic encounters with the DSA that occurred in more affiliative regroups (e.g., regroup number 1). Thus the personalities of the individual animals in a group may have important consequences for the group in terms of group cohesion (also noted by Hanby, 1980).

Much of an individual's behaviour is a function of the complex interaction between his dominance rank and his personality. Furthermore, the personality of an animal may affect the social structure of the group to which he belongs. It follows that if we are to understand more fully the behaviour of an individual and the social structure of any group of primates then along with often studied variables such as dominance, habitat, predation pressures etc. we might do well to include personality variables.

Chapter 10. THE CONCEPT OF DOMINANCE REVISITED

What contribution has this study made to our understanding of the concept of dominance? In the light of the present data what can we conclude regarding the measurement, function, definition and usefulness of dominance?

10.1 Measurement

Section 5.4.1 evaluated the success of various measures of dominance assessment. The best method of assessment in this study in terms of showing (1) high efficiency in ranking all animals in all regroups, (2) high internal validity and (3) high correlations with other measures of dominance assessment (external validity) was a rank order based on the <u>priority of access</u> to a limited resource (milk or orange-juice competition dominance tests), in keeping with the finding of Richards (1974). The success of rank orders based on <u>aggressive behaviour</u> (in terms of the above criteria) was found to be dependent on the type of situation in which it was measured (competitive tests, stimulus animal tests or free social behaviour). In some situations in some regroups aggressive behaviour was infrequent, although where it was possible to derive a rank order based on the direction of aggression in these situations then these rank orders correlated well with other measures of dominance across other situations. The aggressive rank orders (based on both total and direction) derived from the free-social behaviour recording (DTU data) were the most efficient and valid of all the aggressive measures. Dominance orders based on <u>submissive behaviour</u>, both the total and the direction, showed low efficiency, low internal validity and low correlations with other measures (apart from the rank order derived from the direction of submissive behaviour in free social behaviour), because fear behaviour was infrequent. Further, there was no evidence to support Rowell's view that 'it is the lower ranking animals which do most to perpetuate rank distinctions' (Rowell, 1966, p. 437): Table 22 lists the percentage fear shown by the subordinate of a dyad to the dominant with the percentage aggression shown by the dominant to the subordinate; the result of a paired t test was not significant - in some dyads there was more fear than aggression, in others, the reverse was true.

Sexual behaviour was too infrequent to derive any rank orders based on frequency of mountings etc., and rank orders based on total amount of *visual monitoring behaviour*, total amount of *affiliative behaviour* (either amount of grooming received or inititated) did not correlate with rank orders derived from other measures. Neither was there a clearly established dyadic grooming relationship (Table 24).

What might be the reason for the lack of agreement between the various measures of dominance in this study? One reason that rank orders based on one measure do not agree with rank orders based on other measures may be because they are not measuring the dominance rankings of the animals, but some aspect of the animals' personalities or some other aspect of the animals' relationships, such as affiliative bonds.

Chalmers (1981) considers that a dominance relationship is only a subset of the total relationship that exists between two animals; 'dominance may or may not turn out to be the most important aspect of that relationship but we have no a priori justification for judging all other aspects of the relationship in terms of the competitive interactions of the two animals' (Chalmers, 1981, p.437). As discussed in section 5.4.1, the question of whether a particular measure truly reflects a dominance order is a circular issue, as the dominance order can only be inferred from measuring aggression, fear etc. Yet if we can show that there exists a high degree of similarity between rank orders derived from various measures and that it is reasonable to assume that such measures accurately reflect the dominance order of a group _by reason of the functional definition_ of dominance then we can conclude that such measures are a useful method of dominance assessment (the question of function will be dealt with in section 10.2).

If the reason that animals contest a position of dominance is that it yields priority of access to some limited resource which increases their fitness, then it follows that we should be able to infer a valid dominance order from situations of priority of access to incentives. The success of the rank orders based on competitive drinking in the present study (in terms of efficiency, internal and external validity) may be due to the fact that we can be assured that the value of the incentive is constant. In other situations, different animals may put different values on incentives depending on whether they like to groom a dominant animal or not, etc. (Bernstein, 1981).

The composition of a group with respect to the personalities of the animals comprising it may be one reason why there is disparity between rank orders derived from various measures of dominance assessment. While there was a trend over all regroups for dominant animals to show higher aggression levels than subordinate animals, in regroups where aggression was rare - for example regroup number 5 (average amount of aggression over all 5 animals over the 4 week period = 0.79%) - the direction of aggression correlated better with the rank order derived from competitive tests than did the total amount of aggression (see Table 21). That there is an inverse correlation between total aggression and the competitive drinking order within regroup number 5 (the more dominant animals are the least aggressive) can perhaps be explained by the composition of the group with respect to the whole-group rankings of the animals comprising that regroup on aggressive behaviour (Appendix 9). Regroup number 5 comprised animals 10,13,8,2 and 4 (dominant to subordinate), with respective whole-group rankings on amount of aggressive behaviour of 11,10,9,3 and 12. Since the rd4 animal is the most aggressive we would not expect there to be a correlation between dominance and amount of aggression, but can only expect the direction of aggression to reveal the dominance order. This is also true of regroup number 9, with whole-group rankings on aggression of 8 (rd1), 12 (rd2), 4 (rd3) and 1.5 (rd4) (whole-group rank not computable for the subordinate animal); in regroup number 9 the direction of aggression was a better correlate with dominance order derived from competitive drinking tests (on average correlating with 85% of other measures) than total aggression (0%). Thus while the dominance orders in regroup numbers 5 and 9 derived from competitive drinking measurements correlate well with rank orders based on direction of aggression, they do not correlate well with rank orders based on total aggression. This is because the precise levels of aggression expressed by an animal are personality dependent. Just because a dominant animal gains first access to a drinking bottle it does not follow that he will be the most aggressive; on a definition of dominance based on lack of 'limitation of behaviour' we can infer only that other animals will not limit the level he chooses to express (and it is evident that dominant animals differ significantly with respect to how aggressive they are - cf. section 6.1).

The use of fear behaviour to indicate the dominance order is limited by the fact that, in some situations, it rarely occurs. While there was a trend within and over all regroups and within and over all individual animals for total fear behaviour to correlate with increasing subordinance the precise levels of fear were found to be a function of the animals' personalities. This was most evident in position rd4 where there were significant differences between the levels of fear expressed by the animals who occupied this position. As with the measures of dominance deriving from aggressive behaviour, the fear direction order was found with correlate better with other measures of dominance than was a rank order based on total fear. In regroups composed of animals showing an inverse relationship between dominance and relative ranking on fear behaviour (Appendix 9), for example, regroup number 4, comprising animals number 11,10,13,8,2 with respective rankings on fear of 4,11,10,9,8 there was no correlation between total fear and dominance rank as derived from the competitive drinking orders.

Visual monitoring behaviour, though related to dominance in a large stable group (as in P1), was not related to dominance in P2 (contrary to the findings of Keverne et al., 1978) although there was evidence that the amount that rd2 and rd3 animals visual monitored other animals was positively related to the latters' dominance rank (Keverne et al., 1978). Precise levels of visual monitoring were found to depend more on the personality characteristics of the individual animals than on their dominance ranks.

Affiliative behaviour, though related to dominance in a large stable group (as in P1) was not related to dominance in P2. The precise level of affiliative behaviour an animal showed was found to be more a function of his individual personality and whether or not his 'friends' were in the regroup than a function of his dominance rank. There were individual differences in the attractiveness of the animals as groomees when dominant, and total amount of affiliation within a regroup was also found to correlate positively with the former degree of dominance in the stable group (regroups composed of more dominant animals in the stable group showed higher levels of affiliation).

In summary, the composition of the regroup was found to be an important factor in determining the efficiency of various measures of dominance assessment. The greatest similarity was found to be between rank orders based on priority of access in bottle competition tests and rank orders based on direction of fear and aggression, and it is argued that the reason for this is that such rank orders are not based on measures deriving from personality dependent behaviour, such as total aggression, fear, affiliation, visual monitoring, the levels of which are dependent more on the personality of an animal and the complex interaction between his personality and dominance rank than on dominance rank per se.

