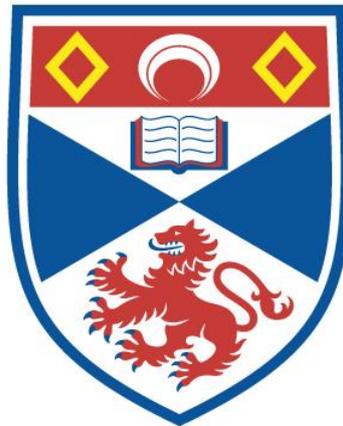


SOCIAL COMPLEXITY IN A LARGE AND SMALL GROUP OF OLIVE BABOONS

THOMAS DANIEL SAMBROOK

**A Thesis Submitted for the Degree of PhD
at the
University of St Andrews**



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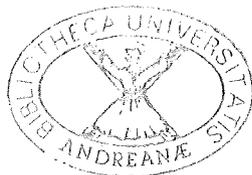
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**Social Complexity in a Large and Small Group of Olive
Baboons**

Thomas Daniel Sambrook

Thesis submitted for the degree of Doctor of Philosophy, University of St.
Andrews, 1995



(i)

I, Thomas Daniel Sambrook, hereby certify that this thesis, which is approximately 40,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Ph.D. in the University of St. Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Acknowledgements

Some Ph.D. students seem to have a hellish time. I have not been one of these and this is thanks entirely to the support of my friends and colleagues that has always been there when I needed it.

More than anyone else, my supervisor, Andy Whiten, deserves credit for this happy state of affairs. He has been constructive rather than prescriptive, always been happy to listen and advise and most of all has been unerringly positive. This thesis is the material aspect of such a spirit of cooperation but in the last three years I have learnt much more than is written here and this, I know, is thanks to Andy's enthusiasm

Studying a fascinating species of wild animal in its natural habitat is a privilege. When those animals are as beautiful and complex as baboons and when the field site is as breathtaking as Chololo the privilege is unparalleled. This privilege I owe to Shirley Strum who kindly allowed me to join her project and smoothed out problems as they arose. She also taught me lots about baboons and how to watch them: quite important under the circumstances. For Chololo, I must also thank John and Sammy Jessel, the owners who were helpful and understanding. Sammy was a very useful neighbour, passing on the odd elephant forecast and dropping off the all important weekly post.

Francis Ngaanga King'waa (aka Charles) was a very kind friend in the field. He not only taught me how to recognise 80 plus baboons but also stoically kept all practical sides of the project running in often difficult times. I could not possibly have studied STT without his help. Also at Chololo, thanks are due to Pascal Muteti, Lawrence Kinyanjui, Thomas King'waa and Martin Sati. These guys are Kenyans which means they are full of good advice, good humour and like drinking beer! Along with Charles they looked after me, their sunburnt mzungu, and problems disappeared in front of me. In Nairobi, David Muiriri and Zippy helped with paperwork and longterm records.

Mum and Dad, still stuck with a student son, carted stuff around for me and also turned up at Chololo bearing two litres of Scotch! When morale was lowest, Rebecca Lawson turned up not only with Scotch but Marmite as well. Rebecca straightened my head out.

Back home, writing up was helped by the support of the Scottish Primate Research Group. Dick Byrne, a font of knowlege concerning obscure references, has also read my work and made useful suggestions. Hannah Buchanan-Smith, Katy Harrison, Rebecca Ham, Patti Teixidor, Heather McKiggan, Debbie Custance, Frances Marsh and Duncan Castles helped along the way and, just by being primatologists themselves, sustained my belief that my work was worthwhile.

Computers and statistics, supposedly tools at the service of scientists, more often seem to be insuperable barriers to progress. Robin Fowler wrote software for me at short notice and Allan Gordon patiently listened to my ramblings on baboons, decoded them into common sense and re-encoded them into statistics.

I am *almost* one hundred percent certain that no baboon at Chololo ever thinks of me. Since thanks will not be heard then, I will only say this: Rebecca and her friends trusted me while they knew me and.... Damn, can't find the words.

I am grateful to the Office of the President and the Institute of Primate Research for permission to conduct research in Kenya. This work was supported by a JCI studentship from the Science and Engineering Research Council of Great Britain.

Abstract

Group size is known to correlate with various indices of brain size in the primates. The possibility that increases in group size foster social complexity forms the central empirical topic of this thesis. A ten month field study of olive baboons, *Papio cynocephalus anubis*, was carried out on the Laikipia Plateau, Kenya. Data were collected on a wide range of social behaviours in two troops, one smaller than the mean group size for *Papio* and one larger.

The concepts of complexity and social complexity are critically examined with a view to their quantification in behaviour and cognition. The status of social complexity in the debate concerning the evolution of high intelligence in the Primate Order is discussed. Dimensions of social complexity are developed and then investigated empirically.

Females in the two troops showed similar grooming frequencies and grooming network sizes. However, the troops differed in the patterning of their grooming with respect to rank: individuals in the small troop groomed those of high rank, individuals in the large troop groomed those of rank similar to themselves.

Cluster analysis of spatial proximities showed no sign of cliquishness in either troop.

Females formed associations with particular males ('friendships') in both troops but there were no clear differences in either the number or stability of these associations.

The rate of interaction was higher in the large troop, but, proportional to total interaction rates, the rates of agonistic and polyadic interactions were not. The rate of interaction was higher for adult and sub-adult females than for adult and sub-adult males. In comparison, the proportion of interactions that were agonistic was greater for the adult and sub-adult males.

The variability of response to affiliation that individuals faced was the same across the two troops. Males, however, faced more variability than did females largely because of a high number of avoidant responses.

The absence of strong differences in social complexity between differently sized troops suggests that, proximally, cognitive complexity limits social complexity. Thus, interspecific comparisons may prove to be the most fertile area of research into complexity in the future.

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Chapter 1: Introduction

The Scope of the Problem

Psychology occupies an interesting niche in science. Historically, its roots are not more than a century old and lie in medicine and philosophy, roots exemplified respectively by the work of Freud and James. The medical model stressed normal and abnormal psychological function in the context of the organism as physiological entity. The philosophical approach was largely concerned with epistemology and the philosophy of mind. These disparate origins characterise the development of a subject which has shown little coherence, in which 'schools of thought' disagree even on the fundamental questions to be asked. Reber (1986) holds psychology to be undefinable in terms of subject matter and simply to be what scientists and philosophers of various persuasions have created in trying to explain mental life and behaviour. The consequence of this lack of direction is that theorists have often used the more established academic disciplines as a secure starting point to begin psychological enquiry.

Biology is one such starting point. Biology advances on psychology on many fronts. The most obvious of these is brain research in which inroads are continually being made concerning the functional structure of the brain. Some may wish to retain the autonomy of psychology in its traditional guise because they equate biological psychology to the reductionist program that neurophysiology often comprises and rightly feel that reductionism is misguided or impossible when applied to the subject matter of psychology. Such a view does not do justice to the scope of modern biology, however. Through their constant interaction, the sub-disciplines of evolution, genetics and animal behaviour have fermented a conceptually exciting picture of nature as an open-ended system, diverse not only in the forms it assumes but equally in the paths it follows. The study of these processes is synthetic as often as it is analytical. From the perspective of ecology, the emergence of minds is a single, though important facet of the ecological whole. Minds are phenomena firmly located in nature.

A further role that biology plays in understanding the human mind concerns the specific contingencies that have shaped the evolution of humans and the Primate order. This is the essence of biological anthropology but also, in its comparative aspects, primatology. The purpose of this chapter is to review some of what is known and some of what has been speculated about primates and primate intelligence. This will set the research agenda and provide the backdrop for the

more specific matter relating to the title of this thesis.

Evolution, Ecology and Sociality in the Primates

Jolly (1985) characterises the evolution of the Primate Order by the emergence of the following features;

- (i) The development of a hand suitable for grasping
- (ii) The development of vision at the expense of the other senses.
- (iii) An increase in the size of the brain, particularly the cerebral cortex.
- (iv) A tendency towards precociality in young.
- (v) An increased lifespan.

These are characteristics of the organism. A further aspect of the anthropoid primates is that, with a few exceptions, they group. This has been hypothesised as a defence against predation since groups, particularly large ones, reduce predation and allow the costs of vigilance to be shared. (Crook 1971; Alexander 1974; Clutton-Brock and Harvey 1977a; van Schaik 1983). Large groups may also be able to displace smaller groups of competing animals, including their own species, from food patches (Wrangham 1980). Humans and chimpanzees (Goodall 1967; Plooiij 1978) and possibly even baboons (Strum 1975) may also benefit from the opportunities groups afford for co-operative hunting.

The particular qualities of the group, such as the nature of the reproductive units contained within it or the transfer of one sex between groups are generally assumed to be a function of habitat. This is the premise of socioecology, typified by Crook and Gartlan's (1966) original classification of primates into five adaptive grades. However, whilst the structure of primate groups may be a consequence of their niche, the effect of this structure is to create an internal environment of competition. For females, this will generally be competition for access to food and for males it will additionally be competition for access to oestrous females (or defence of a harem from males from outside of the group). The effect of this is to create a milieu of social selection which manifests itself in the large amounts of time many primates devote to social interaction.

Primate Intelligence and Social Cognition

Compared to the rest of the mammalian order, primates are intelligent by any of the many definitions of the word. The mean encephalisation quotient of anthropoid primates is around 2.0 (Jerison 1973); that is, compared to other mammals they have a brain twice as big as they 'should have' for their body size.

Intelligence, like all other characteristics of organisms, evolves because it has enabled members of a species to deal with the environment more effectively than their competitors. An increase in the size of an animal's brain changes that animal's niche in so far as it changes the relationship between the animal and its environment. What selective pressures have led primates to evolve their anomalously large brains? The answer to this question may hold the key to understanding how the minds of primates, including humans, are naturally configured.

Broadly, current theories concerning the evolution of primate intelligence come under the headings of ecological or social theories. Instrumental in developing the first variety are Clutton-Brock and Harvey (1980) who have attempted to test whether, within the primate order, frugivory is correlated with brain size. Various species of primate have been shown to make highly directed movements towards particular patches of food (e.g. Altmann and Altmann 1970; Wrangham 1977; Milton 1980; Marsh 1981; Sigg and Stolba 1981). It has been hypothesised (McKinnon 1978) that large brains were selected for in the Primate order because they enabled individuals to use a sophisticated 'cognitive map' of high quality food resources (e.g. fruit) distributed across space and time, modifying the map as fruiting seasons changed and resources were depleted. Clutton-Brock and Harvey also showed that brain size and mean home range size were correlated, implying that the size of the requisite cognitive map helped determine brain size.

A different ecological theory of primate intelligence has been advanced by Parker and Gibson (Parker and Gibson 1977; Gibson 1986, 1990) which suggests that the ability of primates to extract food from an inedible matrix is conceptually as well as manually demanding and that this has been an important factor directing their brain evolution.

The social theory of intellect was hypothesised by Jolly (1966) and Humphrey (1976) and became somewhat transformed into the 'Machiavellian intelligence' hypothesis under the direction of Byrne and Whiten (see Byrne and Whiten 1988). The essence of this hypothesis is that it is the social complexity of primate groups that has selected for intelligence. As Dunbar (1992) has noted, no quantitative evidence has been forwarded in support of this, largely because the

hypothesis is phrased rather vaguely.

Dunbar (1992) is the first scientist to actually make a comparison, across species, of the power of ecological and social explanations of primate brain size. Rather than using total brain size as a variable he concentrated on the neocortex since this accounts for much of the difference between primate taxa. He also notes that, crudely speaking, it is the 'thinking' part of the brain and so should constitute the main index of cognitive capacity. Dunbar used 'neocortex ratio', the ratio of the neocortex to the rest of the brain as his independent variable and examined its ability to predict aspects of primate life that, according to the hypotheses discussed earlier, require increased intelligence. Concerning the ecological theories, he used the variables of; percentage of fruit in diet, mean home range size and mean day range length. For the social theories he used mean group size. After partialling out the effects of body size he found that only group size was significantly correlated with neocortex ratio. Sawaguchi and Kudo (1990) have found similar results; they show that solitary and group living prosimians differ in the relative size of their neocortices.

Dunbar's work lends broad support to the social intellect hypothesis. Whiten and Byrne (1989) have noted, however, that there are three, progressively bold interpretations that can be made of the social intellect hypothesis. The first is simply that social problems require intelligence, that intellect *is* applied in the social domain. The second, stronger level at which the hypothesis can be interpreted is as a statement of the causal factors underlying brain evolution; namely that primate intelligence is a *result* of these intellectually demanding problems. This is the hypothesis that Dunbar's work ostensibly tests. He regressed group size onto neocortex ratio on the basis that, proximally, intelligence limits group size. However, it was assumed that at the ultimate level the causal direction would be reversed: selection for increased group size selected for a concomitant development of intelligence.

The final, boldest interpretation of the hypothesis is that the *mode* of the most sophisticated aspects of primate cognition is specifically social; that selection in the social domain has furnished our order with an intellect geared to solving problems peculiar to the social domain. This final claim sets the study of primate intelligence in the bounds of cognitive ethology for it addresses the question of what specific representations primates hold about the world.

The validity of addressing the nature of animal representations, long championed by Griffin (e.g. Griffin 1976, 1982, 1984) has been furthered recently by Cheney and Seyfarth (1990) in their provocatively entitled book, 'How Monkeys see the World'. They demonstrate how far detailed field observations of vervet

monkey behaviour, coupled with a series of inspired field and lab based experiments can be taken in inferring the attributions that such animals make. A general conclusion the authors draw is that vervet monkeys seem much better at solving problems involving each other than they are at problems that involve objects, even though, formally, the problems may be very similar. This constitutes support for the third level of the social intellect hypothesis.

The Evolution of Social Complexity

The rephrasing of the social intellect hypothesis as the Machiavellian intellect hypothesis conveys an important quality of the idea in its present form. The stress on manipulation and cunning that the title implies, highlights the assumption that the dividends paid to socially sophisticated group members are at the expense of other members of the group.

This is not an uncontroversial claim and Milton (1988) for one has argued that, in the hominids at least, Machiavellianism would have little payoff to the individual and that hypotheses concerning social intellect should stress its *cooperative* nature. She cites food sharing with division of labour in humans as an example. Furthermore, alliances such as those frequently found in baboons (e.g. De Vore 1962; Altmann 1962; Kummer 1965; many authors since) may entail the long term monitoring of reciprocity particularly when the alliances are between unrelated individuals (though the reality or sophistication of such reciprocity has been questioned, see for example, Noe 1990). It is true that reciprocal altruism clearly must ultimately serve selfish ends if it is to prove adaptive (Trivers 1971); hence the need for monitoring. It is also true that primate alliances typically constitute a case of cooperation towards a competitive end (i.e. they are detrimental to those exterior to the alliance). However, the intelligence required to coordinate an alliance, certainly at the short term interactional level, can validly be described as serving a cooperative function.

Yet there is a seductive logic to the Machiavellian hypothesis. The benefits of true cooperation are diffused across the cooperating unit. If all members of a group are cooperative with all others then the adaptiveness of cooperation ultimately becomes a form of group selection. In contrast, the benefits of Machiavellianism accrue purely to the individual and so ought to constitute a much more effective selective pressure. This is all the more the case in that the benefits are at the expense of other group members who are often an individual's closest competitors. It appears that Machiavellianism is a strategy that ought to rather easily, rather

inevitably, invade a population of honest cooperators.

The emphasis on conflict rather than cooperation highlights the fact that the evolution of Machiavellianism accelerates itself. The costs of being manipulated by one's neighbour may be so dire that counter-manipulative abilities are strongly selected for. The consequence is what Humphrey (1976) describes as an evolutionary 'ratchet' increasing the general intellectual standing of the species. A hypothesis positing a process of positive feedback such as this is all the more appealing for the speed of evolution that it can accommodate. This is a pressing issue in the question of how the lineage that led to modern humans tripled the size of its brain in the course of two to three million years, especially since brain size may be one of the less evolutionarily labile characteristics (Deacon 1990).

The evolutionary ratchet concept logically entails a further point. If runaway social selection has characterised primate evolution then we would expect to find primate groups exhibiting social structures and behaviour whose primary function operates with regard to the social rather than ecological environment. This is an important distinction to be made. It is the basic premise of socioecology that social structure (and behaviour that creates that structure) is an adaptation to, and therefore a consequence of, a species' ecological niche. Certainly, it is true that much social behaviour is an attempt to solve ecological problems, e.g. hunting or hive building. Behaviours such as grooming, however, may serve a largely social function in that they may be performed over and above that required for hygiene. Ecological pressures force primates into a primary social behaviour: grouping. This results in a selective environment for a secondary social behaviour; grooming, functioning with regard to the social, rather than ecological environment. This behaviour may itself generate another level of behaviour: competition for access to groom. There may be a limit to the social complexity that ecological factors can directly generate. The route to social complexity probably lies through increasingly self-directed behaviours of groups because they support higher levels of social behaviour as just discussed.