10.2 Definition and function of the concept of dominance

As Altmann (1981) states, dominance relationships are an abstraction inferred from agonistic interactions. 'It follows that questions about the function or adaptive significance of dominance relationships are meaningless, although the corresponding questions about agonistic behavior are not' (p. 431). Dawkins (1976) reminds us that a dominance hierarchy per se cannot be said to have a 'function' in the evolutionary sense, since it is a property of a group, not an individual. 'The individual behaviour patterns which manifest themselves in the form of dominance hierarchies when viewed at the group level may be said to have functions' (p. 89). Dawkins prefers that we abandon the word 'function' altogether and consider dominance in terms of 'evolutionarily stable strategies' (ESSs). Gauthreaux (1981) adopts a similar viewpoint; by treating behavioural dominance as a manifestation of the outcomes of ESSs in asymmetric contests we can discuss more meaningfully the 'ecological significance of behavioural dominance' (p. 441). Before invoking the concept of dominance to explain social behaviour it is necessary to demonstrate that the dominance order derived from agonistic encounters correlates with other orders that are also assumed to be reflective of a dominance order _within the functional definition of dominance_ (Syme, 1974), otherwise we might as well not use the term 'dominance' at all. If the reason animals contest dominance relationships is because there are advantages to being dominant, then one might expect dominance orders derived from agonistic interactions to correlate with orders derived from measures such as priority of access to incentives, or other biologically significant variables. Of course, in any laboratory study the sorts of pressures acting on the animals are few; there is no predation risk, no shortage of food/water, although there are likely to be other pressures, such as restriction of space. It may be therefore that dominance in the laboratory is quite a different sort of phenomenon than is dominance in feral groups of animals, and the reasons for the existence of dominance hierarchies in the two situations may be different. Perhaps in the laboratory where there is less need for an animal to contest dominance relationships in order to increase his fitness then dominance is more dependent on individual characteristics of the animals; one animal possesses greater drive for dominance, prefers to gain first access to prized foodstuffs, to be in a position where he is not likely to suffer aggression, whereas a subordinate animal lacks such a drive for dominance. Certainly in the regroup phase animals rarely contested dominance positions but their ranks remained the same, relative to the other animals in the stable group. This suggests that the animals did not place a high value on contesting dominance and on being dominant, or that they were adopting an ESS. It may be that the present study cannot contribute very much to our understanding of the function of dominance in the wild, but at least it can make us aware of the dangers of assuming that dominance is equated with aggression, subordinance with fear, and has indicated those aspects of an animal's behaviour which reflect his personality rather than his dominance position.

As Wade (1978) notes, there is little agreement about the function of dominance. Dominance has been considered from a general standpoint, where status is a by-product of the use of aggressive behaviour to regulate inter-individual distance (Kummer, 1970), or for group harmony (Kaufman, 1967) to more specific formulations of individual (Lack, 1966), group (Wynne-Edwards, 1962) or sexual (Crook, 1972) selection. Gage (1981) suggests that to discuss the scientific status of dominance and arrive at a useful definition we need first of all to discover how well dominance describes and predicts behaviour - its usefulness as a 'shorthand' term (Candland & Hoer, 1981). Yet as Seyfarth (1981) writes, 'the search for a universal definition of dominance is a fairly sterile intellectual exercise, largely because it is so often divorced from questions of biological function' (p. 447). It is proposed therefore that any study of dominance should first attend to questions regarding function, namely why is it that animals contest dominance relationships? We must explain why animals in some species compete and why in other species they do not (Seyfarth, 1981; Smuts, 1981). With attention focused on the advantages which accrue to the dominant member of a pair one may stress the functional outcome of dominance and frame a definition based on priority of access to incentives, which in turn lends itself to objective measurement (Bernstein, 1981). Yet as Bernstein (1980) points out, there are difficulties in defining and scaling incentives, which may not be equivalent for all animals. However, it is reasonable to assume that the animals' incentives for food/water are more equivalent than their incentives to groom a dominant animal (assuming that they are hungry or thirsty or that the food value is sufficiently high). In other situations, such as when there is no competition for food/water, there is no reason to suppose that incentives are equivalent for all animals; the present study found that there was no relationship between dominance position and the attractiveness of an animal as a groomee, indeed affiliative behaviour was determined more by habitual patterns of association than by dominance status (cf. also Varley & Symmes, 1966), and neither was there any evidence for a clearly established dyadic relationship in terms of whether a subordinate groomed his dominant more or vice-versa (contrary to the findings of Simpson, 1973). Yet unless we can propose why affiliative behaviour might be related to dominance position (for example, by demonstrating that alliances with more dominant animals are of benefit to an individual) then we have no reason to suppose that such a relationship will exist, within our functional definition based on priority of access and desire for increasing fitness. As Bernstein (1981) points out, a wide range of measures of dominance have been proposed, but such measures do not necessarily correlate well with one another. This is hardly surprising if numerous investigators do not agree on the functional definition of dominance. As Bernstein notes, some researchers regard the problem of definition as insoluble and proceed with data collection without formulating a definition, 'but what good are measures in the absence of definition? The validity of a measure is assessed by comparing the measurements to the thing we are trying to define. In the absence of definition, all measures are equally valid' (Bernstein, 1981, p. 449).

Clutton-Brock & Harvey (1978) indicate the importance of the value of a particular incentive for the evaluation of dominance hierarchies. Firstly, the absolute value of an incentive; if the value of an incentive is low then it may not be worth fighting over; if the value is high then contesting may advantageous to the individual. In addition to differences in the values of each resource the value of the same resource may change over time; in male squirrel monkeys dominance rank is only apparent during the breeding season where there is a sudden increase in the benefits of being dominant and it becomes advantageous to contest for dominance (Baldwin, 1968). Further, contests for dominance are more likely in situations where the individuals competing cannot judge the asymmetries of the contest (Maynard Smith, 1974) such as in newly formed groups of animals (Bernstein, 1969).

Gauthreax (1981) suggests that we should consider the concept of dominance from an ecological perspective and that focusing on the restrictive view of dominance relationships among individual animals undermines the utility of dominance in clarifying ecological issues. For example, there is evidence that dominance mediates which individuals stay and which individuals leave a troop when the favourability of a habitat declines and that dominance plays an important role in intra- and inter-specific competitive interactions, habitat selection, spacing movements and predation (Gauthreaux, 1978). However, Deag (1977) holds that we must concentrate on the function of specific behavioural acts, rather than glibly proposing functions for dominance. One 'function' of a dominance hierarchy was thought to be to reduce aggression and preserve peace (Struhsaker, 1967; Bernstein & Gordon, 1974), but as Deag points out, a more parsimonious view is that the reduction of aggression is the effect of individuals adopting strategies to maximise individual fitness. Further, the role of the dominant male in protecting the troop from outside threat (Bernstein, 1964) may not be part of some universal group selection pressure where defence ensures the fitness of all troop members but rather stems from the fact that the high-ranking male is protecting the survival of the infants, most of which are his own (Bernstein, 1976). Thus the attributes which enabled the dominant male to acquire a position of dominance would be passed on to the next generation. Bernstein (1981) stresses that dominance per se cannot be selected for, since dominance can only be determined in a social setting. 'Selection may operate to increase strength, size, swiftness, to improve on the ability to evaluate relative abilities and to remember the consequences of past encounters and the exact contexts in which they occurred, and to increase the ability to select the most favourable contexts for competitions' (Bernstein, p. 422).

10.3 Usefulness of the concept of dominance

To what extent does the concept of dominance increase our understanding of primate social behaviour? The results of this study show that we cannot accept the view that dominance pervades all social relationships, yet unless we can account for why we might expect dominance to have an all-pervasive effect within a functional definition of dominance, then we cannot reasonably expect that it will. If agonistic dominance relationships control and limit competitive conflicts (which have biological significance for those individuals who are competing) then such relationships are an important aspect of social interactions, even if they are only expressed during such contests (Bernstein, 1981).

The concept of dominance is therefore a useful term in predicting the outcome of competitive conflicts, where the winner of an aggressive encounter will gain first access to biologically significant items (such as food, water, or a sexual partner). As well as the utility of knowing dyadic dominance relationships we can predict certain behaviours of animals from their numerical rank within a group, i.e., their levels of aggression and fear relative to other animals in the group, although the absolute levels of aggression and fear will depend on the individual personality characteristics of the animal. Despite Bernstein's (1981) frequent assertion that dominance refers to a relationship between individual animals, he is often guilty of forgetting this fact, and even more guilty of ignoring the role of individual differences in animals; 'In a particular group an N-ranking animal may show a reliable pattern of behaviour, but I ask whether N-ranked individuals in all groups will show the same pattern of behaviour?' (p.428). At least with respect to aggressive/fear levels this study has shown that there are indeed similarities in the behaviour of animals of similar rank relative to other animals in that group, and since dominance cannot be abstracted from a social context this is all we might expect. However the absolute levels of these behaviours will depend on the individual animal.

The present study found that dominance rank was not related to level of affiliative behaviour, in terms of how much each individual animal of a given rank received and initiated. The finding of such a relationship in Phase 1 of the study, in a larger stable group, can be accounted for by the fact that the attractiveness of the dominant animals as groomees and their higher levels of sociability were basic to the animals themselves and not a function of their rank. Neither was there any evidence for a clearly established dyadic dominance relationship in terms of whether it is the dominant or the subordinate of the pair that receives more grooming. Dominance therefore cannot explain affiliative behaviours, which were found in this study to be more dependent on established friendships and personality variables. Neither can dominance explain exploratory behaviour, which was found to be a personality variable independent of rank. There was evidence that dominance rank was related to the amount of solitary behaviour, although it is likely that this might be as a result of the nature of the regroups, where the rd5 and rd1 animals (who show the most solitary behaviour) had lost one of their usual adjacent friends.

Dominance then is useful in describing the outcome of competitive conflict and in describing the relative fear and aggression levels of animals within a group. There is also evidence that some animals, at least in some dominance positions, are aware of the ranks of other animals, beyond the simple discrimination of 'who's above' and 'who's below' them, in that they groom and visually monitor other animals to a level commensurate with the latters' ranks. Thus the utility of the dominance concept is not dependent solely on the correlations between dominance and other behaviour (Eaton, 1981).

One limitation of the present study is that it cannot indicate what are the independent variables which influence dominance, as there were few cases of dominance reversals from those predicted on the basis of the hierarchy in the stable group. However, on the removal of the dominant male in the group of 13, in regroups where another male was present, he assumed the dominant position, unless there were more than 2 animals of higher rank in the regroup. One female, animal number 8, did drop in rank mid-study; relative to the other animals she was one of the least affiliative. Itani (1959) noted that male Japanese macaques who were not 'ambitious' in the central part of the troop and who were unsociable 'were destined to decline in rank'.

By studying animals over a range of dominance positions one can also isolate personality variables, and individual differences in positions of dominance/subordinance. For example, it is evident that animals differ in their 'styles' of dominance, some showing higher aggression than others and some animals, as dominants, are significantly more attractive than others (particularly males). There are similar individual differences in the behaviour of subordinate animals; some show more self-aggressive behaviour, some more stereotypic behaviour and some are more affiliative than others. Any study of animal personality must take into account the situation (dominance position) in which the animals are observed, since some behaviour patterns (e.g., aggression in a position of dominance) are facilitated by the situation, others (e.g., fear in a position of dominance) are absent. Similarly, any study of dominance should realise the individuality of primates; to parody Burns, 'the rank is but the guinea's stamp, the monkey's the gowd for a' that'.

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Appendix 1 Example of some output from the POD programme

```
INPBATCH LOG 1
RESULTS OF ANALYSIS
ZOOM1     Animal number 2, Dominant, Week 1
ON FILE
G6BW1A2  (GROUP #6, Week 1, Animal number 2)

**************************************************
**************************************************
**************************************************
 CODES    FREQU    TIME     % TIME   BOUT      IBI       F PER T
 ERRORS     2        634     0. 163   317.    194713       0. 15
  157700    1        408     0. 105   408.    389651.      0. 08
  211700    15      2706     0. 694   180      25824       1. 15
  212700    8       3836     0. 983   480.     48278       0. 62
  213700    10      2372     0. 608   237      38769       0. 77
  214700    3       1214     0. 311   405.    127615       0. 23
  217700    136    78719    20. 181   579       2289      10. 46
  247700    20     23712     6. 079  1186      13317       1. 54
  257200    3       2523     0. 647   841     129179       0. 23
  257700    100    67032    17. 195   670       3230       7. 69
  258700    1        642     0. 165   642     389417       0. 08
  267700    36     28182     7. 225   783.     10052       2. 77
  277700    9      10161     2. 605  1129.     42211       0. 69
  417700    1        413     0. 106   413.    387646       0. 08
  421700    1        165     0. 042   165.    389894.      0. 08
  422700    2        326     0. 084   163.    194867       0. 15
  424700    1        119     0. 031   119     389940       0. 08
  434700    1        540     0. 138   540.    389519       0. 08
  511700    6      17269     4. 427  2878.     62132       0. 46
  581200    4      15701     4. 025  3925      93590.      0. 31
  584200    5      32527     8. 339  6505      71506       0. 38
  585200    5      21686     5. 560  4337      73675       0. 38
  717700    23     38507     9. 872  1674      15285       1. 77
  737700    27     18573     4. 762   688.     13759.      2. 08
  757700    4       2019     0. 518   505      97010.      0. 31
  767700    2        836     0. 214   418.    194612.      0. 15
  777700    8      10885     2. 791  1361      47397.      0. 62
  851700    3        421     0. 108   140.    129879.      0. 23
  864700    1        105     0. 027   105.    389954.      0. 08
  865700    1        125     0. 032   125     387934       0. 08
  888800    14      7701     1. 974   550.     27311.      1. 08

**************************************************
**************************************************
**************************************************
TOTAL TIME = 390059
TOTAL USABLE TIME = 390059.
TOTAL EVENTS =    454
```

Appendix 2 Definitions of behavioural categories

(1) DTU free social behaviour testing

Fear

still	remain motionless, averting gaze from other animal
present	orient perineum toward other animal, rigid posture
teeth chatter	rapid opening and closing of mouth, lips retracted, baring teeth which chatter
grimace	corners of mouth, drawn back, bare teeth, often accompanied by screams
withdraw	move away rapidly from animal
freeze	tense, rigid posture
scream	high pitched vocalisation

Explore

visual	orient gaze toward animal or aspect of environment
locomotion	walk, climb or run
contact	manipulating specific aspect of environment
suck or mouth	sucking or mouthing specific aspect of environment other than self
forage	manually searching for food (in woodchips in outside area or food hoppers

Play

initiate	invite another animal to play, e.g., by brief contact then run off
play face	mouth open wide, relaxed posture, eyes often closed
chase	as implied, relaxed, often with play-face
wrestle	as implied, relaxed, often with play-face
bite	as implied, relaxed, often with play-face

Aggression/Dominance

bounce	bounce vigorously up and down, rigis posture, tense facial expression
mount	clasp pelvis of other animal with hands and thrust, no erection or intromission
displace	approach other animal and either with or without contact assume that animal's sitting area or activity
brow threat	intense visual fixation, raising and lowering brows
open mouth threat	as for brow threat, but with open mouth, perhaps with bared teeth
chase	as implied, not relaxed, often with brow threat or open mouth threat
grab	as implied, not relaxed, often with brow threat or open mouth threat
bite	as implied, not relaxed
teeth chomp or tension yawn	grind teeth together or head thrown back, eyes often closed, mouth opened slowly, lips withdrawn exposing teeth

Affiliation

groom	searching and picking with fingers or mouth through the fur of another animal
present for groom	offer part of body, other than perineum, to another
lipsmack	lips pursed, mouth opened and closed rapidly producing characteristic 'lipsmacking' sound, eyes directed at other animal
square mouth	muzzle thrust forward, lips pursed to form square
follow	as implied, but not chase
huddle	sit with body contacting another animal
mouth nibble and affiliation rattle	animal directs nibbling movements with mouth to another animal, accompanied by low-pitched 'rattle'

Sex

explore	inspect, either visually, manually or orally the anogenital region of another
present	direct perineum toward other animal, relaxed posture, often accompanied by masturbation
mount	as for dominance mount, but with erection and often intromission and ejaculation