The possible runaway increase of a taxon's social complexity across time is illustrated in Figure 1.1. The function described by this is an exponential one. This does not follow necessarily from the positive feedback mechanism posited for social complexity; all that is assumed there is monotonic increase. It is true, however, that social species tend to evolve faster than non-social ones (Wilson 1992) so there might be a case for viewing evolutionary time as 'compressed' with respect to chronological time, thus creating an exponential function from a linear one.

In any case, it is illuminating to consider the present situation in nature. If

Figure 1.1 Growth of a taxon's social complexity over time

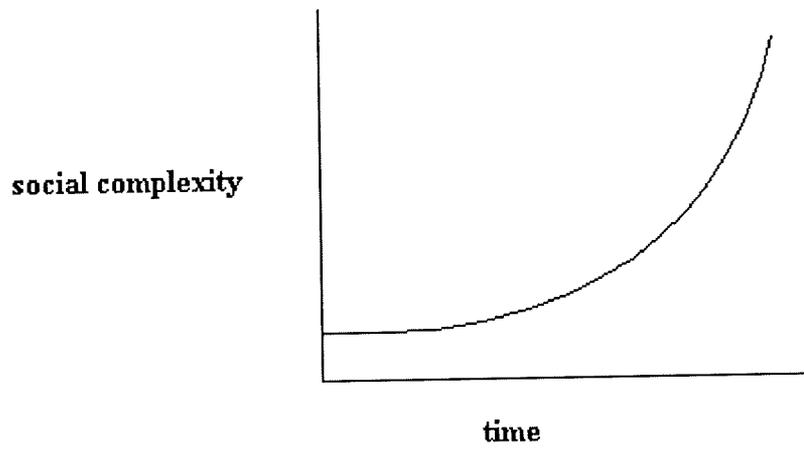
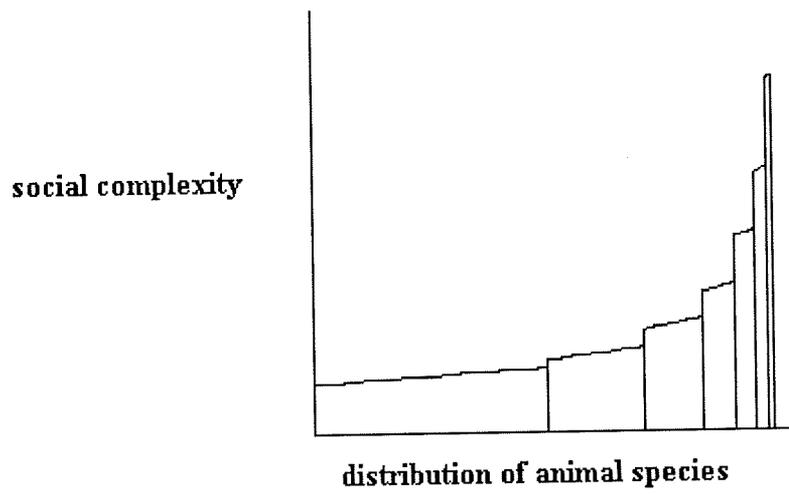


Figure 1.2 Distribution of social complexity across species



one were to plot social complexity (under various reasonable definitions of the term) against the entire distribution of animals in a group, ranked in order of their social complexity, a function such as Figure 1.2 might well emerge. The graph suggests that a large chunk of the social complexity that exists in the animal kingdom (or mammals, or vertebrates, the grade is arbitrary) is concentrated in a disproportionately small number of taxa. (The discrete blocks represent the constraints of phylogeny). Another consequence of this exponential function is that among the few socially complex taxa, the differences in social complexity should get increasingly larger as the overall social complexity grows. It is true that whilst three of the four species of non-human great ape are considerably more socially complex than most of the 130 or so species of monkey, social complexity in the most primitive of human societies is far removed from that of the other apes. To refer this back to Figure 1.1, we should not expect the situation in nature to stand thus unless at least some taxa were susceptible to the runaway acceleration of complexity as depicted.

The Ethics of the Machiavellian Intelligence Hypothesis

Richard Dawkins found himself having to qualify his coining of the 'selfish gene' (Dawkins 1976) as being a statement about biology rather than morality. The Machiavellian Intelligence hypothesis has not attained quite the same degree of publicity but, similarly, it runs the risk of passively condoning exploitation as being in some sense biologically inevitable. It is easier to distance ourselves from selfish genes, since they are, after all, only genes. Intelligence on the other hand is much closer to home. Are studies of human social evolution in danger of further tarnishing humanity's humanity?

A rational and broad line of enquiry need not produce any conflict between studies of human social evolution and ethics, both of which need to be eclectic to fulfil their function. On the one hand, scientific explanation can only suffer from a naive expectation of cooperation in the animal kingdom, which expectation may be fostered by an anthropomorphic extension of features of our own behaviour to other animals. Dawkins and Krebs (1978), for example, were responsible for something of a paradigm shift when they remarked that animal signals, being products of natural selection, should not be assumed to be an accurate readout of the signaller's internal state except in cases where this was adaptive or, in the more frequent case, unavoidable because of design features of the signal. In retrospect, it seems obvious that signals mediate competition and so should be expected to be

manipulative rather than honest. Perhaps like group selection, so central a dogma in the sixties, it requires a close examination of the mechanism of a process to escape our human biases.

On the other hand, it is absurd to ignore the universality of moral codes in human societies and the existence of apparently genuine altruistic behaviour. The longevity of humans and the accountability that sophisticated communication brings might well be expected to favour genuinely honest behaviour. At some point in human evolution, society and culture may have started to penalise anything other than the most adroit of Machiavellianism. Earlier, it was said that Machiavellian strategies ought to rather easily invade a population of honest strategies. Machiavellianism entails exploiting others in such a way that they do not realise that they have been exploited; this distinguishes Machiavellianism from blatant 'cheating'. It is true that a small advantage in intelligence might enable a Machiavellian individual to operate this way on a one to one basis. However, the growth of group size and the emergence of language in our ancestors must have resulted in a much larger and much more disclosive net of communications. The prospects of Machiavellianism may have waned at this point in favour of genuine honesty. A cheater's exposure in his or her interaction with a single individual would affect its reception by all other individuals who had access to that information.

The converse effect of such accountability is that altruism can theoretically extend beyond the classic reciprocal dyad which underlay Trivers (1971) original conception of reciprocal altruism. Connor and Norris (1982) suggest that reciprocal altruism in dolphins (for example in aiding conspecifics to the surface) cannot account for all such instances of altruistic acts. Since dolphins have been shown to form alliances (Connor ^{et al.} 1992), it is possible that altruistic animals would find it easier to form cooperative bonds with 'onlookers' and there might consequently be selection for generalised altruism.

Erdal and Whiten (1994) review the question of selfishness with regard to contemporary hunter-gatherer societies. The norm in these is egalitarianism rather than the dominance hierarchies typical of other primates and, arguably, agricultural and industrial human societies. Erdal and Whiten coin the term 'vigilant sharing' for the division of resources in such groups and posit it as an ESS under certain conditions. Intriguingly, they also suggest that it might result from the evolutionary spiral of Machiavellianism and counter-Machiavellianism 'blowing itself out' as the exercise of such skills became prohibitively costly in time and energy. The result, in a large group would be that vigilant sharing was an evolutionarily stable strategy.

However, even on a one to one basis, honesty may be a safer ploy than

Machiavellianism in cases where individuals are repeatedly interacting. The results of Axelrod's (1984) famous computer tournament of the Prisoner's Dilemma game are pertinent here. The Prisoner's dilemma relates directly to the formal aspects of reciprocal altruism in that it sets a scenario in which the long term benefits of cooperating with one's partner can be improved if one is able to cheat often enough and get away with it. A great variety of strategies were submitted to Axelrod's tournament which was operated in a context of natural selection; low scoring strategies were knocked out and the contest repeated at each stage. The winner, across many variations of the tournament, was 'tit-for-tat', a strategy that cooperated in the first instance of the game and then on subsequent occasions repaid its partner's previous action in kind. The entirely trusting strategies that always cooperated were quickly weeded out by the entirely selfish ones who themselves waned once they had exhausted this trusting population. The overtly Machiavellian strategies, complex decision makers which attempted to get away with just as much cheating as their partner appeared willing to take, did not do much better than the blatantly selfish ones. Very few strategies were as simple as tit-for-tat. Axelrod classed tit-for-tat and the other most effective strategies as being *nice* (they always tried to cooperate at the start), *retaliatory* (they didn't allow cheating), *forgiving* (the other aspect of retaliation: they cooperated as soon as their partner cooperated) and *clear* (other strategies knew what to expect). To extend the results to aspects of human cooperation, clarity of motive is perhaps one of the greatest losses to result from being suspected a Machiavellian.

There appears to be a link between genuine emotional states and the expression of those states in facial signals. That is to say, most people are not able to feign emotions very well (Ekman 1985). Thus, honesty motivated by genuine moral sentiments ought to be distinguishable from the Machiavellian pretence of honesty. Where individuals seek out such genuinely honest others to form cooperative bonds with, and where individuals in such cooperative alliances can out-compete those who are not, there will be selection for honesty. A typical rejoinder to this might be that there would be even greater selection for the successful pretence of honesty. However, as discussed earlier, because it is not possible to fool all of the people all of the time, Machiavellianism will only be adaptive in certain situations.

The assumption of selfishness and the neglect of altruism in scientific theories of human behaviour can be pernicious. Ever since the coining of the phrase 'survival of the fittest' our expectations of what to expect from one another have suffered from the negative assumption that all are relentlessly competing. In its extreme form, this is endorsed: 'greed is good' and the greatest good will

emerge from our all striving to outcompete one another. Frank, Gilovich and Regan (reported in Frank 1993) investigated the possible psychological effects of the selfish models of behaviour that form the core paradigms of economics. They found that economics students were more than twice as likely as other students to cheat whilst playing one shot games with strangers. The authors claim that this was not a reflection of the type of person who chose to study economics. For example, the difference in cheating grew larger the longer a student had studied economics. Questionnaires revealed that first year economics students were more likely to expect opportunistic behaviour from others by the end of their first term than they were at the beginning.

Such can be the effect of science on society. Science aside, if Machiavellianism has played a part in the shaping of our rational faculties then it is important to appreciate that fact. Dawkins (1976), in the aforementioned defence of his ethical stance, claims that we have to understand our selfish genes in order that we may trick them and thus behave unselfishly. The same applies to a study of Machiavellianism in primate evolution. It provides a base line from which to look for evolutionary routes to unselfish behaviour, routes that are presumably to be found in how groups behaved both with respect to one another and internally. Such knowledge may have considerable application to all instances where cooperation needs to be fostered in our society.

A Research Program for Social Complexity

This chapter has examined in general terms both the causes of social complexity and its consequences, these including self reinforcement of social complexity through positive feedback and consequent selection for heightened intelligence. The relevance of the study of social complexity to cognitive ethology was also touched upon. Application of these principles allowed the discussion of possible roles of social complexity and Machiavellian intelligence in human evolution. This discussion was set in the broader context of the paradigmatic exchange between scientists' models of human evolution and societal norms and those of our own 'folk anthropology'.

These considerations remain implicit in following chapters. Since this is an empirical thesis, much of the remaining discussion will relate this quantity, social complexity, solely to the study animals: olive baboons. As savannah baboons are an extensively studied species for whom many of the quirks of species specific behaviours have already been established, they constitute an ideal departure point

for the primatologist investigating social complexity. I hope, however, that where applicable the results of this study can be generalised at least to other primates and, where they cannot, the *methods* used will remain valid tools for investigating social complexity.

The implications of the construct of 'complexity' as a descriptor, form the substance of the following chapter. Chapter 3 extends this dissection of complexity by an examination of qualities peculiar to its social guise, leading to a battery of hypothesised indices of social complexity. Baboons and the relentless flux of their society dominate the remainder of the thesis until the final discussion.

Chapter 2: On Complexity

* A revised version of this manuscript has been submitted to *Theory and Psychology*

Introduction

The study of complexity, like that of chaos a few years before, is emerging as a discipline in its own right, with theorists from disparate fields in pursuit of a common theory (Waldrop 1992; Lewin 1992, 1994). Much of the recent literature is concerned with the processes by which complexity arises, often with an underlying assumption that the nature of the phenomenon itself is relatively unproblematical. Kauffman (1991), amongst others, has extensively considered the evolution and perpetuation of complexity in dynamical systems. The aim of this chapter, however, is perhaps more fundamental: to examine the concept of what complexity *is* in ways that are useful to behavioural and cognitive scientists. In this chapter I will consider only 'freeze-frame' aspects of complexity and will not be concerned with its temporal aspects.

The term complexity is frequently found in biology and psychology. This is particularly the case in evolutionary biology and ethology, where there has been an apparent progression towards greater complexity in organisms, both morphologically and behaviourally (e.g. Darwin 1854). It is uncontroversial to state that mammals, as a group, are more complex than flatworms, and flatworms more complex than bacteria. Such a judgement is a descriptive measure, albeit an intuitive one. However, when complexity is invoked as playing a *causal* role in evolution, a more rigorous examination of the concept needs to be made. Primate cognition provides a good example. Patterns of behaviour, cognition and neuroanatomy have been loosely summarised as 'complex' in primates, and these features are hypothesised to be adaptations to problem solving in a 'complex' environment (e.g. Humphrey 1976; Whiten and Byrne 1988; Dunbar 1992). But unless the nature of this complexity in all of the contexts outlined above can be more formally and accurately characterised, little can be said about why certain features rather than others exemplify adaptation. What follows is a review of some of the more important concepts of complexity found in the information sciences and an attempt to relate them to problems in biology more generally.

Randomness

Grassberger (1986) presents for inspection three two dimensional patterns. Of these, one is a chess board pattern and another, a pattern of random dots. The third is a 'chaotic function' tracing its progress in whorling semi-periodic orbits. Belied somewhat by their name, chaotic patterns of this sort do appear to contain structure, but structure of which the individual elements are arranged in unpredictable ways. For readers unfamiliar with the chaos concept, envisaging a satellite picture of cloud formations over the earth might be useful; such a picture would probably appear chaotic in the sense of the word intended here.

The question is: which of the three patterns is the most complex? Intuitively, many would say the chaotic pattern. The chessboard is very simple in its regularity. The random dot pattern is far from being simple in regularity; instead it must be judged less complex because it is 'just random'. These extremes of simplicity thus appear at opposite poles with respect to randomness, complexity being perceived between them. What measure of complexity will show this?

In order to discuss this question, the nature of randomness itself should first be discussed. Fortunately, this concept has proved itself to be easily formulated. Chaitin (1970, 1975) has discussed randomness with respect to the most primitive kinds of systems imaginable: strings of binary digits. Chaitin's position is that randomness is essentially 'patternlessness' and that any string of 1's and 0's in which a pattern can be discerned is non-random.

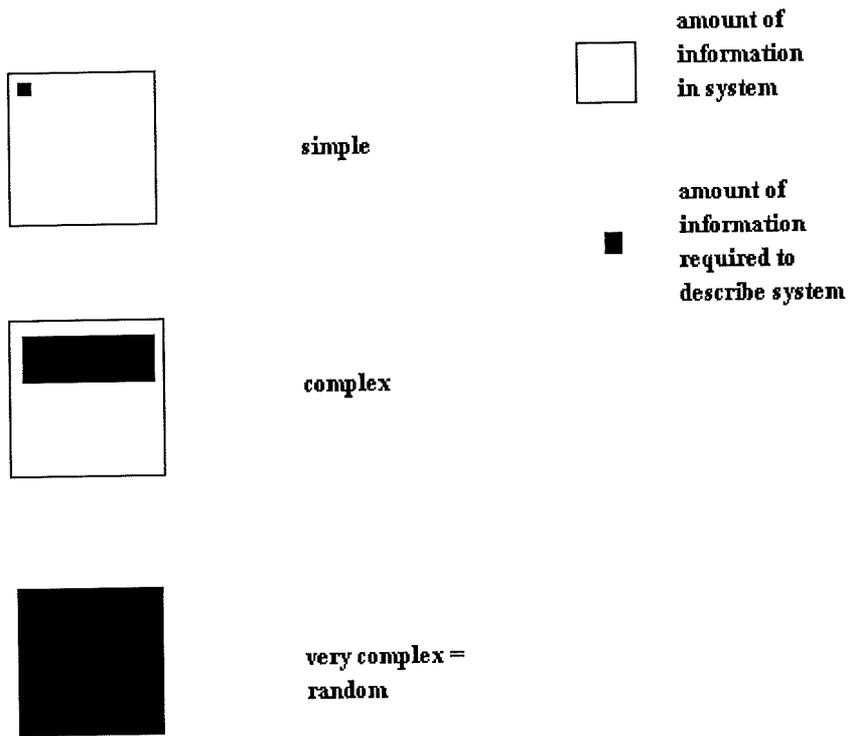
Formally, any patterned string can be generated by a string shorter than itself: that is to say the algorithm (embodied perhaps in a computer program) for describing a patterned system is smaller than the system itself. In the case of a truly random string of 1's and 0's, however, the simplest way to reproduce the string is to specify it verbatim.

As such, non random systems are *compressible* into a set of rules. This compression can be continued until the 'minimal program' is found which most succinctly describes the system. This is itself random, by definition (since otherwise it could be further compressed).

For some, this process is itself enough to identify complexity. Kolmogorov complexity (Chaitin 1975) of a pattern is the length of the program needed to generate a pattern divided by the size of the pattern itself. Figure 2.1 illustrates this in a simple manner. The squares represent the amount of information contained in the system, the shaded area the amount contained in the minimal program required to generate the system.

The unattractive aspect of this definition is that random systems are

Figure 2.1 Kolmogorov complexity



accredited maximum complexity. In the context of evolution, it is generally hypothesised that animals have evolved complex characteristics in response to complexity in their environments. A perfectly random environment however, cannot be expected to select for complex behaviour and intelligence since the possessors of these attributes gain no advantage over their conspecifics. As Strum (in press) notes, a monkey faced with trees which fruit randomly may as well take a random walk to find some food. Only when the environment is patterned but patterned in non-obvious ways can it be expected to select for intelligence.

The three-way distinction between orderedness, randomness and complexity, with the latter quality considered intermediate between the others, is characteristic of the emerging discipline of complexity. Kauffman (1991) has described complexity as 'the edge of chaos', as the point where 'frozen' systems 'melt' towards chaos. Clearly then, complexity is an intuitively meaningful term and there is a common desire to see it distinguished from randomness.

Predictability

The concept of predictability is closely linked with those of pattern and randomness as discussed above. In fact, the common sense notion of randomness (as opposed to the formal one discussed earlier) is very close to that of unpredictability. Predictable systems are strongly patterned whilst unpredictable ones are not. The level of apparent predictability of a system results from an observer's knowledge of: (i) the rules that govern the system, and, (ii) the current state of all variables used in the rules.

A useful way to gauge the predictability of a system is to count the *number of factors* that are required to predict the next state of a system. Consider three different strings;

- (a) 11111111111111111111111111111111
- (b) 10101010101010101010101010101010
- (c) 110011001100110011001100110011

The first requires no factors to predict the next digit since this is always 1. The second requires a consideration of the previous digit only and the third requires knowledge of the previous digit and the previous one to that. The corresponding

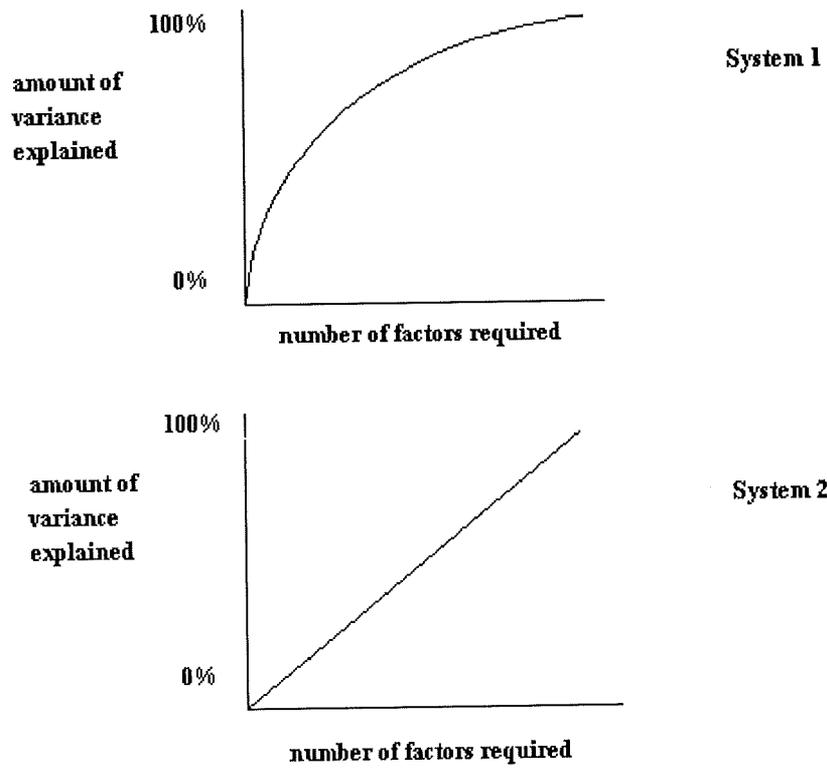
rules can be expressed as follows.

- (a) $\text{next} = 1$
- (b) if $\text{previous} = 1$ then $\text{next} = 0$
if $\text{previous} = 0$ then $\text{next} = 1$
- (c) if $\text{previous} = 1$ and $\text{previous}(\text{previous}) = 1$ then $\text{next} = 0$
if $\text{previous} = 1$ and $\text{previous}(\text{previous}) = 0$ then $\text{next} = 1$
if $\text{previous} = 0$ and $\text{previous}(\text{previous}) = 1$ then $\text{next} = 0$
if $\text{previous} = 0$ and $\text{previous}(\text{previous}) = 0$ then $\text{next} = 1$

Chaitin (1970) defines the *algorithmic complexity* of a string as the number of bits of information required to generate it. If it is assumed that a high proportion of the aspects of living organisms are rule-governed then unpredictability can be used as a rough index of complexity. However, on both theoretical and methodological grounds, it is not practicable to attempt to measure the unpredictability of an entire system where many factors are at play. Rather, an attempt should be made to specify the number of factors that are required to predict a given amount of the system's variance. In this manner, the unpredictability of the entire system is 'sampled' by investigating the unpredictability of a portion of it. Consider the two systems distinguished in Figure 2.2. Both systems require the same number of factors in order to be entirely explained but in System 1, 50% (or indeed any other fraction) of the variance is explained by many less factors than in System 2.

Note that this definition of complexity does not depart from that of Chaitin (1975) previously described which, itself, is very close to that of randomness. However, the point to be emphasised here is that when a system is very large and organised, most apparent randomness may well reflect the perceiver's ignorance of the rules that govern the system rather than 'genuine' randomness. For example, the rules that govern the feeding behaviours of either a baboon or an amoeba may each, on average, predict four times as much information regarding the observed behaviour (which in this case constitutes our system) as the rules themselves contain. By our earlier definitions the two sets of behaviours are equally random (randomness = system divided by size of minimal program). The feeding behaviour of the baboon is, however, more complex in so far as the absolute size of the program required to describe its behaviour (or, say describe 50% of its

Figure 2.2 Cumulative efficacy of a number of factors in explaining the variance of two systems



variance) is larger. This situation is represented in Figure 2.3.

Where the number of rules required to specify a system is a reasonably modest fraction of the system itself (say, less than 50%) we should be confident that we are explaining variance by the discovery of genuine rules that govern the system. We would always want to limit ourselves to explaining a fraction since in all living systems there is likely to be a residual amount of variance that is not rule governed (or in the parlance previously used, variance which requires as much information to explain it as is contained in the variance itself). However, in complex organisms, a new rule which explains only 1% more of the variance is still going to code for much more information than is required to code itself. Thus, to return to the choices outlined at the beginning of the section on randomness, we need henceforth to consider only the difference between the chaotic pattern and the chessboard pattern, since living systems so little resemble the random dot pattern. As long as this remains the case we can usefully retain the definition of complexity as algorithmic complexity.

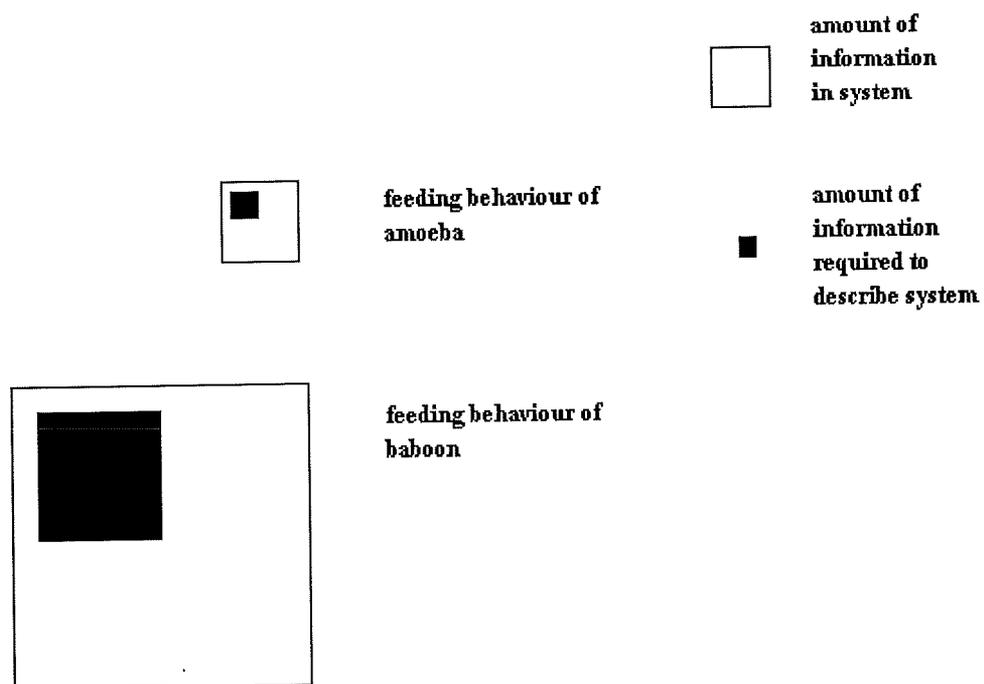
Organisation

So far, the attempt to define complexity in such a way that explicitly excludes random systems, or rather, assigns them maximum simplicity has been avoided. Rather, it has been suggested that the large amount of information that constitutes a description of an organism can (within a given level of confidence) be compressed into a much smaller set of rules for generating the system. As such, living organisms tend to be nearer the ordered end of simplicity than the random end.

The primary attribute of life is that it is organised. Random systems are clearly not, whilst very simple ones may be merely periodic, showing none of the complex connectedness of living organisms. Most notably, the organisation of living things can be described at many levels such that *emergent characteristics* can be identified.

Organisation, like randomness has been subject to attempts at formalisation (e.g. Chaitin 1979). The information that makes up a minimal program for describing a system (i.e. the complexity of a system) can be partitioned. Assume that the minimal program splits up the system it describes into patterns. Some of the information in the minimal program will refer to these patterns and some to the way they are organised. In the equation given below, H is a convention that refers to the amount of information in a system.

Figure 2.3 Relationship between algorithmic complexity and Kolmogorov complexity (randomness)



$$H(\text{minimal program}) = H(\text{patterns}) + H(\text{organisation})$$

Three important expressions have now been considered. The one given above is a breakdown of the original expression $H(\text{minimal program}) =$ algorithmic complexity. It should also be recalled that $H(\text{minimal program}) / H(\text{system described})$ is Kolmogorov complexity which can be taken as essentially a measure of randomness. Obviously, any of the terms in the expressions can now be isolated and expressed in terms of the others.

The nature of the organisation term in the equation above should now be given some consideration. Two very simple strings, say 101 and 110 can be used to generate an extremely random looking string if multiple instances of each are randomly assembled. In such a case, the information in the minimal program that describes the string will mostly be contained within the organisation term and not within the 'patterns'. This conceptual partitioning allows us to assess the amount of organisation in a system relative to the amount of information in the patterns that are being organised.

Note however, that the organisation part of a program may be considered a program in its own right and subject to compression. Consider a minimal program that recognises a long string to be composed entirely of the two substrings 101 and 110. The $H(\text{patterns})$ part of this minimal program will be very small and the bulk of the program will consist in $H(\text{organisation})$, being the most economical specification of how these substrings are ordered. One possibility is for $H(\text{organisation})$ simply to specify the order of the substrings verbatim. However, if the substrings are ordered non-randomly, then $H(\text{organisation})$ may be able to capitalise on this by specifying a rule for ordering the substrings. In essence this is the recognition that the substrings are elements arranged in consistent ways to form larger substrings. It may thus be most economical for $H(\text{organisation})$ to function by specifying how the smaller substrings can be used to construct the larger ones and then how these larger substrings are themselves organised.

Formally the process described above constitutes breaking down $H(\text{organisation})$ into a new minimal program composed of $H(\text{patterns})'$, that is, the larger substrings, and $H(\text{organisation})'$, how *these* are arranged. Since each such breakdown generates a new organisation term the process can be continued indefinitely. The potential embedding of levels of organisation should now be clear. Where hierarchical levels exist in a system and the overall amount of information in the system is large compared to that required to specify the organisation at each level, a minimal program for describing a system will contain

information about the organisation at each level. This process will continue until a level of organisation is found at which the elements are organised randomly.

Consider an example from social behaviour. Members of a social species have a number of social acts in their behavioural repertoire; some aggressive, some affiliative. An observer who records an individual repeatedly interacting with one or more others is in a position to describe that individual as having social *relationships* defined by the identities of the interactants and the forms of social act involved. This is the paradigm outlined by Robert Hinde (1976) for describing social structure in human and non-human primate groups and is summarised in Table 2.1.

It is the *consistency* in the interactions that allows the identification of certain types of relationships. Were all individuals to interact randomly with each other, we would have no basis for identifying relationships. A further pattern of emergence may be identifiable at a level above relationships. If the relationships held by an individual bear a non-random relation to one another than we have a basis for saying that the individual occupies some kind of *role* in the group, in the same way that relationships are defined by consistencies at the level of interactions.

The way in which primate social behaviour is structured is just one example of this stratification of phenomena in living systems. The general case is that a phenomenon at one level is composed of patterns of phenomena at the level below.

It was stated earlier that our intuitions about complexity led to a wish to characterise it such that both uniformly patterned and random systems had low complexity. But the fact that these types of systems represent, respectively, minima and maxima of randomness, jeopardises the use of randomness as a direct measure of such complexity. What these two extremes share however, is a common failure to support emergent properties. Thus, one way of conceiving of randomness is as that from which naught emerges. Likewise, a simple periodic system can be described at one, simple level.

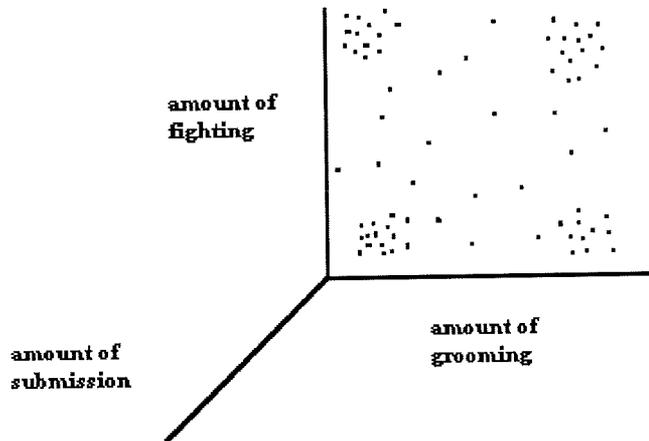
Maximally patterned systems, those which people tend to judge the most complex, will occur when a system is at a point between randomness and uniformity. The scheme for describing primate society outlined above can be extended further to illustrate this. Figure 2.4 shows the interactions of a hypothetical individual with all others. Ignoring the z axis for the moment, it can be seen that there are two acts in its repertoire: groom and fight. Each data point represents the frequency of each act directed at other group members.

The pattern in Figure 2.4 would lead us to define four types of relationship, which might be labelled: friendship, animosity, indifference and temperamentality. Were the data points to be randomly distributed over the space then no relationships

Table 2.1 Levels of social phenomena in a primate group

| Level 1 (interactions) | Level 2 (relationships) | Level 3 (roles) |
|--|---|---|
| fight greet show submission etc | friendship animosity ambivalence etc | top rank scapegoat conciliator etc |

Figure 2.4 An individual's relationships shown as a clustering of its interactions with other group members



would be identifiable.

As soon as another dimension is added, however, (say submission) the space for clustering to occur increases. Figure 2.4 shows that, geometrically, this clearly must be the case. But intuitively also, the potential subtlety and depth of a relationship will always be dependent on the number of dimensions along which it is free to vary. Clusters are (by definition) relatively discrete. As the number of clusters grows, their discreteness diminishes unless the volume they are clustered in grows correspondingly. Alternatively, we can say that if an animal lacks an act then this immediately restricts the diversity of relationships it can experience.