Self or solitary behaviours

groom	as for affiliative groom, but self-directed
sleep	as implied
play	non-aggressive activity, involving running, rolling, leaping etc. not involving other animal(s)
masturbate	manually or orally contact own genitals
stereotypy	performing an unusual repeated movement, such as somersaulting, back-flipping, cage swinging
huddle	sit with arms and head tucked into body, often with bizarre posture, such as leg(s) behind neck
aggression	threaten, shake, grab, pull or bite any part of own body, often accompanied by threat vocalisations

DTU behavioural change

rate score	computed by dividing total testing time by total number of events within that testing time (see POD output in Appendix 1). Thus low score indicates high rate of behavioural change

(2) Novel object tests (other than those behaviours defined above)

dominance to environment	threaten, shake, grab, pull or bite any aspect of environment other than self, often accompanied by threat vocalisations
epimeletic object	affiliative behaviour to object, such as lipsmack, sit close to object

(3) Isolation tests (other than those behaviours defined above)

whimper	low-pitched vocalisation
scream	high-pitched, more intense vocalisation

(4) Scan sampling (other than those behaviours defined above)

alone	sitting alone
sit with others	sit in contact with other animals
within arms length of other animals	sit within arms length reach of other animals
climb	locomotion off-floor
be positive	engage in affiliative or playful interaction with other animals
be negative	engage in aggressive interaction with other animals
visual monitor	visually explore environment
pace	stereotypic locomotion

(5) Dominant stimulus animal tests (other than those behaviours defined above)

harrass mating	approach and lunge at mating pair, often accompanied by hitting or grabbing movements

Appendix 3 Percentage behaviour of each animal in each dominance position

Means over 4 weeks

Rd1 animals

Animal number	Fear	Explore	Play	Behaviour Aggression	Affiliation (total)	Sex	Self
15	0	13.68	0	2.09	139.49	0	25.60
17	0	24.72	0	0.49	19.48	0	48.59
5	0	9.61	0	0.14	84.40	0	39.63
11	0	16.48	0	0.12	38.62	0	42.88
10	0	24.10	0	0.49	24.23	0	45.04
13	0	13.90	0	0.53	34.17	0.35	48.27
2	0	38.48	0	1.00	19.57	0	39.47
3	0	38.11	1.43	0.18	19.75	1.67	39.80
Rd2 animals							
17	0.20	28.57	0	0.38	100.71	0	19.60
5	0.14	18.33	0	0.36	18.65	0	65.59
11	0.05	16.31	0.26	0.40	62.38	0	34.16
10	0.10	23.14	0.51	0.30	45.97	0	30.85
13	0.05	17.38	0	0.04	53.89	0	41.67
8	0.18	20.81	0	0.42	19.47	0	51.10
2	0.42	10.37	0	0.87	58.51	0	24.86
4	0.07	13.00	0	0	10.79	0	64.15
Rd3 animals							
5	0.29	22.12	0	0.57	47.25	0	39.86
11	0.77	18.49	0.13	0.32	32.95	0	46.89
10	0.05	8.74	0.33	0.07	65.08	0	40.08
13	0.12	16.01	0	0.08	69.52	0	35.42
8	0.21	12.77	0	0.19	53.49	0	44.19
2	0.49	19.91	0	0.45	24.66	0	52.64
4	0.69	10.37	0	0.06	30.49	0	45.34
25	0.34	16.82	0.14	3.28	21.29	0.44	42.57
Rd4 animals							
11	0.58	21.91	0	0.16	53.71	0	35.11
10	0.06	24.78	0.10	0.07	35.54	0	46.59
13	0.19	11.22	0.23	0.05	66.87	0	23.79
8	0.05	10.13	0	0	21.26	0	65.58
2	0.16	13.13	0	0.28	46.75	0	37.87
4	0.23	7.25	0	0.03	38.89	0	62.76
3	0.04	21.51	0	0.09	39.20	0	34.84
25	0.66	34.25	0.11	0.04	6.70	0	53.43
27	0.37	21.62	1.51	0.29	14.09	0	57.92
Rd5 animals							
10	0.32	15.10	0	0	20.17	0	71.44
13	0.55	21.20	0	0	16.39	0	54.47
8	0.66	9.49	0	0	15.94	0	73.38
2	0.15	17.67	0	0	34.16	0	46.83
4	0.49	15.41	0	0	34.20	0	48.45
25	0.75	30.62	0	0	0.15	0	67.03
27	0.45	28.75	0.16	0	7.62	0	60.82
6	1.17	44.11	0	0	0.28	0.28	50.75

continued/

Animal number	Behaviour							
	Visual monitor	Locomotion	Displace	Affiliation		Stereotypy	Self aggress	Behavioural change rate
				inititate	receive			
Rd1 animals								
15	8.65	2.93	0.41	33.74	76.79	0.31	7.46	13.47
17	12.48	4.24	0.31	17.14	0.32	0.09	1.53	10.12
5	5.24	2.55	0.14	26.64	18.42	0.13	1.61	16.34
11	10.86	3.53	0.07	8.47	11.16	0.50	0.92	14.06
10	13.11	4.92	0.40	13.57	9.06	12.14	1.56	11.59
13	6.53	2.79	0.12	21.01	2.91	0	3.56	14.00
2	20.65	12.55	0.45	7.54	8.39	0.27	1.03	10.25
3	23.33	7.13	0.07	0.76	18.99	0	2.01	9.53
Rd2 animals								
17	12.14	3.44	0.23	67.09	9.02	0.14	0.92	10.79
5	8.56	5.65	0.29	7.66	7.89	0.44	6.15	12.28
11	8.70	3.55	0.31	22.21	25.20	0.57	0.64	16.16
10	13.55	6.20	0.25	10.81	17.06	4.87	0.82	10.73
13	9.35	4.48	0	39.15	0.38	0.43	1.10	13.25
8	9.82	2.91	0.26	4.87	14.60	1.65	0.28	17.93
2	4.03	3.69	0.13	22.63	17.08	0.16	3.43	13.97
4	9.06	2.91	0	9.15	1.64	0.03	0.52	18.75
Rd3 animals								
5	11.04	6.24	0.17	8.82	31.81	3.31	4.88	8.99
11	11.02	5.30	0.18	20.16	9.82	0.02	1.12	13.25
10	5.50	2.62	0.03	14.91	39.10	1.29	0.20	16.72
13	8.97	4.41	0.06	36.03	27.15	0.03	1.34	11.91
8	6.42	2.42	0.03	28.46	14.73	0.14	2.20	22.99
2	9.55	6.72	0.29	13.53	5.92	1.61	3.34	9.00
4	4.22	2.85	0.07	30.49	6.47	0	1.22	16.63
25	11.41	4.72	0.16	21.29	3.38	0	1.29	12.11
Rd4 animals								
11	12.15	4.77	0.13	30.76	12.57	1.17	1.47	10.07
10	10.95	9.10	0.05	7.97	22.61	5.62	0.25	10.81
13	5.41	2.99	0.05	58.81	0.50	0.30	1.74	14.49
8	7.98	2.56	0	0.93	19.95	0	0.82	20.55
2	7.45	4.45	0.17	24.32	22.10	0.34	2.29	15.55
4	4.07	1.75	0	5.68	33.21	0.31	0.48	23.52
3	14.04	4.22	0.02	1.19	17.66	0.06	1.01	12.51
25	16.74	6.45	0.04	2.90	2.09	0.15	0.37	9.67
27	10.72	4.12	0	12.18	1.60	15.27	1.43	8.02
Rd5 animals								
10	8.58	3.47	0	1.70	14.45	18.78	0.35	11.48
13	12.09	6.13	0	15.46	0.93	2.66	2.94	7.81
8	3.27	1.89	0	0.32	10.56	0.04	1.01	24.55
2	9.71	3.72	0	24.39	9.17	0.06	2.96	15.52
4	7.01	4.18	0	24.16	9.69	0.03	0.25	14.95
25	19.66	6.47	0	0.08	0.07	1.50	1.21	11.53
27	15.87	6.29	0	3.02	1.45	2.57	0.70	8.33
6	18.07	23.45	0	0.08	0.20	3.31	3.29	8.60