There is clearly something special about systems which, though specifiable by less information than they contain, have that information structured in 'interesting' ways. Neither random nor chessboard patterns are very interesting. They are also not complex in the intuitive sense we have considered. Random patterns are complex in the manner outlined by Chaitin's algorithmic complexity, but the complexity is not organised in interesting, *complex* ways. In this manner, intuitively complex systems contain a kind of second order complexity.

Reconsider the three systems in terms of randomness: the random dot pattern and the chessboard representing extremes, and the chaotic function an intermediary. Consider such classes of system in terms of their minimal program:

$$H(\text{program}) = H(\text{patterns}) + H(\text{organisation})$$

In highly periodic, chessboard-like systems all three of the terms above are always low. In random systems, the partitioning of a system's description into $H(\text{pattern})$ and $H(\text{organisation})$ is not really meaningful. At its extremes, a random string can be seen either as a single information rich pattern with no need of organisation, or alternatively as a large number of very simple patterns (1's and 0's) requiring a great deal of information to specify how they are put together. In either case the minimal program will be the same size. Only in the intermediate area between randomness and periodicity are the contributions of pattern information and organisation information meaningful and free to vary with respect to each other. Only in such cases are the relative contributions of these terms difficult to specify *ad hoc*. *Systems which are intuitively complex are those for which the minimal program, the best method of description, is not clear, a priori.* In contrast, we can always specify the best method of describing a random system: repeat it verbatim.

Given a large enough system, there are many more ways for it to be random than non-random. Despite this, it is common for us to consider all random systems as somehow being the same as each other regardless of the uniqueness of each

particular instance. The perspective from which random systems *are* all the same is that given above: the meaninglessness of considering the relative contribution of pattern information and organisation information to a description of a system.

It is the assessment of the relative contributions of $H(\text{patterns})$ and $H(\text{organisation})$ which constitutes an assessment of a system as random or complex. The manner in which humans class systems as simple, random or complex ought to be functional. I suggest that the classification represents a case of metacognition. The appraisal of a system as random or complex is an estimate of the amount of cognitive effort that will have to be devoted to understanding the system. This is functional in so far as effort is not wasted on attempting to understand random systems. In terms of selective pressures, systems as we have discussed them should have a temporal aspect; the purpose of understanding them is to predict how they will behave next.

The special properties of intuitively complex systems, namely their (potentially hierarchical) organisational aspect and the variability of the way in which this and the system's constituent patterns are related have been elucidated. However, whether such complexity can be quantified remains to be seen.

One formalism that might be appropriate for identifying that area between randomness and simple periodicity which seems to constitute intuitive complexity is suggested by Alessandro and Politi (1990). They use the terminology of 'vocabulary' and 'grammar' which are analagous to patterns and organisation. They suggest that the complexity of the vocabulary of a string be a function of the logarithm of the number of admissible sequences plus the logarithm of the number of inadmissible sequences. This makes the chessboard and random dot type patterns minima of complexity.

Complexity and Cognition

Just as the complexity of an animal's behaviour can be expressed as the amount of information required to describe it, so can the complexity of an animal's cognition be expressed as the amount of information that it can process in attempting to solve problems. The addition of a speed measure to this would constitute one measure of an individual's cognitive ability.

The separation of complexity into pattern and pattern organisation has some interesting implications for cognition. Patterns at the lowest level of organisation are the basic element. Organisational information specifies how they are to be assimilated, possibly into higher order patterns. The process of organisation and the

generation of further levels of patterns adds *depth* to a system in so far as the more abstracted patterns and levels of organisation are achieved only after passing through the simpler ones. This is to be compared to the amount of information at any one level, that which can be dubbed *breadth*. The niche which some animals fill might contain many important patterns but patterns which are simply organised; the niche is complex in the sense of its breadth. We would expect animals in such niches to note and act on many environmental cues but with little assimilation. In contrast, where the patterns of an environment are organised in a complex way, where events are highly contingent on one another, the interaction of factors results in a complexity that could be characterised by depth.

Human cognition is notable for its capacity to understand contingency and conditionality and I suggest that it is this deep, rather than broad, form of complexity in problem solving that merits the greatest attention as regards its evolution in the natural world. This is not anthropocentrism. It is the processing of factor interaction that moves an animal's decision making away from the behaviouristic realm of signals as 'releasers' and into the realm of true computation. It is the intentionality, the 'aboutness' of cognition, that is intriguing and as cognitive models become more abstracted from the real world they become ever more remarkable for their retaining the property of mapping it.

Connectionism (for overview see Rumelhart et. al. 1986) realises the distinction of deep and broad complexity of cognition in a rather more tangible manner. Neural nets in their most common form contain a layer of input units connected to a layer of output units, possibly via one or more layers of 'hidden units'. It is a classic demonstration that problems in which one factor in the input reverses the effect of another cannot be solved by neural nets without a 'hidden layer' of units in between input and output layers. These hidden units code for the interaction of factors: they create an internal representation. (The problem usually used to exemplify this is the exclusive OR problem in which the neural net computes the meaning of "A or B" as meaning A or B but not both.) The essential character of networks without hidden units is that they map similar input patterns to similar output patterns (Rumelhart et. al. 1986)

Breadth of computation consists in the breadth of the array of input and output units, depth in the number of layers of hidden units. The former architecture is suitable for recognising a large number of patterns, the latter for recognising relationships between patterns. In some ways, connectionist modelling conceptually integrates a formal, algorithmic expression of cognitive complexity with cognitive complexity as it exists in the brain.

Complexity and Behaviour

Algorithmic complexity as defined by Chaitin (1970), though imperfect as a general definition of complexity for the reasons discussed above, is probably the most practicable approach in the case of describing living organisms. In practical terms, unpredictability can be used as an equivalent term for complexity in describing an animal's behaviour; rather than writing a program for describing an animal's behaviour one can count the number of factors that will predict a given amount of that behaviour's variance. As a heuristic device, it is reasonable to propose that the number of acts in an animal's behavioural repertoire should index its behavioural complexity. (This mirrors the proposal of Bonner that morphological complexity should be gauged by the number of different cell types in an organism: see McMahon and Bonner 1983). Of course, the question is then begged of how to determine the number of acts in an animal's repertoire.

The validity of this approach is likely to be greatest when applied to comparable systems; say, the complexity of foraging decisions in folivorous versus frugivorous primates. If it is assumed that both types of animal are foraging as optimally as their intelligence will allow, then, by virtue of the way it has been defined here, the predictability of their behaviour will perfectly mirror the complexity of their decision making. Or, to put it another way, it will perfectly mirror the complexity of the environment *for* that animal.

One nice aspect of this is that we avoid getting caught up in a fruitless debate over the 'objective' complexity of the environment as divorced from the animal's behaviour with respect to it, and go straight to the amount of complexity that is actually grasped by the animal.

In discussing the relationship between an animal's ecological niche, its behaviour and its intelligence it is complexity cognisable by the individual rather than 'objective', environmental complexity that is the most relevant measure. Baboons and chimpanzees both live in large groups in forest habitats, for example, but we can relate the discrepancy of their brain sizes to discrepancies in their behaviour. As such, they occupy slightly different ecological, or more specifically, 'cognitive' niches within the same habitat, illustrating the different qualities and quantities of the overall environmental complexity grasped.

Whilst we expect a species' niche, behaviour and cognition to be of appropriately matched complexity in the long run, the complexity faced by an individual at any one moment is likely to vary. Because of this, it can become worthwhile speculating on the discrepancy between the complexity of an animal's cognition or behaviour and the complexity of the problem at hand. Clearly, the

frequency and importance of these occasions is going to chiefly determine the evolution of a species' intelligence. The distinction between the amount of complexity grasped and the amount 'out there' provides a framework that bears directly on the difference between two major candidates for selection forces shaping human and non-human primate evolution: the social and non-social (or 'ecological'). The application of an animal's intellect to a problem in the ecological domain, such as planning a day's ranging or fashioning a tool, does not contribute to the problem itself: the complexity of the animal and the complexity of the system are separate. So whilst there may be seasons and food items which prove to be more complex than an individual is able to cope with, we do not expect this to occur frequently within the range of ecological variation that the species has survived to date.

This dissociation of individual complexity and problem complexity is not the case in the social domain. Simply put, as long as they are competing with each other socially, the harder individuals work to act optimally in the social domain, the harder the problems become; one animal's Machiavellian skill is another's social problem (Humphrey 1976; Byrne and Whiten 1988; Whiten and Byrne 1988). This exemplifies the generality of the power of social complexity to beget complexity, with spiralling selection pressure producing 'arms races' (Dawkins and Krebs 1978). The most stark example of this is the case of 'mindreading', where individuals infer states of mind in others (e.g. Premack and Woodruff 1978; Krebs and Dawkins 1984; Astington et al. 1988; Whiten 1991). The ability of non-human primates to do this remains a topic of debate (Whiten 1993) but it cannot be doubted as being a crucial aspect of human cognition. If I, ape A, infer that you, ape B, know something (say about the location of a hidden food item), then it is useful for you to appreciate this fact (so you could lead me off in the wrong direction for example). In order to avoid being fooled I would need to know that you know that I know what you know. This recursion can obviously continue infinitely in principle; the relevant point here is that each level is necessary only because of one's opponent's ability to grasp the previous one. It is in this manner that the sophistication of the problem constantly exceeds the sophistication of the problem solvers.

The concepts and methods reviewed and developed in this chapter deliberately lack specificity. Formal definitions work best in formal systems. The scope of biology requires flexibility of method and this should be so in the quantification of complexity as elsewhere. That this quantification is of theoretical and experimental importance in the study of the natural world has been a central proposal of the chapter. The following chapter attempts to ground some of these

considerations in operational measures of social complexity.

Chapter 3: On Social Complexity

Introduction

The aim of this chapter is to closely examine the concept of social complexity, integrating the approach discussed in Chapter 2 with aspects of primate behaviour. This section reviews the contributions of previous authors to the field. The following section explores some of the interesting questions that emerge from a detailed examination of what the concept of social complexity entails. The final section outlines an operational framework for research.

Discussions of social complexity are most likely to be found in ethological works. For the behaviourist it is immediate contingencies that matter, not the flux of cause and effect beyond or within the organism. Ethology, however, is an inherently complex subject. From the outset it recognises four different ways of explaining of behaviour: causal, developmental, functional or evolutionary. There is a tacit assumption that systems in which the validity of a method of explanation varies are necessarily going to be complex.

Robert Hinde has done much to illustrate the scope of the problem involved in describing the social world of humans and other primates. He notes (1983a) that whilst laws of learning may remain basic to primate social behaviour, constructs taken from human social psychology such as attribution and exchange may be profitably applied to other primates. Thus, he argues, we may move away from the data language used for describing behaviour and employ new concepts not present in the data.

This line of reasoning underlay Hinde's (1976) description of sociality at the three, hierarchical levels of interaction, relationship and social structure. One of the chief values of this 'scaffolding' of the problem was that it stressed the dynamic aspects of social phenomena, an important aspect of social complexity. Hinde (1983a) notes that since each of the interactions that make up a relationship affects all subsequent ones, any observed stability will be dynamic in its nature. The same dynamism applies to social structure given that each relationship can affect each other.

Hinde's perspective is perhaps the most encompassing. Other authors have chosen to highlight particular phenomena as characteristic of social complexity in anthropoid primate groups. The principal ones are considered below.

The existence of long term relationships, especially between non-kin is often taken as an indicator of social complexity. These relationships are not formed

exclusively in the context of mating (Seyfarth 1978b; Altmann 1980; Smuts 1985). The most tangible aspects of these relationships are grooming and association but the relationships may also manifest themselves in terms of aid given in fights (e.g. Seyfarth 1978b; Smuts 1985). Since such aid is directed against a party outside the relationship it is clear that complexity exists not only for those within the relationship (e.g. in terms of judging cost/benefits) but also for those without.

This introduces a second phenomenon often cited in support of the case for primate social complexity: polyadic interactions. Early observation of these was made by De Vore (1962) and Altmann (1962) and, in more detail, Kummer (1967). Many authors have documented the phenomenon since and Harcourt (1987) estimates that up to 30 percent of contests in Old World primate groups involve the intervention of a third animal; outside of primates there is little documentation of alliances and what there is tends to be support of kin.

One obviously complex aspect of polyadic interactions is that additive increases in the number of protagonists result in geometric increases in the number of relationships between them (Menzel and Johnson 1976; Harcourt 1988). Beyond this, it has been argued that the alliances that typically make up polyadic interactions involve skills not apparent in dyadic contests. In particular, Harcourt (1988) notes that consideration of the relationship between the other two animals in a triadic interactions requires a comparison without reference to oneself. Note that if primates *do* actually compute such a thing this constitutes a crucial overcoming of egocentricity. Harcourt makes the further point that, once the possibility of third party intervention is introduced, decisions must be made about possible allies (both one's own and one's opponent's) not immediately involved in a contest. This must further increase cognitive load.

A third aspect of social complexity often cited is that of cooperation. Whilst the status of cooperation in primates with regard to formal models of reciprocal altruism remains undecided (e.g. Noe 1990) it seems clear that some form of exchange does occur (e.g. Packer 1977; Seyfarth 1977; Chapais and Schulman 1980; de Waal 1977, 1982; Seyfarth and Cheney 1984). Clearly, the monitoring of such exchange involves the evaluation of costs and benefits across an extended period. Maintaining such a 'credit rating' does not of itself appear terribly complex: cost/benefit analysis by animals tends to be assumed as a universal basis for their decision making. Therefore, one might suppose that the absence of reciprocal altruism in taxa other than primates results from purely demographic constraints such as too short a period of association. However, social exchange in primates is complicated by at least two factors. One is that there are observed asymmetries in payoffs (e.g. Bercovitch 1988; Noe 1986, 1988, 1990, 1992).

These may reflect an expectation on the part of cooperators that payoffs *should* be uneven: Noe (1991) refers to this as 'bargaining power'. Whilst certain features of individuals might mark them out for higher payoff (e.g. high rank), in part the dues individuals expect will rely on their own perception of their role in the alliance. A related point is that even if cheated of one's 'fair' share in an alliance, the benefits might still outweigh the costs of losing the alliance and perhaps having no alliance at all.

This raises the question of how far one individual can blatantly exploit the other: a form of natural psychology. I am not suggesting that a baboon, for example, consciously expresses the problem in these terms (though neither am I dismissing that possibility). However, an optimal strategy for employing reciprocal altruism would include these factors.

The second complication regarding social exchange is that different 'currencies' (Whiten and Byrne 1989) are in play. Thus, agonistic aid appears to be exchanged for grooming (Seyfarth and Cheney 1984). Since the relative costs of each currency differ according to the individual (e.g. aid may be cheap for high-rankers but not low-rankers, grooming may be equally costly to all), computing the 'correct' payoff becomes very difficult.

Clearly all three phenomena discussed above are closely intertwined. Social complexity occupies a kind of middle ground between demography and cognition. The disciplines of ecology and psychology have equipped us with the conceptual tools for describing these latter two features and we can use these to approach the less easily characterised phenomenon of social complexity. Whiten and Byrne (1989) make explicit the causal chain of demography, social complexity and social cognition in primates. Thus they note that large permanent groups lead to long term relationships requiring knowledge about such relationships. Similarly, the long residency primates hold in their group permits the possibility of cooperation setting up pressure for 'natural psychology' to monitor this.

The discussion to date has concentrated on particular features of primate groups that appear complex. In the next section I consider, more generally, the opportunity for special complexities that exist, *a priori*, in social systems.

Theoretical aspects

Relational and Interactional complexity

In Hinde's (1976) analysis of social structure, relationships and interactions are perceived as phenomena occurring at different social levels. Any attempt to

measure social complexity should separate complexity at these two levels before trying to integrate them.

This distinction can also be made at the cognitive level. A 'theory of mind' is a faculty that enables the prediction of behaviour by the inference of mental states in others; it presumably uses a set of rules about how knowledge is acquired and manipulated by others. A theory of mind is one tool in a more global 'theory of interactions' which may be possessed by socially sophisticated animals. Such a theory would contain rules dictating how interactions tend to proceed and how they can be altered. A 'theory of relationships' would be a corresponding set of rules about how relationships (which are merely constructs, like mental states) arise, decline and affect other relationships and the interactions of which they are comprised. Cheney and Seyfarth (1990) both review and provide their own evidence for this faculty in non-human primates. I leave the interpretation of 'rule' ambiguous at this point and refer the reader to Cheney and Seyfarth (1990) since they do an admirable job of discussing the epistemological aspects of non-human knowledge.