Measure Number	Method
1	Day 1 Drinking order
2	Day 1 Aggression (direction)
3	Day 1 Fear (direction)
4	Day 19 Drinking order
5	Day 19 Aggression (direction)
6	Day 19 Fear (direction)
7	DSA test Aggression (direction)
8	DSA test Fear (direction)
9	SSA test Aggression (direction)
10	SSA test Fear (direction)
11	Day 26 Drinking order
12	Day 26 Aggression (direction)
13	Day 26 Fear (direction)
14	DTU data Fear (total)
15	DTU data Fear (direction)
16	DTU data Aggression (total)
17	DTU data Aggression (direction)
18	DTU data Visual monitor (total)
19	DTU data Initiate groom (total)
20	DTU data Receive groom (total)

Appendix 4 Ranks assigned to each animal in each regroup using various measures of dominance assessment

* = rank not assignable ** = no DTU data for this animal

Regroup number	Animal	Measure 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	15	1	*	1	1	1	*	*	1	*	*	1	1	*	1	1	1	1	2	2	1
	17	2	*	*	2	2	*	*	*	*	*	2	2	*	2	2	2	2	4	5	5
	5	3	*	*	3	3	*	*	*	*	*	3	5	*	3	3	3	3	3	3	2
	11	4	*	2	4	4	*	*	*	*	*	4	3	*	4	4	4	4	5	4	3
	10	5	*	*	5	5	*	*	*	*	*	5	4	*	5	5	5	5	1	1	4
2	17	1	1	*	1	*	*	*	*	*	1	1	1	*	2	1	1	1	5	3	5
	5	2	2	1	2	*	*	*	*	*	2	2	2	*	3	2	2	2	1	1	2
	11	3	3.5	2	3	*	*	*	*	*	*	3	3	*	5	4	3	3	3	5	3
	10	4	3.5	*	4	*	*	*	*	*	*	4	4	*	1	3	4	4	2	2	1
	13	5	5	3	5	*	*	*	*	*	*	5	5	*	4	5	5	5	4	4	4
3	5	1	2	*	1	1	*	*	2	1	2	1	*	*	3	1	2	1	2	2	2
	11	2	2	*	2	2	*	*	*	*	*	2	2	*	2	2	1	2	5	4	3
	10	3	2	*	3	3	*	*	*	2	*	3	2	*	1	3	3	3	4	3	1
	13	4	4	*	4	4.5	*	*	*	3	*	4	2	*	4	4	4	4	3	5	5
	8	5	5	*	5	4.5	*	*	*	4	*	5	4	*	5	5	5	5	1	1	4
4	11	1	2.5	*	1	*	*	*	*	1	*	1	*	*	4	1	2	1	4	2	1
	10	3	2.5	*	2	*	*	*	*	*	*	5	1	*	2	2	1	2	5	3	3
	13	4	2.5	*	3	*	*	1	*	2	*	2	2	*	3	3	3	3	2	5	5
	8	2	2.5	*	4	*	*	3	*	4	*	3	3	*	1	4	4.5	4.5	1	1	4
	2	5	5	*	5	*	*	2	*	3	*	4	*	*	5	5	4.5	4.5	3	4	2
5	10	1	1	*	1	1	*	*	*	*	*	1	1	*	2	1	1	1	5	1	3
	13	2	2	*	2	2	*	1	*	*	*	2	2	*	1	2.5	4	3	4	3	5
	8	3	3	2	3	3	2	*	1	*	*	3	3	*	4	2.5	3	2	1	2	4
	2	4	4	1	4	4	*	2	*	*	*	4	5	*	3	4.5	2	4	3	4	1
	4	5	5	*	5	5	1	*	2	*	*	5	4	*	5	4.5	5	5	2	5	2
6b	13**	1	1	*	1	*	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*
	8	2	2	*	2	*	*	*	*	*	*	2	*	*	1	1	2	1	3	1	3
	2	3	*	*	*	*	*	*	*	*	*	3	*	*	2	2	1	2	2	3	2
	4	*	3	*	*	*	*	*	*	*	*	*	*	*	3	3	3	3	1	2	1
	25**	*	4	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*

cont/

Key to
measures

Regroup number	Animal	Measure																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
7	13	1	1	*	1	1	*	1	1	1	*	1	1	*	2	1	2	1	3	3	3
	2	2	2	*	2	2	*	2	2	2	*	2	2	*	3	2	1	2.5	1	4	1
	4	3	3	*	3	3	*	3	*	3	*	3	3	*	4	3	4	2.5	2	5	4
	3	4	4	*	*	*	*	4	*	*	*	4	*	*	1	4.5	3	4	4	1	2
	25	5	5	*	*	*	*	*	*	4	*	*	*	*	5	4.5	5	5	5	2	5
8	3	1	1	1	1	1	*	3	*	*	*	1	1	*	1	1	1	*	3	1	1
	2**	2	2	2	2	2	*	1	*	*	*	2	2	*	*	*	*	*	*	*	*
	4**	3	3	*	3	3	*	2	*	*	*	3	3	*	*	*	*	*	*	*	*
	25	*	4	*	*	*	*	*	*	*	*	*	4	*	3	2	2	1	2	3	2
	27	*	5	*	*	*	*	*	*	*	*	*	5	*	2	3	3	2	1	2	3
9	3**	1	1	1	1	1	*	1	*	*	*	1	*	*	*	*	*	*	*	*	*
	4	2	2	2	2	*	*	*	*	*	*	2	*	*	1	1	4	*	1	3	1
	25	3	3.5	3	3	2.5	*	2.5	*	*	*	3	*	*	2	2	1	1	3	2	3
	27	4	3.5	*	4	2.5	*	2.5	*	*	*	4	*	*	3	3	2	2	2	4	3
	6	5	5	*	5	4	*	4	*	*	*	5	*	*	4	4	3	3	4	1	4
Number of groups all ranked		7/9	3/9	0	6/9	2/9	0	0	0	0	0	6/9	4/9	0	6/6	4/6	5/6	4/6	6/6	6/6	6/6
% groups all ranked		78	33	0	66	22	0	0	0	0	0	66	44	0	100	67	83	67	100	100	100

note: regroup number 8b excluded from analysis, as only one animal was observed during the period of this regroup (number 2) who was always dominant in the competitive drinking tests and there was no reason to suspect her dominance position otherwise.

Appendix 5 Regroup means, summed over all animals, over all weeks

Regroup				Behaviour				Average
number	Fear	Explore	Play	Aggression	Affiliation total	Sex	Self	D13
1	1.15	81.10	0	2.73	289.05	0	153.29	3
2	1.27	86.02	0.06	0.99	98.42	0	209.71	4
3	0.81	44.30	0.16	0.52	235.74	0	168.83	5
4	0.44	67.77	0.10	0.40	167.62	0	177.26	6
5	0.80	66.23	0	0.79	170.04	0	173.78	7
6b	1.22	72.67	0.04	1.18	120.46	0.07	213.64	8.2
7	1.63	69.41	0	1.24	138.95	0.07	176.27	8.8
8	1.32	108.20	0.37	0.97	101.01	0.35	191.13	10
9	1.60	92.51	0.37	3.33	87.32	0.20	205.44	11

Appendix 6 **Means - over each regroup dominance position over 4 weeks over regroup numbers 1,2,3,4,5 and 7.**

Behaviour	Regroup dominance position				
	rd1(n=6)	rd2(n=6)	rd3(n=6)	rd4(n=6)	rd5(n=6)
Fear	0	0.71	1.41	0.72	1.94
Explore	68.33	76.03	59.00	69.30	73.00
Aggression	2.57	1.71	0.85	0.43	0
Affiliation					
total	226.91	226.74	206.63	175.57	80.67
initiate	80.40	113.03	92.59	82.67	44.07
receive	79.11	51.09	86.27	63.58	29.91
Self	166.68	144.49	167.85	162.52	241.07
Self-aggression	11.09	8.71	7.30	5.05	5.81
Behavioural change	13.26	12.85	15.08	13.52	14.32
Stereotypy	2.20	1.10	0.80	1.26	3.85
Displace	0.24	0.20	0.09	0.07	0.00
Locomotion	3.49	4.50	3.97	5.05	4.31
Visual monitor	9.48	9.39	7.89	9.19	10.05