The point to be made here, is that interactional and relational complexity are partially dissociable aspects of social complexity. (By complexity I mean the number of factors required for successful prediction: the definition that emerged in Chapter 2.) In small groups, for example, there might be limited relational complexity in so far as the number of different, stable configurations of relationships might be limited. This need not bound interactional complexity, however. Indeed, in small groups each animal might be relatively well informed about every other; this would necessitate the most socially adept animals moving the complexity of interaction to a higher level in order that they may exercise their advantage.

System complexity, cognised complexity and confusion.

This section follows on from ideas developed in the discussion in Chapter 2. *System complexity*, I define as the total number of factors that are required to perfectly predict a system. This is obviously not something we can hope to quantify at all accurately, not least because the level of reduction at which one sets one's 'factors' is entirely up to the researcher and their chosen level of analysis. So this is a theoretical quantity, whose changes we can often only hope to deduce from a priori grounds.

Cognised complexity, I define as the number of factors actually processed by an individual: it is thus a quantity that varies according to the subject doing the

cognising. We can thus talk about social complexity for individuals, adults, juveniles, species, observers and so on, all within the context of the actual *system complexity* defined above.

Confusion is what remains: potentially predictable aspects of the environment that are not in fact predicted by the subject under study. Thus

$$\text{System complexity} = \text{Cognised complexity} + \text{Confusion}$$

The terms in the equation are dynamically related to each other. Any increase in cognised complexity will necessarily produce an increase in system complexity *because cognisance is a factor that itself contributes to the system*. This is best illustrated by the example given in Chapter 2 of the recursive, open-ended nature of mindreading. The general consequence, however, is that confusion can never be completely removed from the equation.

Factor interaction

Chapter 2 introduced the notion of broad and deep complexity, with depth of complexity being obtained by the interaction of factors, potentially generating deeper 'levels'. The nature of the way in which factors interact will determine the demands which are made of animals attempting to cognise them. The manner in which factors interact, if it is eccentric, can pose quite important limitations on the performance of simple computers (be they animal or machine).

The variable a animal wants to maximise is the general 'attractiveness' of some state of affairs. Different factors, taken singly, will generate different functions against this. The attractiveness of rank in a dominance hierarchy is probably fairly linear. The attractiveness of oestrous female baboons around the point of greatest swelling is a bit like a parabola, and so a more complex function. As more and more factors are added a multidimensional 'landscape' is generated. The topographical complexity of this landscape is analogous to the complexity of a baboon's decision-making demands.

A particularly complex form of factor interaction arises when an otherwise desirable factor becomes undesirable when combined with another. This can be dubbed 'valence reversal' and was touched upon in Chapter 2 in the context of neural nets and the exclusive OR problem. An example is the choice of coalition partners. Table 3.1 shows the six permutations of dominance possible in a triadic coalition. If my aim is to create a coalition of the strongest weight as regards pooled rank, I would normally want my ally to be higher ranked than myself. This is the case in permutation (1), the strongest coalition. However, the rank relations

Table 3.1 Permutations of rank in coalition formation. Order denotes rank, first being highest rank

| | | |
|----|------------------------|----------------------------|
| 1. | ally me opponent | strongest coalition |
| 2. | me ally opponent | strong coalition |
| 3. | me opponent ally | weaker coalition |
| 4. | opponent me ally | weakest coalition |
| 5. | ally opponent me | classic 'protected threat' |
| 6. | opponent ally me | danger of backfiring |

between all members of the triad must be borne in mind in assessing the valence of having a high ranked partner. Thus in permutation (6), an animal higher ranked than myself might be a liability, in that, faced with a third individual higher ranked than both of us it might end up re-directing aggression at me. Thus the valence of high ranked animals changes by virtue of this factor's interaction with the rest of the context.

Another example pertains to the class of resource a coalition is formed in pursuit of; a high ranked animal is well chosen for haranguing an enemy but may be a poor ally as regards winning an oestrous female from another male.

Consequently, factors must be simultaneously considered in order to perceive their interference or, alternatively, a schema (a set of rules for frequently occurring factor interactions, such as triadic configurations) must be followed as a means of alleviating processing demands. In most cases it is probably the latter, but such a schema must be learnt and is not available simply as a gross biological 'signal' in the environment. An individual that can perceive the interaction of factors may enjoy considerable advantages. Tactical skill is evinced when individuals are able to hold different factors simultaneously in mind, and deduce their interaction, *in the course of ongoing behaviour*. The vervet monkey that Cheney and Seyfarth (1990) reported alarm calling to deceive its peers who then wandered around unconcernedly while they fled, failed to appreciate how the latter behaviour affected the former (though it did not seem to affect the efficacy of the deception, which says something about vervet monkeys generally). In mindreading as a whole, many errors can be characterised by the failure to keep the factor of one's own knowledge separate from the factor of another's. It seems quite possible that a fair proportion of normal 3 year old children who fail false belief tasks (e.g. Wimmer and Perner 1983) are capable of metarepresentation but simply *forget* in the excitement of the experiment that the actor in the story does not have the same knowledge as themselves. As children (and possibly non-human primates) become more familiar with concepts such as "A has belief P" they become better able to simultaneously and independently process them, and so become more Machiavellian. Paradoxically, the key to understanding the interaction of factors in the world is first to be able to isolate them from one another, *then* to integrate them.

Below are three levels of complexity of factor interaction and the cognitive demands they make with regard to deducing factor interaction.

1. Additive. No interaction of factors, each factor can be processed once and a tally of optimality kept. Example: estimating quality of food patch by number of food items.

2. Multiplicative, no valence reversal. Factors may augment one another

but the valence of a factor is fixed. A single processing of each factor is inaccurate but may be a viable heuristic and record the improvement or deterioration of a situation as more factors are processed. Example: estimating quality of ranging route which may incorporate both a salty food and a drinking site.

3. Multiplicative, valence reversal. Factors which may reverse the valence of others *must* be integrated to avoid big mistakes. Example: coalitions as discussed above.

In the mammalian brain it is the neocortex that shows the greatest interconnectedness and re-entry and so ought to have the greatest ability to deal with factor interaction. Environmental correlates of high neocortex ratio such as group size in Dunbar's (1992) regression are thus implicated as being high in factor interaction.

We might conjecture that some equivalence would be shown between the ratios of **neocortex/rest of brain** and **factor interaction/number of factors** (which has previously been characterised as deep complexity/broad complexity). Dunbar's (1992) regression of group size and neocortex ratio represents a specific example of the proportionality of the two ratios above. If group members are considered as 'factors' and the relationships between them, 'factor interactions', then the second ratio will tend to grow as group size increases and promotes increases in the the first ratio.

Dimensions of Social Complexity

Table 3.2 is intended as a pragmatic outline of what aspects of social complexity are empirically accessible to ethologists and the text that follows here is essentially notes on the table.

Rows in the table are dimensions of social complexity. Columns are the social level at which the complexity is generated and are based on the scheme proposed by Hinde (1976). I have chosen the term 'role' rather than social structure since this seems to best capture the formal equivalence with which the levels arise out of each other: a relationship is a pattern of interactions and a role is a pattern of relationships. A relationship exists between one individual and another and a role exists between one individual and a number of others, perhaps the whole group. Roles and networks are not the same thing: networks are merely sums of relationships, roles are patterns within networks. Examples of roles are alpha male, scapegoat, social climber and kingmaker.

Cells in the table are proposed as the (measurable) manifestation of each

Table 3.2 Dimensions of social complexity

| | INTERACTION | RELATIONSHIP | ROLE |
|-------------------------|--|---|---|
| Frequency | | | |
| dyadic | frequency of interactions | number of relationships held | n/a |
| polyadic | frequency of polyadic interaction | number of polyadic relationships | n/a |
| Diversity | | | |
| dyadic | number of different acts faced | number of different relationships held | number of different roles in group |
| polyadic | number of different polyadic acts faced | number of different polyadic relationships held | ? |
| Rate of change | speed with which acts exchanged in an interaction | stability of an individual's relationships | stability of an individual's role |
| Demographic turnover | n/a | n/a | n/a |
| Variability of response | variability of respondent's act | n/a | n/a |
| Unpredictability | number of factors required to predict each event in an interaction at a given level of success | number of factors required to predict formation of a relationship at a given level of success | number of factors required to predict formation of a role at a given level of success |

dimension of complexity at each social level. Some cells are empty; this illustrates how the dimensions change as new levels emerge. The characterisation of complexity as existing at various levels is particularly important for a thesis such as this which is making comparisons within a single species. I am investigating the possibility that olive baboons experience more complexity as their troop size grows. At the cognitive level, adult baboons may differ very little in their complexity. This provides us with a null hypothesis in comparing across group size: same species, same complexity. Quite possibly, this could hold at the level of interactions: troop size should not affect the behavioural repertoire of the animals although it might affect frequencies of acts. However, even in the unlikely event that each individual acts in the same way, oblivious to the size of its troop, relationships may be apt to become configured differently. This would be a consequence of demographic factors such as the number of females in oestrous at any one time and social factors such as the number of potential allies available.

A few introductory notes should be made concerning the dimensions of complexity chosen, i.e. the rows of the table: where data pertaining to the dimensions is presented in following chapters, that dimension is discussed in greater detail.

Frequency and diversity comprise the two most basic measures of complexity: thus, not only the rate at which individuals must interact is considered, but also the range of actions that they must select from. Similarly, in the context of relationships, individuals face complexity not only in the number of relationships that they must monitor, but also in their range, say, from alliance through affiliation and appeasement to antagonism.

The special complexities of polyadic interactions have already been addressed. Table 3.2 also recognises the possibility of polyadic relationships. These raise complexity in so far as the relationship an individual holds with two others may be affected by the relationship those individuals hold with one another. Heider (1958) introduced the idea of 'balance theory': if A is positive towards B but negative towards C, then balance is only possible if B is also negative towards C. (The general case is that the triad of relationships is balanced only if the product of the three polarities is positive). In this context, then, a polyadic relationship is one in which relationships between more than two animals mutually, overtly affect each other. The qualifying 'overtly' recognises that each relationship potentially affects all others concurrent with it, just as any interaction is potentially influenced by all other interactions occurring at that time.

Stability, or rate of change, introduces a temporal aspect into what has so far been more of a 'freeze-frame' characterisation of social complexity. Formally

speaking, systems that change clearly require more information to describe them since, unless the changes are themselves predictable (e.g. cyclic), the descriptions can only 'compress' information in the static periods. From the point of view of the cognising animal operating under real-world constraints, rate of change clearly poses complexity.

Demographic turnover is included in the table despite the fact that itself it is not a social quantity. This is to stress that it is likely to have a pervasive effect on all the other aspects of social complexity, particularly measures of stability.

The last two dimensions, variability and unpredictability, essentially represent equivalent ideas. The importance of unpredictability and its relation to formal definitions of complexity was raised in Chapter 2. Variability of response is a more superficial and therefore easily implemented form of this in which variance itself is deemed complex rather than the extent of information required to explain the variance.

Chapter 4: Methods

General aspects of ecology

The Soitataishe and Uaso Ngiro Baboon Projects are directed respectively by Dr. Andrew Whiten at the University of St. Andrews and Professor Shirley Strum at the University of California at San Diego. They are based at Chololo Ranch, owned by the Jessel family, which is roughly 40 kilometres north of Nanyuki, Kenya.

The habitat is savannah type with undulating hills and a number of small rocky hills or kopjes. The vegetation is chiefly characterised by various species of acacia tree and, in wetter periods of the year, a layer of herbs and grasses. A greater density and variety of plant life is typically found in the (typically dry) watercourses. A more detailed description of the habitat can be found in Strum (1987), Barton (1989) and Marsh (1992).

Other animals

The baboons ranged on Chololo and adjacent ranches but also on the adjacent Ndorobo reserve. On the ranches, the only humans are occasional cattle herders with the livestock of the ranch owner. A wide variety of animals are to be found, including zebra, buffalo and many species of antelope but also large cats including cheetahs, leopards and lions. Migratory elephants are occasional visitors. The large cats were possible sources of predation, whilst young antelopes, dik-diks and hares were occasionally taken as prey by the baboons.

On the Ndorobo reserve, wild animals were much rarer and the baboons' movements were more often influenced by the local Ndorobo tribesmen and their herds of goats. There were various cases of Ndorobo claiming that baboons had killed their livestock, however, an agreement between the baboon projects and these people ostensibly ensured that they would drive baboons away from their herds in preference to killing them.

The study troops frequently shared sleeping sites with other, non-habituated baboon troops.

Climate

Conditions in the area have been described as marginal (Strum 1987) and the habitat type as 'dry savannah' following Delany and Happold's (1979) rainfall-based classification. The climate is typically characterised by two rainy seasons and

monthly precipitation for the study year is shown in Figure 4.1 (data provided by Strum). The temperature also varies seasonally with highest temperatures reached in the two dry seasons (Barton 1989).

As a broad estimate of the amount of food available, pin frame samples were taken of the herb layer biomass. These data are presented in Figure 4.2 (data provided by Strum). No animals died or deteriorated to very poor condition during the study period. The most noticeable effects of food shortage were an increase in the daily range length (particularly in STT) and a drop in the frequency with which females came into oestrous.

For the baboons, obtaining water was always possible since the ranches contained a number of man-made dams for the use of cattle.

The Baboons

Three troops of baboons are studied at Chololo: STT (short for Soitataishe: Masai for 'white rocks', one of their sleeping sites), The Pumphouse Gang and Malaika ('angel' in Swahili). STT are indigenous to the area but the other two troops were translocated from the Gilgil Baboon Project in The Rift valley, by Strum in 1984 (see Strum 1987; Eley et al. 1989).

Malaika and the Pumphouse Gang have been studied by Strum for nearly 20 years and so the genealogies and kin of all natal animals are well known. Robert Barton habituated STT in 1986 and although they have been studied continually since then, the kinship of adult individuals can only be inferred in some cases.

The habituation of all study troops is superb allowing observers to record fine details of social interaction.

Demography of study troops

Baboons were placed in age-sex classes according to Gilgil/UNBP protocols which are described in Nicolson (1982) and Smuts (1985). Table 4.1 shows the demographic breakdown for STT and MLK at the beginning and end of the study period.

Sampling Methods

Three methods of sampling were used; focal sampling of a small pool of mature animals (see note at end of chapter for a definition of this class), scan

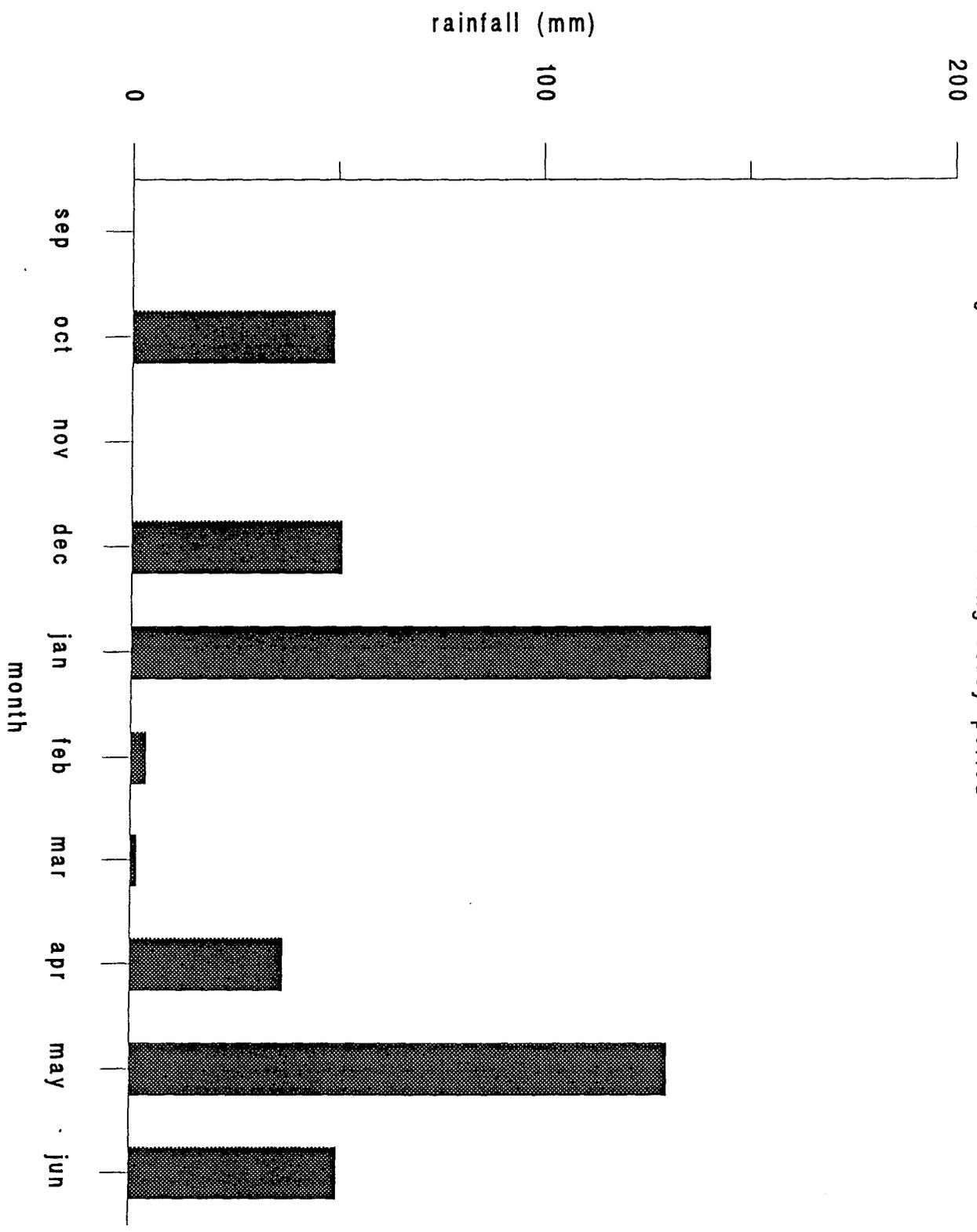


Figure 4.1 Rainfall during study period

Figure 4.2 Mean herblayer biomass totals (gms / sq m). Months split into two halves. Half-months without a column were not sampled.