Appendix 7 Means - behaviour to animals in particular dominance positions by rd1, rd2, rd3, rd4 and rd5 animals

(i) all dominant (rd1) animals, n = 8. Behaviour to rd2, rd3, rd4 and rd5 animals (means)

Behaviour	rd2	rd3	rd4	rd5
Fear of	0	0	0	0
Present to	0	0	0	0
Visual monitor	2.81	1.56	1.42	1.06
Groom	11.16	0.92	2.95	3.79
Aggress	0.41	0.44	0.43	0.29
Displace	0.37	0.22	0.26	0.13

(ii) all rd2 animals, n=8. Behaviour to rd1, rd3, rd4 and rd5 animals (means)

Behaviour	rd1	rd3	rd4	rd5
Fear of	0.36	0	0	0
Present to	0	0	0	0
Visual monitor	3.21	1.50	1.05	0.97
Groom	14.82	17.84	4.03	0.79
Aggress	0	1.41	0.63	0.36
Displace	0	0.20	0.33	0.20

(iii) all rd3 animals, n=8. Behaviour to rd1, rd2, rd4 and rd5 animals (means)

Behaviour	rd1	rd2	rd4	rd5
Fear of	0.72	0.52	0	0
Present to	0.10	0.11	0	0
Visual monitor	2.94	2.69	1.65	0.89
Groom	6.48	10.98	11.95	3.34
Aggress	0	0	0.38	1.52
Displace	0	0	0.20	0.29

(iv) all rd4 animals, n=9. Behaviour to rd1, rd2, rd3 and rd5 animals (means)

Behaviour	rd1	rd2	rd3	rd5
Fear of	0.29	0.24	0.41	0
Present to	0.09	0.06	0.14	0
Visual monitor	1.81	1.85	3.24	1.50
Groom	7.55	3.76	16.01	3.75
Aggress	0	0	0	0.1[illegible]
Displace	0	0	0	0.1[illegible]

(v) all rd5 animals, n=8. Behaviour to rd1, rd2, rd3 and rd4 animals (means)

Behaviour	rd1	rd2	rd3	rd4
Fear of	0.40	0.37	0.61	0.65
Present to	0.12	0	0.15	0.04
Visual monitor	2.33	1.91	1.93	2.62
Groom	5.85	0.02	9.11	3.85
Aggress	0	0	0	0
Displace	0	0	0	0

Appendix 8 Correlations between behaviours for each regroup dominance position

*p=<0.05 **p=<0.01

(a) rd1 n=8

	Behaviour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Fear	-														
2	Explore	n.c.	-													
3	Play	n.c.	0.36	-												
4	Aggression	n.c.	0.07	-0.21	-											
5	Affiliate (total)	n.c.	-0.71*	-0.21	-0.07	-										
6	Sex	n.c.	0.15	0.73*	-0.05	-0.16	-									
7	Self	n.c.	0.07	-0.07	-0.14	-0.36	0.16	-								
8	Self groom	n.c.	-0.36	-0.07	-0.71*	0.36	0.05	0.29	-							
9	Stereotypy	n.c.	-0.04	-0.44	-0.04	0.18	-0.64*	-0.18	-0.03	-						
10	Self huddle	n.c.	-0.43	-0.21	-0.36	0.43	0.05	0.21	0.64	0.18	-					
11	self-agg	n.c.	-0.36	0.21	0.29	0.36	0.37	-0.14	-0.14	-0.33	0.07	-				
12	Initiate affiliation	n.c.	-0.64*	-0.50	0.29	0.50	-0.26	0.00	0.00	0.11	0.07	0.43	-			
13	Receive affiliation	n.c.	-0.29	0.36	-0.07	0.57*	0.05	-0.64*	-0.07	0.11	0.00	0.36	0.07	-		
14	Locomotion	n.c.	0.86**	0.36	0.07	-0.57*	0.05	-0.07	-0.36	0.11	-0.43	-0.21	-0.65*	-0.14	-	
15	Visual monitor	n.c.	0.79**	0.50	0.00	-0.50	0.16	0.00	-0.29	0.04	-0.36	-0.14	-0.71*	-0.07	0.93*	-
16	Behaviour change	n.c.	-0.64*	-0.50	-0.14	0.64*	-0.26	-0.14	0.43	0.25	0.50	0.00	0.43	0.21	-0.64*	-0.71*

(b) rd2 n=8

	Behaviour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Fear	-														
2	Explore	0.14	-													
3	Play	-0.26	0.16	-												
4	Aggression	0.64*	0.21	-0.16	-											
5	Affiliate (total)	0.14	0.14	0.16	0.50	-										
6	Sex	n.c.	n.c.	n.c.	n.c.	n.c.	-									
7	Self	-0.28	-0.14	-0.26	-0.50	-0.71*	n.c.	-								
8	Self groom	0.04	-0.33	-0.43	-0.18	-0.54	n.c.	0.54	-							
9	Stereotypy	-0.07	0.36	0.58	0.00	-0.07	n.c.	0.07	-0.04	-						
10	Self huddl	-0.64*	-0.50	0.16	-0.71*	-0.36	n.c.	0.50	0.25	0.00	-					
11	self-agg	0.14	0.00	-0.16	0.07	0.14	n.c.	-0.14	-0.18	-0.07	-0.21	-				
12	Initiate affiliation	-0.14	0.00	-0.05	0.21	0.57*	n.c.	-0.57*	-0.62*	-0.36	-0.21	0.29	-			
13	Receive affiliation	0.29	0.00	0.47	0.36	0.43	n.c.	-0.29	-0.11	0.36	-0.21	-0.14	0.00	-		
14	Locomote	-0.11	0.18	0.37	-0.18	-0.11	n.c.	-0.04	-0.30	0.40	-0.11	0.55	0.11	0.04	-	
15	Visual monitor	-0.07	0.64*	0.26	0.00	0.07	n.c.	-0.21	-0.25	0.26	-0.14	-0.36	0.07	-0.07	-0.04	-
16	Behaviour change	-0.14	-0.57*	-0.16	-0.21	-0.29	n.c.	0.43	0.62*	-0.07	0.50	-0.43	-0.43	0.00	-0.62*	-0.21

(c) rd3 n=8

	Behaviour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Fear	-														
2	Explore	0.28	-													
3	Play	-0.09	-0.27	-												
4	Aggression	0.25	0.69*	0.05	-											
5	Affiliate (total)	-0.64*	-0.36	-0.09	-0.47	-										
6	Sex	0.07	0.07	0.45	0.51	-0.36	-									
7	Self	0.57*	0.14	-0.09	0.11	-0.64*	-0.07	-								
8	Self groom	0.57*	0.14	0.00	0.25	-0.79*	0.21	0.57*	-							
9	Stereotypy	-0.25	0.25	-0.23	0.15	0.11	-0.44	-0.11	-0.11	-						
10	Self huddl	-0.36	-0.07	0.36	0.11	0.43	0.50	-0.64*	-0.50	-0.11	-					
11	self-agg	-0.07	0.50	-0.62*	0.47	-0.14	-0.07	-0.07	0.07	0.47	-0.14	-				
12	Initiate affiliation	-0.07	-0.50	-0.18	-0.40	0.29	0.07	-0.07	-0.21	-0.62*	0.14	-0.14				
13	Receive affiliation	-0.43	-0.14	0.00	-0.40	0.64*	-0.50	-0.42	-0.57*	0.47	0.36	-0.07	-0.07	-		
14	Locomotion	0.36	0.79*	-0.18	0.47	-0.43	0.07	0.21	0.36	0.18	-0.14	0.29	-0.43	-0.21	-	
15	Visual monitor	0.29	0.57*	0.27	0.76*	-0.36	0.50	0.00	0.14	-0.04	0.21	0.21	-0.21	-0.29	0.36	-
16	Behaviour change	-0.07	-0.64*	0.27	-0.47	0.29	-0.07	0.07	-0.21	-0.33	0.00	-0.57*	0.29	0.07	-0.71*	-0.36