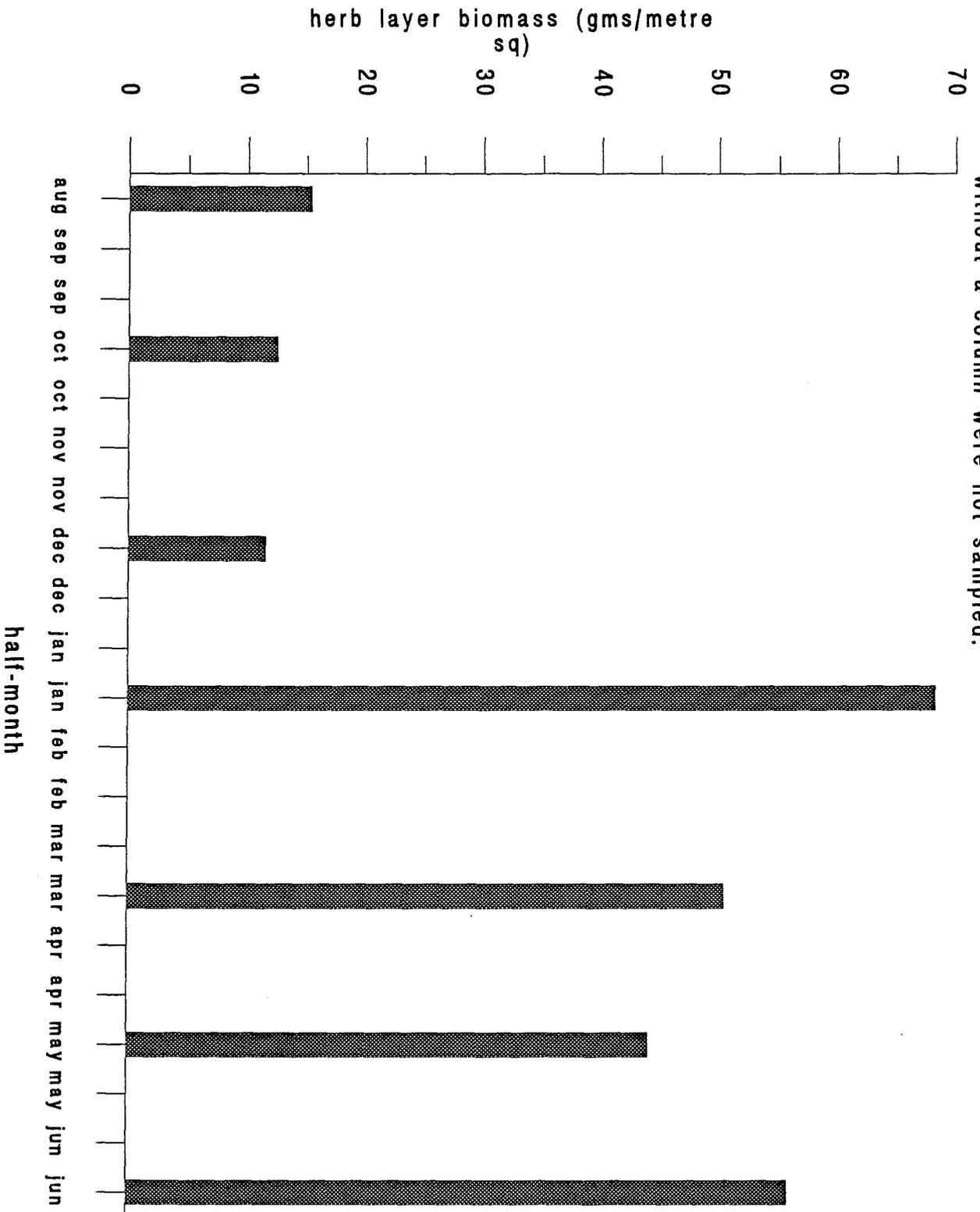


Table 4.1 Breakdown of age-sex classes in study troops. Class criteria taken from Nicolson (1982)

| | MLK | | STT | |
|------------------|---------|---------|---------|---------|
| | Sep '92 | Jun '93 | Sep '92 | Jun '93 |
| Adult female | 10 | 10 | 21 | 18 |
| Adult male | 4 | 6 | 5 | 6 |
| Sub-adult female | 1 | 2 | 3 | 4 |
| Sub-adult male | 2 | 3 | 12 | 12 |
| Juvenile female | 7 | 10 | 15 | 15 |
| Juvenile male | 3 | 2 | 15 | 14 |
| Infant female | 5 | 3 | 7 | 6 |
| Infant male | 2 | 1 | 6 | 4 |

sampling of entire troops and *ad libitum* records taken during the above samples. Broad details of what these types of sampling method entail can be found in Altmann (1974). All data were recorded on a 'palm-top' computer using MBUNI, a program for focal data collection (see Marsh 1992). Sampling began in September 1992 and ended in June 1993.

Scan sampling

The rules for scan sampling were as follows.

1. In each scan an attempt to scan all animals in the troop was made.
2. The scan was discontinued either when all animals had been sampled or when several minutes had elapsed without the observer finding unsampled animals.
3. When the animals were located before they left the sleeping site, they were always scanned. Thereafter they were scanned at intervals of no less than one and a half hours. The decision to scan was made on the basis of practicability in STT which essentially required them to be in reasonably open terrain and not moving fast. The decision to scan MLK was made similarly, though in this case it was for reasons of comparability to STT data.
4. The activity in which the majority of the group was engaged was recorded from November onwards. Possible activities were; (i) moving/feeding, (ii) feeding and (iii) resting/grooming.
5. Each animal was the subject of a record in a scan sample once only, in which animals proximal to it and animals it was grooming or being groomed by were recorded. However, an animal once scanned could appear in the sample for another animal as a proximal animal or a groomed animal.
6. Scan samples were instantaneous. The observer, directing his attention to an individual recorded;
 - (i) the identity of any individual the sampled animal was grooming or being groomed by.
 - (ii) the identities of animals in three proximity grades; contact, arms reach and within five metres. When no animals were within these grades the identity of the nearest animal was recorded or nearest animals (up to a maximum of three) when no one animal was clearly nearest.

7. On the sleeping site in the mornings, it was impracticable to record all animals within five metres of each other. For scans on the sleeping site this proximity grade was reduced to one and a half metres.

Notes on scan sampling rules

A possible source of bias is that scans were not controlled across the two troops for any variable other than absence of dense vegetation. However, an analysis of troop activity during scans (see Table 4.2) using the X^2 statistic reveals that the factors of troop and activity during scans are independent ($X^2=3.84$, $N=351$, $df=2$, $p>0.10$). This implies that troop activity is naturally controlled to an extent in the data set (though the X^2 statistic is not as small as might be hoped and there is always danger in using the retention of a null hypothesis as a 'result'). It is difficult to know what the best way to proceed would be in any case however, since troop activity probably did differ consistently, activity samples from focal data (see Chapter 6) suggesting that STT spent more time moving than MLK. Thus, controlling scans for group activity might well have injected artificiality: such activity differences might be caused by group size differences and in turn influence social complexity.

Table 4.3 shows the number of scans and the number of minutes of scan sampling for each troop for each month. Because the sampling was instantaneous and each animal was the subject of a sample only once in a scan, it is the number of scans rather than their total duration that is the more relevant measure.

Focal sampling

Adult females and adult and large sub-adult males were selected from each troop to form a pool of focal animals. The decision to concentrate on only these age-sex classes was based on various factors. Such individuals are most immediately involved in the process of determining their reproductive success through the birth and care of their offspring. Hence there may be a case for saying that their behaviour is most clearly related to discernible strategies for reproductive fitness. In contrast, infants and juveniles may not have had time to learn fully coherent social strategies. Furthermore, in the non-reproductive phase of their life they may in some sense be 'programmed' to experiment with a diversity of behaviour, some of which may not be adaptive *per se*. This reasoning is analagous to the notion of play as experimentation with motor patterns; juveniles might need to learn the scope of social interaction and relationships before selecting appropriate, moderate behaviour (Fagen 1976). Other reasons for the choice were

Table 4.2 Frequency of scan samples made during different troop activities. Data available on troop activity from Nov '92 only.

| GROUP | | ACT | | | total |
|-------|-------|----------------|---------|------------------|-------|
| | | moving/feeding | feeding | resting/grooming | |
| | MLK | 56 | 32 | 61 | 149 |
| | STT | 77 | 28 | 97 | 202 |
| | TOTAL | 133 | 60 | 158 | 351 |

Table 4.3 Scan sampling size

| | SCANS (FREQUENCY) | | SCANS (MINUTES) | |
|-------------|-------------------|-----|-----------------|------|
| | MLK | STT | MLK | STT |
| SEP | 15 | 12 | 513 | 497 |
| OCT | 11 | 11 | 264 | 422 |
| NOV | 17 | 24 | 273 | 749 |
| DEC | 13 | 18 | 227 | 593 |
| JAN | 29 | 33 | 302 | 995 |
| FEB | 19 | 16 | 239 | 507 |
| MAR | 13 | 18 | 161 | 517 |
| MAY | 28 | 19 | 301 | 483 |
| APR | 24 | 37 | 246 | 965 |
| JUN | 15 | 19 | 199 | 438 |
| TOT | 181 | 207 | 2725 | 6166 |
| GRAND TOTAL | | 388 | | 8891 |

the supposition that the more mature age-sex classes would exhibit social complexity at its greatest and also the recognition that these individuals would be less susceptible to confounding maturational processes.

At the outset, an attempt was made to have individuals in the two troops matched for various characteristics. However, for STT, factors such as a female's rank often only became apparent towards the end of the study so this match was only partially successful. The focal animals, along with characteristics relevant to their matching, are listed in Table 4.4.

The rules for focal sampling were as follows;

1. Focal samples were 30 minutes long unless interrupted (e.g. by focal animal entering thick or dangerous bush). Interrupted focals of less than 15 minutes were discarded.
2. Focal samples for each animal were balanced across time blocks on a weekly basis. The day was divided into six time blocks; 6.30-9.00, 9.00-11.00, 11.00-13.00, 13.00-15.00, 15.00-17.00 and 17.00-19.00.
3. A new focal sample could not be made of an animal until one and a half hours had elapsed since the previous sample of that animal finished.
4. The size and dispersal of STT made selection of focal animals by a predetermined order impractical. The following compromise was reached. On any one day, a pool of three to four animals that had been undersampled in that time zone was identified. The first of these animals found by the observer that was not an immediate neighbour of the previous focal animal was chosen. The disqualification of neighbours guarded against a spurious apparent association of focal animals; however, it threatened to exert a small bias in the data towards showing focal animals *not* sharing proximity. To compensate for this, a neighbouring animal was chosen when it was the sole most undersampled animal in that time zone on that day.
5. Focal samples incorporated both instantaneous and continuous recording. At the commencement of a focal sample, and at two minute intervals thereafter, the following information was recorded;
 - (i) animals grooming or groomed by the focal animal
 - (ii) animals within those proximity grades described for scan samples.
 - (iii) the activity of the focal animal (see Table 4.5)

Table 4.4 Characteristics of focal animals

| <i>Females</i> | | | | |
|----------------|---------------|-------------------|---------------|------------------------|
| | Rank* | Age | Began cycling | No. offspring in troop |
| MLK | | | | |
| Desiree | 1/11 | 19 | 1980 | 3 |
| Michelle | 4/11 | 11 | 1985 | 2 |
| Davina | 7/11 | 8 | 1989 | 1 |
| Rima | 10/11 | 10 | 1987 | 2 |
| STT | | | | |
| Maxine | 2/23 | not known | before 1986 | 3 |
| Withania | 3/23 | not known | 1986 | 2 |
| Karen | 4/23 | not known | 1987 | 1 |
| Amanda | 11/23 | not known | 1988 | 1 |
| Alison | 19/23 | not known | 1988 | 1 |
| Opuntia | 22/23 | not known | before 1986 | 2 |
| | | | | |
| <i>Males</i> | | | | |
| | Age Class | "Promotions" | Immigration | |
| MLK | | | | |
| Ndovu | Old adult | adult before 1986 | 1986 | |
| Herakles | Young adult | adult 1990 | 1987 | |
| Robert | Old sub-adult | sub-adult 1988 | 1987 | |
| Sharman | Mid sub-adult | sub-adult 1990 | 1987 | |
| STT | | | | |
| Stilton | Mid adult | adult 1987 | before 1986 | |
| Denine | Young adult | adult before 1992 | 1992 | |
| Deejay | Old sub-adult | adult 1992 | 1989 | |
| Gregar | Old sub-adult | adult 1992 | 1991 | |
| Grumpy | Mid sub-adult | sub-adult 1990 | 1989 | |

* See chapter 5 for criteria used to determine dominance

Table 4.5 Information recorded in 2 minute point samples for focal animals

| | |
|--|--|
| PROXIMITY (all animals within each grade recorded) | contact arms reach five metres ¹ nearest ² |
| ACTIVITY (one of the following selected) | |
| feeding/moving behaviours | moving feeding whilst moving feeding on ground feeding in tree feeding in bush |
| resting/grooming behaviours | grooming being groomed grooming self nothing resting (i.e eyes closed) |

¹ This grade reduced to 1.5 metres on the sleeping site

² This grade only used when no animals in the other grades

6. Continuous recording was made of all social behaviours shown by the focal animal. These behaviours are shown in the ethogram in Table 4.6. The MBUNI program automatically recorded the time at which an entry was made. However, since entries of some behaviour sequences took up to 5 seconds to type in, intervals between acts that were shorter than this period cannot be reliably ascertained in the data.

Table 4.7 shows the number of hours of focal sampling per animal per month. Sampling of Gregar (GM), Karen (KN) and Opuntia (OP) ceased when these animals disappeared from STT. Sampling of Herakles ceased when he had transferred to STT. A reasonable understanding of the female dominance hierarchy in STT had emerged by December. Sampling of Alison was begun in order to address the problem of the lack of a low ranking female in the STT focal pool and sampling of Karen was greatly reduced as too many high ranking females were already being sampled. Sampling of Grumpy began when it was appreciated that a previous member of the STT focal pool was probably natal.

Figures 4.3 and 4.4 show the amount of focal sampling on a monthly and bi-monthly basis respectively.

Logistics largely determined what periods of the day were spent in the field. The possibility that this varied across bimonthly periods was checked as this would constitute a possible confound. Figure 4.5 shows the amount of sampling in each time block across bimonthly periods. A X^2 test confirms that that the period of the day sampled is independent of the bimonthly period ($X^2=26.7$, $N=1730$ $df=20$, $p=0.143$)

Ad libitum records

With the exception of a few, frequently occurring behaviours such as grunts and passive approaches or departures, the ethogram for focal samples was used in *ad libitum* recording of behaviour of non-focal animals. These records were secondary in priority to sampling the current focal animal. As an *ad libitum* behaviour, grooming was recorded in a one-zero fashion; an interval of half an hour was required to elapse before a new grooming incident could be registered for the same groomer-groomee dyad.

Biases likely to exist in *ad libitum* data are the over-representation of animals that associated with focals and an over-representation of events accompanied by vocalisations (since these draw the attention of the observer). Also, between the two troops, the *ad libitum* coverage of MLK was much better in so far as a greater

Table 4.6 Ethogram. Frequencies of each behaviour are shown in right hand column. Behaviours followed by bracketed values were assessed for intensity on the number of points there indicated (when these are italicised the intensity constitutes a *fear* grading). Footnotes for behaviours which are not self-explanatory shown overleaf.

| OBSERVATION | | AGONISM | | AFFILIATION/GREETING | |
|---------------------------------|------|--|-----------------|--|------|
| avoid by quickened movement | 1 | bark (1-2) | 93 | attempt mount ¹⁴ | 89 |
| avert gaze | 0 | bite (1-2) | 77 | come hither | 75 |
| look at (1-2) | 273 | buffer using ⁶ | 1 | embrace ¹⁵ | 166 |
| scan quadrepedally | 10 | chase (1-3) | 256 | grunt | 3381 |
| scan bipedally | 15 | counter-chase ⁷ | 1 | excited grunt | 71 |
| search | 1 | circle | 3 | hip grasp ¹⁶ | 185 |
| vigilant of | 18 | charge | 0 | lipsmack (1-2) | 889 |
| | | fight | 32 | mount | 400 |
| AVOIDANCE | | grapple | 2 | mount with backbite | 48 |
| leave 5m actively | 751 | groom in agonistic context ⁸ | 35 | non-aggressive bite ¹⁷ | 4 |
| leave 5m passively ¹ | 1826 | group mob ⁹ | 4 | present (1-3) | 930 |
| leave 1m actively | 0 | lunge | 60 | stand rigid | 224 |
| leave 1m passively | 10 | molar grind | 35 | solicit versus ¹⁸ | 47 |
| herd versus ² | 44 | non-specific aid in polyad ¹⁰ | 13 | side present (1-2) | 25 |
| hide behind | 6 | threaten (1-2) | 213 | reach to body | 52 |
| hide from | 1 | pin down | 0 | reach to genitals | 8 |
| run away from | 229 | protected threat ¹¹ | 2 ¹¹ | touch body | 426 |
| run to follow | 59 | push | 25 | touch genitals | 30 |
| run towards | 145 | mount | 400 | touch ano-genital region | 120 |
| run proximal to | 29 | victorious over | 10 | | |
| turn back on | 1 | wounded | 0 | COPULATION | |
| | | yawn | 28 | copulate with ejaculate | 71 |
| ASSOCIATION | | | | copulate without ejaculate | 53 |
| approach 5m passively | 1839 | SUPLANT | | copulate ejaculate unknown | 54 |
| approach 5m actively | 1087 | feeding supplant | 165 | copulation grunt (1-3) | 106 |
| approach 1m actively | 139 | grooming supplant ¹² | 7 | copulation grunt : dishonest ¹⁹ | 2 |
| approach 1m passively | 295 | proximity supplant ¹³ | 50 | copulation harass | 30 |
| follow | 250 | reverse supplant | 22 | | |
| move towards | 57 | | | FEAR | |
| pass close by | 603 | SNIFF | | be startled | 85 |
| run to follow | 59 | sniff ano-genital | 201 | scream (1-3) | 303 |
| run proximal to | 29 | sniff body | 15 | fear-face/vocalistaion (1-2) ²⁰ | 286 |
| | | sniff mouth | 56 | | |
| GROOMING | | | | MISC | |
| attempt groom ³ | 1 | INFANT INTERACTION | | backbite | 48 |
| groom | 1105 | infant climbs on other | 7 | interpose | 7 |
| groom briefly ⁴ | 41 | carry infant | 4 | masturbate | 13 |
| groom present ⁵ | 255 | hold infant to chest | 14 | play | 0 |
| groom self | 8 | steal infant from mother | 1 | predate | 0 |
| stop grooming | 453 | | | take prey from | 2 |

- ¹ A passive leave is one in which something other than the animal left is causing the movement. Same distinction applies to approaches.
- ² Herding is typically done of oestrous females by their consorts: the male butts the female away from other males.
- ³ A grooming attempt was made but the other animal moved off.
- ⁴ Grooming for less than 5 seconds. Typically done by the dominant animal in a dyad prior to the subordinate beginning resuming a more protracted bout.
- ⁵ Animal presents a part of its body for grooming by another.
- ⁶ A mature male holds an infant between itself and an aggressor.
- ⁷ In this context a counter-chase is performed by the chased, losing animal in an aggressive encounter.
- ⁸ Grooming performed by a threatened animal apparently either for the purposes of protection or as a displacement activity.
- ⁹ Typically follows a mature male's maltreatment or suspected maltreatment of an infant. Many individuals (especially mature females) chase the male, screaming.
- ¹⁰ Non specific aid includes threatening vocalisations, movements and solicitation of further parties.
- ¹¹ An individual (often a juvenile) threatens another whilst in the vicinity of (and often grooming) a powerful ally.
- ¹² A proximity supplant is one in which an individual has to leave the proximity of another with whom it was not interacting because of the approach of a third.
- ¹³ A reverse feeding supplant is one in which an individual has to wait to get access to a resource.
- ¹⁴ An animal attempts to mount another who moves away.
- ¹⁵ One or two arms encircle another's body.
- ¹⁶ Usually a response to a present: other's hips are grasped with both hands.
- ¹⁷ The jaws are slowly closed on another's body.
- ¹⁸ Rapid head-movements made from solicited individual to adversary.
- ¹⁹ Dishonest copulation grunts are those where a female is neither copulating nor defecating.
- ²⁰ Fear vocalisations are a repeated 'ah' sound accompanied by shuddering and jactitation of body.

Table 4.7 Minutes of focal sampling

| | SEP | OCT | NOV | DEC | JAN | FEB | MA R | APR | MAY | JUN | TOT | |
|-------------|------|------|------|------|------|------|---------|------|------|------|-------|-------|
| MLK | | | | | | | | | | | | |
| HK | 280 | 175 | 296 | 146 | 356 | 263 | 240 | 210 | 421 | | 2387 | |
| ND | 237 | 205 | 300 | 237 | 360 | 232 | 240 | 383 | 636 | 236 | 3066 | |
| RT | 210 | 217 | 330 | 176 | 330 | 240 | 212 | 450 | 537 | 258 | 2960 | |
| SQ | 258 | 237 | 235 | 240 | 353 | 256 | 146 | 600 | 523 | 285 | 3133 | |
| DE | 198 | 210 | 321 | 219 | 356 | 164 | 237 | 558 | 556 | 264 | 3083 | |
| DQ | 192 | 240 | 346 | 220 | 360 | 258 | 180 | 504 | 478 | 194 | 2972 | |
| MC | 222 | 150 | 291 | 120 | 446 | 267 | 188 | 497 | 506 | 210 | 2897 | |
| RM | 169 | 240 | 271 | 230 | 330 | 265 | 243 | 534 | 480 | 320 | 3082 | |
| TOT | 1766 | 1674 | 2390 | 1588 | 2891 | 1945 | 1686 | 3736 | 4137 | 1767 | | 23580 |
| STT | | | | | | | | | | | | |
| DE | 138 | 320 | 258 | 196 | 370 | 150 | 270 | 532 | 521 | 236 | 2991 | |
| DJ | 170 | 300 | 375 | 198 | 290 | 180 | 230 | 416 | 605 | 211 | 2975 | |
| GG | | 240 | 368 | 230 | 409 | 120 | 327 | 520 | 600 | 291 | 3105 | |
| GM | 187 | 204 | 316 | 176 | 384 | 26 | | | | | 1293 | |
| SI | 136 | 322 | 266 | 258 | 281 | 177 | 236 | 416 | 567 | 333 | 2992 | |
| AL | | | | 120 | 296 | 220 | 390 | 480 | 665 | 210 | 2381 | |
| AM | 180 | 234 | 290 | 243 | 330 | 205 | 210 | 413 | 540 | 325 | 2970 | |
| KN | 150 | 286 | 307 | 60 | 90 | 60 | 30 | | | | 983 | |
| MA | 176 | 270 | 259 | 270 | 326 | 210 | 376 | 433 | 550 | 201 | 3071 | |
| OP | 180 | 207 | 357 | 201 | 412 | 141 | 42 | | | | 1540 | |
| WT | 180 | 300 | 300 | 207 | 394 | 183 | 174 | 366 | 662 | 304 | 3070 | |
| TOT | 1497 | 2683 | 3096 | 2159 | 3582 | 1672 | 2285 | 3576 | 4710 | 2111 | | 27371 |
| GRAND TOTAL | | | | | | | | | | | 50951 | |

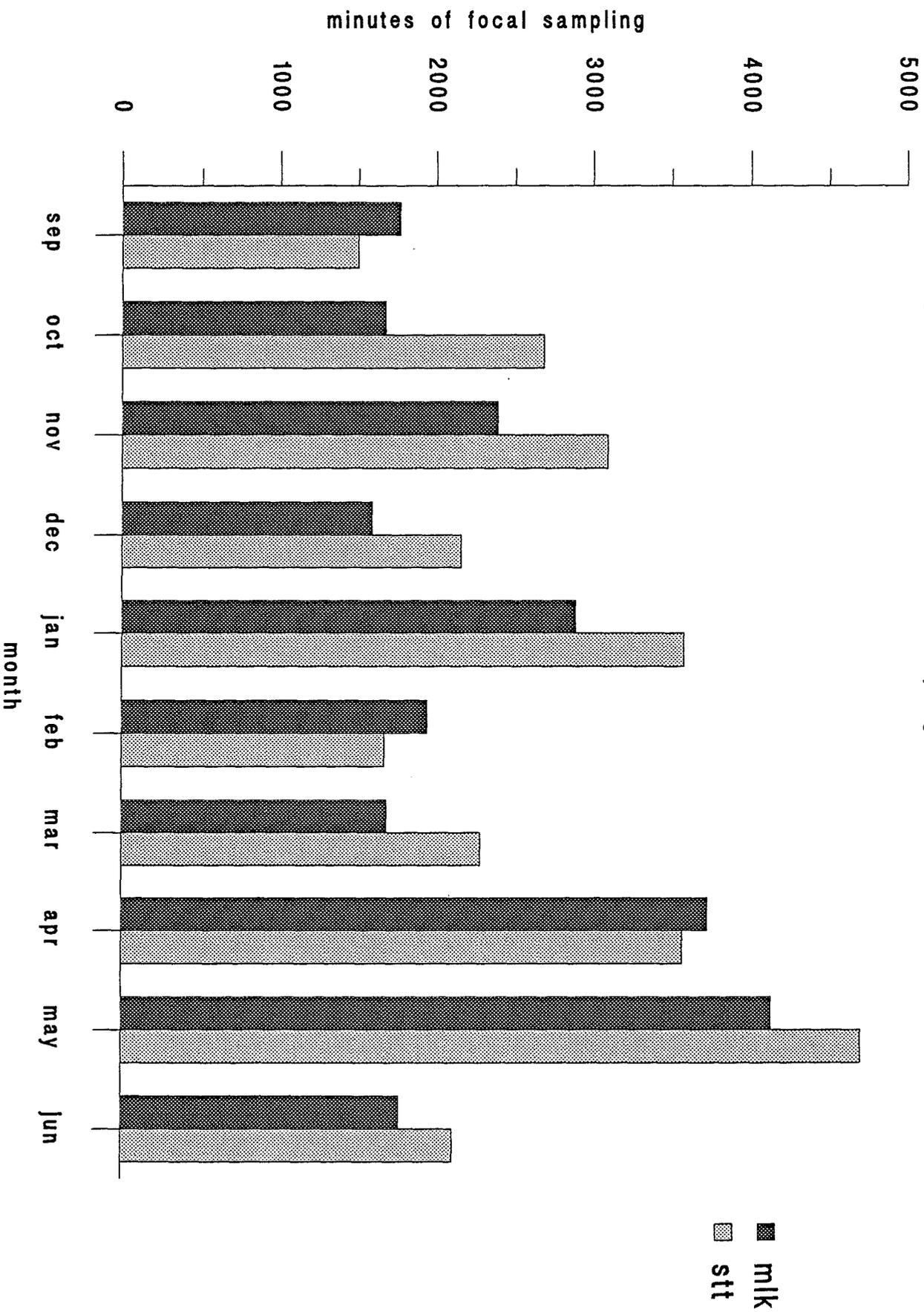


Figure 4.3 Minutes of focal sampling in each month

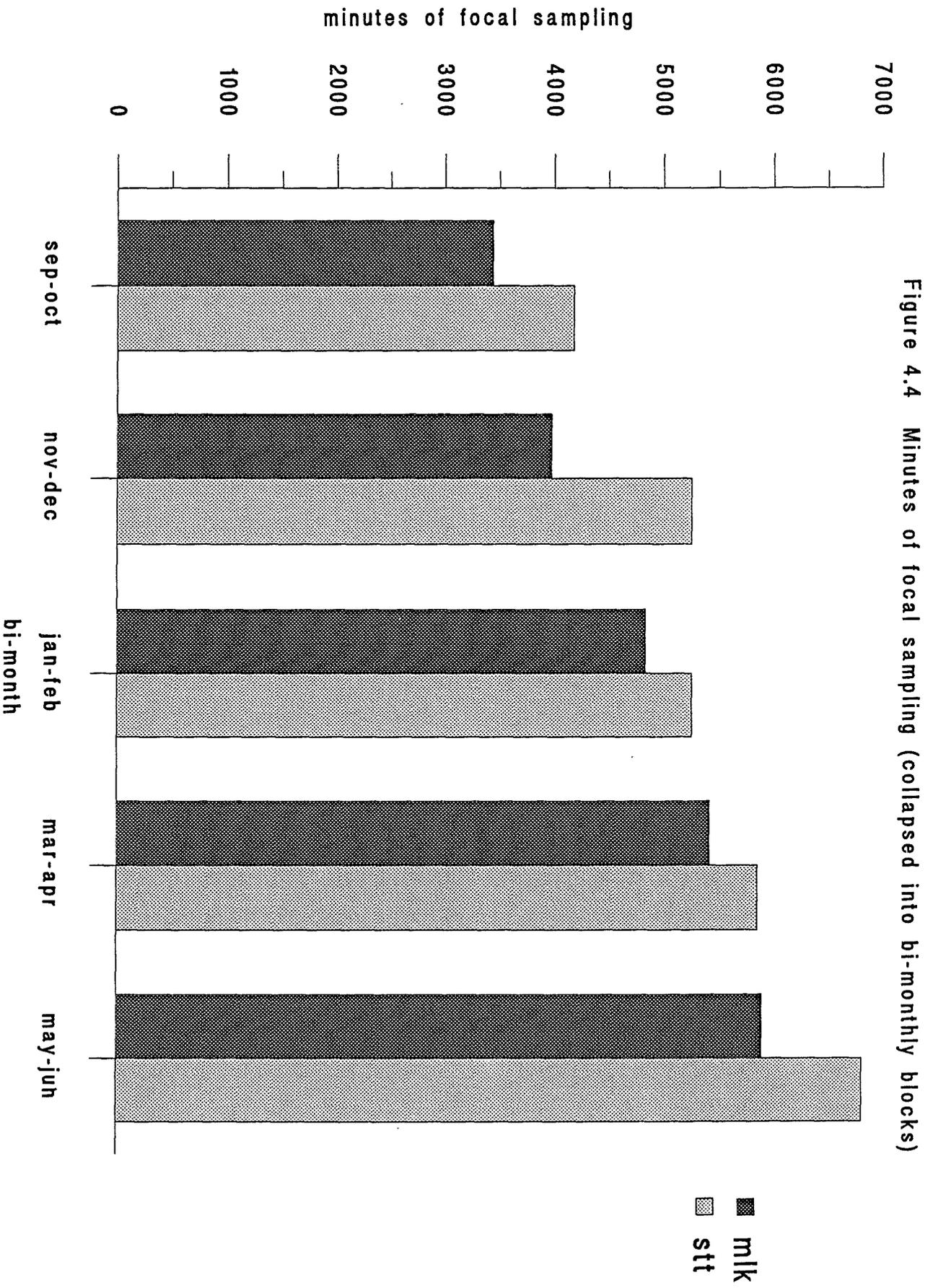
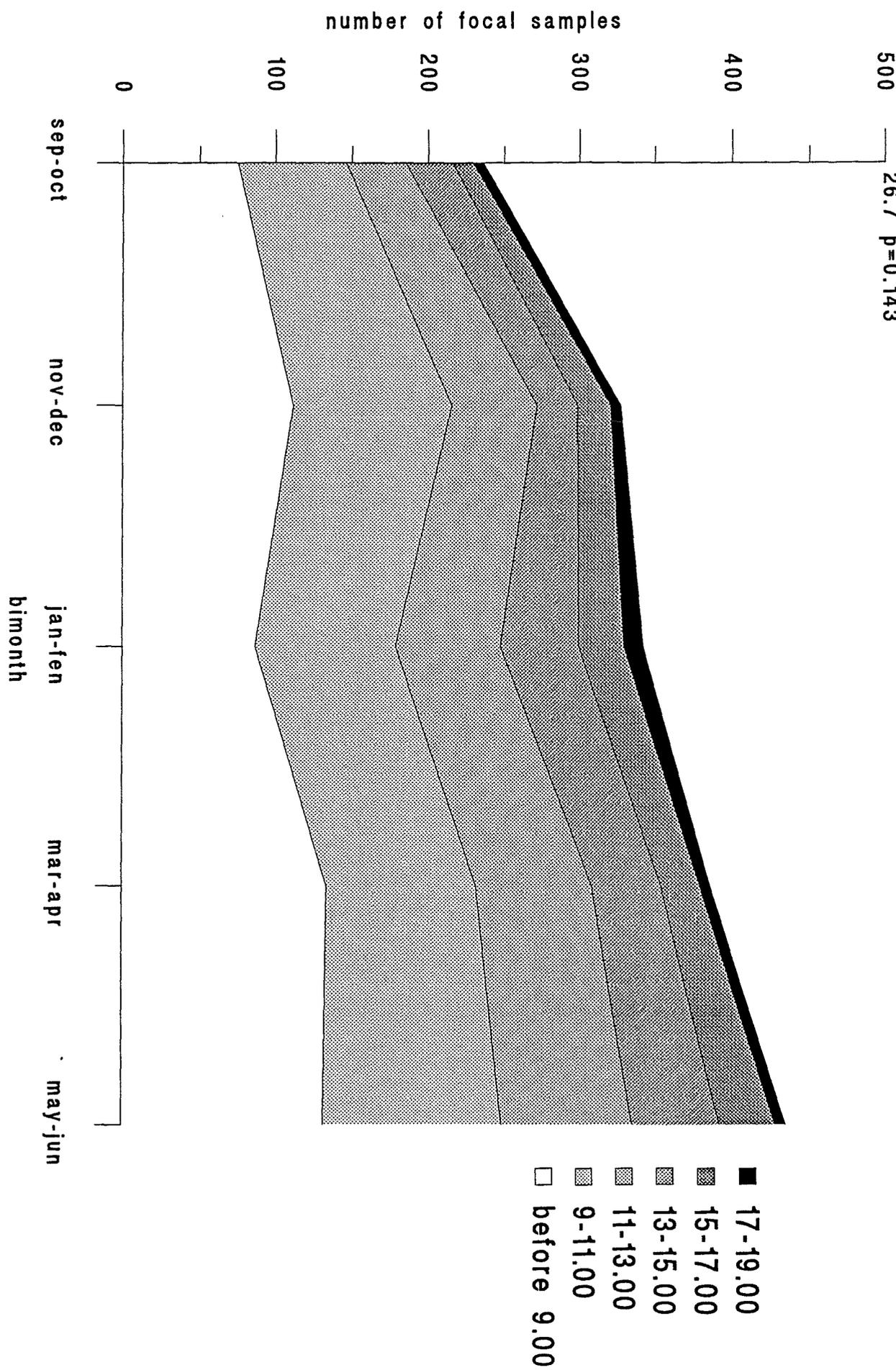