(d) rd4 n=9

	Behaviour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Fear	–														
2	Explore	0.22	–													
3	Play	0.32	0.26	–												
4	Aggression	0.06	0.17	0.13	–											
5	Affiliate (total)	-0.11	-0.33	-0.26	0.17	–										
6	Sex	n.c.	n.c.	n.c.	n.c.	n.c.	–									
7	Self	0.00	0.00	0.00	-0.28	-0.56*	n.c.	–								
8	Self groom	0.06	-0.28	-0.26	-0.33	-0.39	n.c.	0.50	–							
9	Stereotypy	0.22	0.22	0.33	0.50	0.00	n.c.	0.00	-0.39	–						
10	Self huddle	0.06	-0.28	-0.20	0.00	0.28	n.c.	-0.06	0.00	-0.06	–					
11	self-agg	-0.06	-0.17	-0.07	0.33	0.50	n.c.	-0.28	-0.33	0.06	0.33	–				
12	Initiate affiliation	0.28	-0.06	0.26	0.33	0.50	n.c.	-0.50	-0.56*	0.50	0.22	0.44	–			
13	Receive affiliation	-0.17	-0.17	-0.52	-0.22	-0.06	n.c.	0.28	0.22	-0.06	-0.22	-0.33	-0.33	–		
14	Locomotion	0.17	0.72*	0.13	0.22	-0.06	n.c.	-0.17	-0.44	0.28	-0.44	-0.11	0.11	0.00	–	
15	Visual monitor	0.06	0.72*	0.07	0.11	-0.28	n.c.	-0.17	0.00	-0.06	-0.22	-0.22	-0.22	-0.22	0.56*	–
16	Behaviour change	-0.33	-0.67*	-0.52	-0.39	0.22	n.c.	0.00	0.28	-0.33	0.17	0.06	-0.17	0.50	-0.50	-0.50

(e) rd5 n=8

	Behaviour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Fear	-														
2	Explore	0.36	-													
3	Play	-0.21	0.21	-												
4	Aggression	n.c.	n.c.	n.c.												
5	Affiliate (total)	-0.57*	-0.50	-0.21	n.c.	-										
6	Sex	0.50	0.50	-0.14	n.c.	-0.36	-									
7	Self	0.14	-0.21	0.07	n.c.	-0.29	-0.21	-								
8	Self groom	0.00	-0.21	0.21	n.c.	-0.29	-0.50	0.43	-							
9	Stereotypy	0.07	0.29	0.07	n.c.	-0.21	0.36	0.07	-0.21	-						
10	Self huddle	0.43	0.21	-0.50	n.c.	-0.14	0.50	0.14	-0.29	0.36	-					
11	self-agg	0.29	0.36	-0.21	n.c.	-0.29	0.50	-0.29	-0.14	0.21	0.14	-				
12	Initiate affiliation	-0.64*	-0.29	0.07	n.c.	0.64*	-0.50	-0.50	-0.21	-0.29	-0.50	-0.21	-			
13	Receive affiliation	-0.43	-0.79**	0.07	n.c.	0.57*	-0.36	0.14	0.14	-0.21	-0.14	-0.43	0.21	-		
14	Locomotion	0.42	0.93**	0.21	n.c.	-0.43	0.50	-0.14	-0.29	0.21	0.29	0.29	-0.36	-0.71*	-	
15	Visual monitor	0.21	0.86*	0.21	n.c.	-0.64*	0.35	-0.07	-0.07	0.28	0.21	0.36	-0.29	-0.79**	0.79**	-
16	Behaviour change	-0.14	-0.36	-0.36	n.c.	0.14	-0.21	0.00	0.29	-0.50	-0.29	-0.14	0.07	0.29	-0.43	-0.36

Appendix 9 Relative ranking orders from Phase 2 testing

Summmed over all regroup dominance positions each animal experienced. Based on number of animals 'x' showed higher mean levels of a given behaviour in the same positions, expressed as a % of total animals with whom he shared common dominance ranks,
1 = highest rank (e.g., relatively most fearful animal).
* = relative rankings only computable from some dominance positions

Animal number	Fear*	Explore	Behaviour Aggression*	Affiliation total	Affiliation init	Affiliation rece	Self	Self agg	Visual monitor	Behaviour change rate (1=lo)	Stereotypy	Locomotion	Displace*
15	n.c.	12	1.5	1	1	1	13	1.5	11.5	4	7	11	1
17	2	2	5	6.5	3	11	8	8	4	12.5	12	9	6
5	8	8.5	7	5	9	5	7	3	11.5	6	5	7	4
11	4	6	6	3	7	6	6	11	6	3	4	6	3
10	11	8.5	11	4	8	2	5	12	7	7	1	5	7
13	10	10	10	2	2	10	10.5	4.5	9	8	8	10	8
8	9	11	9	10	11	4	1	9	10	1	9	13	10
2	7	7	3	6.5	6	8	10.5	4.5	8	5	6	3	2
4	5	13	12	8	5	7	3	13	13	2	11	12	11
3	12	4.5	8	9	12	3	12	7	2	10	13	4	9
25	3	3	4	13	10	13	4	10	1	11	10	2	5
27	6	4.5	1.5	11	4	9	2	6	5	12.5	3	8	12
6	1	1	n.c.	12	13	12	9	1.5	3	9	2	1	n.c.

Appendix 10 Distribution of χ^2 under various conditions.

A. Complete data set (hypothetical 'best-fit')

Animal	Dominance position				
	1	2	3	4	5
15	1	1	1	1	1
17	2	2	2	2	2
5	3	3	3	3	3
. . . . .	(relative ranks on a particular behaviour in identical dominance positions)				
6	13	13	13	13	13

degrees of freedom = 12 $\chi^2 = 60.0$ $p<0.00001$ W=1.0

B. Incomplete data set (hypothetical 'best-fit')

(i) 13 x 5 matrix

Animal	Dominance position				
	1	2	3	4	5
15	1	M	M	M	M
17	2	1	M	M	M
5	3	2	1	M	M
11	4	3	2	1	M
10	5	4	3	2	1
13	6	5	4	3	2
8	M	6	5	4	3
2	7	7	6	5	4
4	M	8	7	6	5
3	8	M	M	7	M
25	M	M	8	8	6
27	M	M	M	9	7
6	M	M	M	M	8

degrees of freedom = 12 $\chi^2 = 35.7$ $p<0.001$ W=1.00

(ii) 12 x 4 matrix

a. omits Rd1

Animal	Dominance position			
	2	3	4	5
17	1	M	M	M
5	2	1	M	M
11	3	2	1	M
10	4	3	2	1
13	5	4	3	2
8	6	5	4	3
2	7	6	5	4
4	8	7	6	5
3	M	M	7	M
25	M	8	8	6
27	M	M	9	7
6	M	M	M	8

degrees of freedom = 11 $\chi^2 = 28.9$ $p<0.005$ w=1.00

Cont

b. omits Rd5

Animal	dominance position			
	1	2	3	4
15	1	M	M	M
17	2	1	M	M
5	3	2	1	M
11	4	3	2	1
10	5	4	3	2
13	6	5	4	3
8	M	6	5	4
2	7	7	6	5
4	M	8	7	6
3	8	M	M	7
25	M	M	8	8
27	M	M	M	9

degrees of freedom = 11 $\chi^2 = 28.8$ $p < 0.005$ W=1.00

Appendix 11 Relative ranks from Phase 2 persistence tests on behaviours showing relative consistency and reliability

Behaviour	Look through divider	Arm through divider	
	f	%	f
Animal			
15	13	9	10
17	3.5	8	13
5	9	6	1
11	8	7	6
10	5	2	3
13	12	13	12
8	6	3	7
2	10	11	9
4	11	10	10
3	7	5	8
25	1	1	4
27	2	4	2
6	3.5	12	5

Appendix 12

Results from Dominant stimulus animal tests

Table showing number of 15 second periods each animal in their respective regroup dominance positions exhibited the following behaviours:

	Regroup dominance position																			
Animal in that pos	1/15	2/17	3/5	4/11	5/10	1/17	2/5	3/11	4/10	5/13	1/5	2/11	3/10	4/13	5/8	1/11	2/10	3/13	4/8	5/2
		Regroup 1					Regroup 2					Regroup 3					Regroup 4			
Behaviour:																				
To DSA:																				
lipsmack	0	0	0	0	0	2	1	0	0	2	1	0	0	0	0	0	2	0	1	0
present	0	2	1	4	2	12	5	14	4	4	4	13	3	4	1	6	8	7	7	7
withdraw	0	0	0	0	0	4	1	2	1	3	4	3	3	7	1	1	6	1	1	1
aggress	21	4	4	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
follow/approach	6	2	2	1	1	7	4	3	1	0	1	3	1	2	1	1	0	0	3	0
affiliate	7	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
harrass mating	0	0	0	0	0	3	0	5	2	0	3	1	2	0	2	2	2	1	4	3
From DSA:																				
Mate	0	0	0	0	0	0	5	0	0	0	0	2	1	0	0	3	2	0	0	0
Fear	4	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aggress	2	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Group dominance maintenance	11	9	1	2	9	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
Group affiliation	0	5	5	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Self-aggress	0	0	0	0	0	0	0	0	0	0	2	0	0	3	0	0	0	0	0	1
Total aggressive interactions + DSA	23	4	4	0	21	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Total interactions + DSA	41	9	7	5	27	29	16	25	8	9	14	28	10	13	5	13	20	9	16	11

	Regroup dominance position																			
Animal in that pos	1/10	2/13	3/8	4/2	5/4	1/13	2/8	3/2	4/4	5/25	1/13	2/2	3/4	4/3	5/25	1/3	2/2	3/4	4/25	5/27
		Regroup 5					Regroup 6b					Regroup 7					Regroup 8			
Behaviour:																				
To DSA:																				
lipsmack	0	1	0	0	0	3	1	0	0	0	9	5	5	1	0	0	0	0	0	0
present	4	19	8	2	7	7	4	4	1	0	7	12	3	3	0	0	18	9	2	2
withdraw	1	0	0	1	1	4	6	0	5	5	2	1	1	0	0	3	8	0	4	1
aggress	0	0	0	0	0	0	0	0	0	0	0	19	5	36	0	1	0	0	0	0
follow/approach	1	6	9	0	0	6	1	5	0	0	0	0	0	0	0	0	10	0	0	2
affiliate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
harrass mating	5	1	5	4	0	0	3	0	1	0	1	0	2	0	1	0	3	0	2	1
From DSA:																				
mate	0	0	0	0	10	2	1	4	0	0	0	2	0	0	0	0	0	4	0	0
Fear	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aggress	0	0	0	0	0	0	0	0	0	0	2	2	3	7	0	3	0	0	0	0
Group dominance maintenance	0	0	0	0	0	2	0	0	0	0	31	15	6	13	0	1	1	1	0	0
Group affiliation	1	2	0	0	0	5	0	0	0	0	15	14	0	0	0	0	0	0	0	0
self-aggress	0	5	4	0	1	0	2	0	0	0	0	0	0	0	0	0	7	0	0	0
Total aggressive interactions + DSA	0	0	0	0	0	0	0	0	0	0	2	21	8	43	0	4	0	0	0	0
Total interactions + DSA	11	27	22	7	18	22	16	13	7	5	21	41	19	47	1	7	39	13	8	6

	Regroup dominance position									
Animal in that pos	1/2	2/4	3/25	4/27	5/6	1/3	2/4	3/25	4/27	5/6
	Regroup 8b					Regroup 9				
Behaviour:										
To DSA:										
lipsmack	1	0	0	0	0	2	0	0	1	1
present	8	2	1	5	0	2	5	3	3	0
withdraw	6	4	4	1	0	0	0	4	0	0
aggress	0	0	0	0	0	1	1	0	0	0
follow/approach	3	0	0	3	0	9	0	0	0	0
affiliate	0	1	0	0	0	18	0	0	0	0
harrass mating	0	1	0	1	0	0	0	0	0	0
From DSA:										
mate	3	0	0	0	0	0	0	0	0	0
Fear	0	0	0	0	0	0	0	0	0	0
Aggress	0	0	0	0	0	0	0	0	0	0
Group dominance maintenance	1	0	0	2	5	13	30	60	70	1
Group affiliation	0	0	0	0	0	0	0	0	0	0
self-aggress	7	0	0	0	0	1	0	0	0	1
Total aggressive interactions + DSA	0	0	0	0	0	1	1	0	0	0
Total interactions + DSA	21	8	5	10	0	32	6	7	4	1

Appendix 13
Results from Subordinate stimulus animal tests

Table showing number of 15 second periods each animal in their respective regroup dominance positions exhibited the following behaviours:

	Regroup dominance position																			
Animal in that pos	1/15	2/17	3/5	4/11	5/10	1/17	2/5	3/11	4/10	5/13	1/5	2/11	3/10	4/13	5/8	1/11	2/10	3/13	4/8	5/2
	Regroup 1					Regroup 2					Regroup 3					Regroup 4				
Behaviour:																				
To SSA:																				
Fear	1	2	2	7	9	7	4	0	0	0	0	0	0	0	0	0	2	1	0	0
Aggress	6	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	3
affiliate	2	3	5	0	0	2	0	0	0	0	3	1	1	1	0	0	0	0	0	0
follow/approach	0	0	0	0	0	0	0	0	0	0	7	1	0	1	1	0	0	0	0	0
From SSA:																				
Fear	45	3	5	0	1	3	0	0	0	0	6	0	2	1	2	0	0	0	0	0
Group dominance maintenance	9	1	0	0	0	0	0	0	0	0	2	1	2	0	0	1	0	1	0	0
Group affiliation	2	7	5	0	0	0	0	0	0	0	0	1	1	3	0	0	1	1	0	1
self-aggress	6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total interactions + SSA	54	8	12	7	10	12	4	0	0	0	16	2	3	3	4	0	2	2	0	3

Regroup dominance position

	Regroup 5					Regroup 6b					Regroup 7					Regroup 8				
Animal in that pos	1/10	2/13	3/8	4/2	5/4	1/13	2/8	3/2	4/4	5/25	1/13	2/2	3/4	4/3	5/25	1/3	2/2	3/4	4/25	5/27
Behaviour:																				
To SSA:																				
Fear	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aggress	0	0	0	2	0	0	0	0	0	0	0	15	0	1	30	6	0	0	18	8
affiliate	0	0	0	0	0	3	0	0	0	2	30	13	0	0	8	0	0	0	3	8
follow/approach	2	0	0	0	1	0	0	0	0	0	11	7	0	0	0	10	0	0	9	7
From SSA:																				
Fear	2	0	0	0	0	2	0	0	0	2	0	2	0	0	2	3	0	0	10	11
Group dominance maintenance	0	0	0	0	0	0	0	0	0	0	6	0	2	0	0	1	0	0	0	0
Group affiliation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
self-aggress	0	3	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total interactions + SSA	4	0	0	2	1	5	0	0	0	4	41	37	0	1	40	19	0	0	40	34

Regroup dominance position

	Regroup 8b					Regroup 9				
Animal in that pos	1/2	2/4	3/25	4/27	5/6	1/3	2/4	3/25	4/27	5/6
Behaviour:										
To SSA:										
Fear	2	2	2	0	0	0	0	0	0	0
Aggress	0	0	0	0	0	8	0	4	0	0
affiliate	2	0	0	0	0	9	41	11	14	0
follow/approach	1	0	0	0	0	2	2	5	2	0
From SSA:										
Fear	10	0	1	0	0	3	0	1	1	0
Group dominance maintenance	2	0	0	0	0	0	0	0	0	0
Group affiliation	0	0	0	0	0	0	0	0	0	0
self-aggress	0	0	0	0	0	2	2	0	0	0
Total interactions + SSA	15	2	3	0	0	22	43	21	17	0

The results of Tables 34, 35 and 36 should not be taken as anything except an indication of absolute consistency, since for each measure the sign test analysis was performed on the erroneous assumption that, on a null hypothesis, half the animals should show significant variation associated with dominance position. This expectation is not justifiable and the procedure of selecting only statistically significant results as indicating variable behaviour greatly exaggerates the impression of consistency. Reliance can be placed on the analyses of relative consistency in Section 7.4.

III