Figure 4.4 Minutes of focal sampling (collapsed into bi-monthly blocks)

Figure 4.5 Times of day sampled across bi-monthly blocks. (Chi sq of time zone vs bi-month = 26.7 p=0.143)



proportion of individuals were visible at any one time in this smaller troop.

Long term records

Both UNBP and STT projects keep long term records of many aspects of baboon ecology. These include the characteristics of reproductive cycling in females, instances of predation and inter-troop encounters. The local ecology is closely monitored with the daily recording of rainfall and temperature. There is also a monthly assessment of food biomass available to the baboons. A census of other baboon troops in the area is attempted monthly.

Statistical methods

The diversity of data collected and the scope of analysis required for an investigation of social complexity in baboons requires a concomitant eclecticism in statistical methods. Where a statistical test is used some rationale is usually given. Necessity requires that parametric tests are used in some instances where data is strictly ordinal (e.g.) rank. In these cases some rationale is always given and an attempt is made to find corroborating evidence from other analyses.

A note on terminology

Throughout the thesis I use the term *mature* to refer to the classes of adult and sub-adult collectively, and *immature* to refer to juveniles and infants. Unless qualified, *female* means mature females only and *male* means mature males only.

Chapter 5: Dominance

Introduction

Dominance is a key feature of primate social organisation. The term itself is imprecise but typically refers to consistencies in the aggressive or submissive behaviour of interacting individuals (e.g. Sade 1967; Hausfater 1975). Whilst some have questioned the value of the dominance concept in primates (e.g. Gartlan 1968; Rowell 1974), it is probably true to say that it is a useful construct for primatologists provided that it is made clear what *kind* of dominance is being displayed with respect to what *kind* of resource. With respect to the kind of dominance, a large cluster of acts that appear overtly 'dominant' may be observed in a dyad consistently occurring in one direction. Thus the existence or description of general agonistic dominance in many primate groups may not be in any way controversial.

However, the effects of dominance on resource acquisition vary according to the resource. In olive baboons, for example, a male's rank in an agonistic hierarchy can be very poorly related to its success in winning consorts with oestrous females (e.g. Strum 1982). This is a consequence of the social complexity surrounding this type of resource acquisition. Dominance hierarchies are constructed on the basis of purely dyadic interactions but consorts in baboons are often turned over by coalitions of males. Furthermore, the oestrous female herself may be in a position to affect the outcome. Bachmann and Kummer (1980) found that male hamadryas baboons were more likely to attempt to win an oestrous female from another male when that female showed a lack of preference for the current consort-holder. Also, at the moment of a consort turnover, there is typically an aggressive episode where several of the consort followers may attempt to secure the female for themselves without receiving aggression from the dispossessed consort-holder. The direction in which the female runs at this moment may affect the followers' success (Smuts 1985). Since female choice is not related in any simple way to male-male agonistic dominance, this factor alone considerably complicates the picture of how agonistic rank may relate to reproductive success.

The relationship between dominance and complexity is difficult to pin down. A hierarchy would seem to be a simplifying process for interactions. However, since dominance hierarchies may themselves become structures around which and into which social behaviour is directed, they can plausibly be seen as *adding* complexity. The situations are different for the two sexes as is considered below.

Female and Male Dominance

In Old World Monkeys, females typically stay in the troop into which they are born and their rank is *inherited*. (though the validity of the concept of inheritance of rank has been questioned, e.g. Dewsbury 1990; Capitano 1991; Hoekamp and Smale 1991). Generally immatures acquire a rank below that of their mother but above that of the matriarch ranked below their mother. Within a matriline, rank is usually inversely related to age (Walters and Seyfarth 1987) resulting in 'youngest ascendancy' in which immatures rise in rank above their older siblings through support from their mother. The mother's support for her youngest child has been variously explained as investment in the higher reproductive value of the youngest child (Schulman and Chapais 1980) and as an attempt on the part of the mother to form a coalition to prevent her oldest child rising above her in rank (Horrocks and Hunte 1983). The possibility that youngest ascendancy is the consequence of a tactical decision on the part of matriarchs can offer an explanation of cases where the pattern fails to appear. Demography can affect the availability of allies; Dunbar (1988) notes that where inter-birth intervals are long, as in gelada baboons, an aging mother cannot count on a young second daughter providing enough support to form an alliance against an older daughter. Under these circumstances a better strategy would be for the mother to form an alliance with the older daughter. Datta's (1992) recent attempt to model demographic effects on female dominance structure concluded that such effects were likely to be very complex and that an absence of rigorous cross-population data precluded the assumption of hard and fast rules.

In contrast, the dominance of mature males who (in Old World monkeys) are typically immigrants into a group, is more a question of fighting ability. This is a function of a number of factors such as size, strength and possibly nerve. In baboons, male rank is typically related to age and duration of residence in groups. Rank tends to be high shortly after a male's immigration into a group and declines as the male ages and becomes a less effective fighter (Packer 1979a, 1979b; Rasmussen 1980; Strum 1982; Smuts 1985).

As noted above, female baboons inherit rank by the operation of a simple rule based on permanent kinship relations and, as such, the female dominance hierarchy is a stable one. In contrast, the factors that determine a male baboon's rank are various, unstable over time and, to a greater extent, reflect the behaviour of the male. In effect, male baboons make their own rank and females have theirs

conferred upon them. This suggests that males experience more social complexity in this regard.

This is perhaps an overstatement of the dichotomy since rank changes in female baboons do occur. Apart from the fall off in a female's rank in old age (e.g. Hausfater et al. 1975) there is at least one account of a female baboon systematically working her way up the hierarchy (Ron 1993). More common are cases of whole matriline falling below others (e.g. Koyama 1970; Chance, Emory and Payne 1977; this study) and whole matrilines rising (e.g. for vervets, Cheney and Seyfarth 1990). However, the catastrophic but logical nature of these 'coups' seems to highlight a tendency for dominance relations in females to create their own internal order. This can be compared with the more local dominance changes in male hierarchies which result primarily from the reversal of dyads (Hausfater 1975). The mechanism of this self organisation in the female hierarchy is unclear but we should assume a causal status of facets of the social structure beyond each individual animal's relationships, i.e. a strong top down effect of group structure on network structure. This is because the efforts of individuals will presumably all be aimed towards increasing their rank, leading the group towards instability. However, since each individual must, by its choice of actions, be contributing to the emergence of a new hierarchy it seems reasonable to posit that female baboons *expect* stable dominance relations and thus help bring them about, in part by a passive disinclination to disturb an emerging new hierarchy. The stability of female dominance hierarchies reflects this supposed expectation. It presumably also reflects the fact that in most cases a challenge to a stable hierarchy will necessarily have a negative outcome and that, whilst low rank may have disadvantages, such animals may benefit more from knowing their rank and avoiding time consuming and possibly life-threatening negotiations of it than they would by enjoying the benefits of high rank.

The relative stability of male and female rank in vervet monkeys is neatly summarised by Cheney (1983). She showed that in a four year period females changed ranks at the rate of 0.11 ranks per female per year, whilst adult males did so at 0.75 ranks per male per year.

The purpose of this chapter is partly a methodological one; since many of the analyses in subsequent chapters use rank as a factor for exploring complexity, I explain here the methods used to identify rank. However, the question of linearity and stability across sexes is discussed in so far as it bears on social complexity in its own right.

Creating dominance matrices for the study troops

An agonistic dominance hierarchy was sought both for mature females and males in the troops. Focal and *ad libitum* records were used for this purpose. Only dyadic interactions were used. In selecting the behaviours that indicated agonistic dominance or submission, the scheme of Hausfater (1975) was followed closely. With respect to my own ethogram the following behaviours were used;

Dominance

bite, chase, grapple, lunge, molar grind, threaten, victory in fight, yawn

Subordinance

avert gaze, avoid, counter-chase, fear face/vocalisation, present with fear, run away, scream, be vigilant of

The rationale of the choice of behaviours is that, in the case of dominance they should show an aggressive stance, and in the case of subordinance they should show a fearful or avoidant stance.

Supplants, both feeding and social, were excluded on the basis of possible observer bias. Since the dominance hierarchy became known to me I may not have been able to impartially judge when a supplant had taken place and when it was simply the coincidental moving of two animal with respect to each other. Whilst this bias may be tolerable enough to merit the inclusion of supplants in the study's ethogram, it is too clearly a self fulfilling criterion to be used in *determining* dominance.

Linearity of Hierarchies

The instability of male baboon rank hierarchies over time has already been discussed. Concomitant to this is the question of their linearity. Since the dataset for a whole ten month study period is being used to determine hierarchies, these two factors, linearity and stability are confounded. They may, however, be not so much confounded as inseparable: on a very small time scale, non-linearity in a hierarchy cannot be distinguished from change in the hierarchy since the demonstration of non-linearity requires reference to previous interactions.

The linearity of the dominance hierarchies of mature males and females was tested in both groups using a procedure outlined by Appleby (1983). This compares

the number of expected circular triads $E(d)$ in a dominance matrix (given random dominance relationships) with the observed number (d), resulting in a X^2 statistic. The results of this test are given in Table 5.1.

There is clearly a strong linear hierarchy in the case of the females of both troops ($p < 0.02$) but, using the same behavioural criteria, no clear hierarchy exists for the males ($p > 0.30$).

A more sensitive consideration of male agonistic behaviour might reveal a real dominance hierarchy based on different principles but that analysis lies beyond the scope of this study. As such, this thesis proceeds without the use of rank as a factor pertaining to male interactions.

Determining the female dominance hierarchy

I could find no satisfactory algorithm for putting the subjects of a dominance matrix into rank order. The method proposed by de Vries et al. (1993) orders individuals by the total number of others that they show a net dominance over and then uses an iterative 'flipping' procedure (Roberts 1990) to remedy local errors by reversing the positions of adjacently placed animals for which the dyad's dominance is in error. The problem with the procedure is that individuals who are rarely involved in agonistic encounters, i.e. those for whom most cells in the dominance matrix are empty, can be grossly mislocated in the original ordering.

For MLK, the hierarchy is well known through the efforts of the UNBP research team who monitor dominance instances and transgressions of dominance. (It is worth noting that the de Vries et al. procedure assigned an incorrect hierarchy to my data for this troop.) The hierarchy I constructed for STT is based on the principle that the least number of transgressions of linearity should occur in the hierarchy. As can be seen in Tables 5.2 and 5.3 this solution is not hard to compute since there are so few transgressions. Where no dominance incidents existed for individuals closely ranked by this scheme, the placing was achieved using suspected kinship (using the youngest ascendancy rule) and the dominance hierarchies documented by Lohead and Barton (see Barton 1989).

Changes in the STT Dominance Hierarchy

Table 5.4 is a comparison of the STT female dominance hierarchy computed above with that computed by Deborah Lohead in 1987. Only animals common to

Table 5.1 Linearity of dominance hierarchies: E(d) is expected number of circular triads given random assignment of dominance relationships to dyads, (d) is observed number.

| | E(d) | (d) | X^2 | d.f | p |
|-------------|-------|-------|-------|-------|-------|
| MLK females | 41.3 | 27.3 | 36.8 | 20.2 | <0.02 |
| STT females | 442.8 | 380.3 | 56.0 | 29.4 | <0.01 |
| MLK males | 5.0 | 5.5 | 30.0 | 30.0 | >0.30 |
| STT males | 113.8 | 116.8 | 20.74 | 22.56 | >0.30 |

Table 5.4 Changes in the STT female hierarchy over a 6 year period

Dec '86-Nov '87 (Lochead)

Maxine
Withania
Karen
Tura
Marina
Greta
Mali
Faith
Nina
Opuntia
Turkana
Twala
Billie
Janny
Liz

Sep '92-Jun '93 (Sambrook)

Maxine
Withania
Karen
Tura
Greta
Faith
Betty (daughter of Billie)
Twit (daughter of Twala)
Janny
Mali
Liz
Marina
Turkana
Opuntia
Nina

both hierarchies or with known kin are included.

At some point between studies, a segment of STT comprising Billie, Janny, Twala and Liz moved up the hierarchy. An analysis of demographic records in STT reveals an interesting property common to all individuals that have *fallen* in rank since 1987. When STT split shortly after Lohead's study the bottom third of the hierarchy ultimately formed the daughter troop. The process of splitting was a protracted process however and some animals who remained in STT spent a number of days in the emerging daughter troop and a third, ephemeral mini-troop. All animals in STT who have fallen in rank spent periods away from the main troop in these daughter troops. No animals who did not move away have fallen in rank.

Discussion

The fact that both troops exhibited a strong linear hierarchy for the females but not for the males was not surprising given the review of previous work at the beginning of the chapter. If one could get inside the head of the males a much clearer picture of dominance might appear. However, it remains the case that, at a gross behavioural level, dominance relationships are far more mutable in males. The fact that many agonistic encounters between males are in the context of consortships and consequently involve coalitions contributes to this situation.

For males, two sorts of unpredictability present themselves as a consequence. The first is that at the level of interactions; where dominance relations are susceptible to contravention or reversal, individuals may not be sure of the level of dominance or submission they should show in greetings or of the precedence they should enjoy concerning a resource such as food. The second level of unpredictability is at the level of relationship. As alluded to above, male baboons probably do have an idea of the dominance they hold with respect to others. Unlike the relative immutability of the female hierarchy, males have greater scope for improving their dominance and so face a set of strategic decisions on how to accomplish this. That conflicts can be initiated largely for the sake of establishing dominance seems likely. Strum (1987) relates how males will contest a consortship but, having forced the holder away from the female, will opt to further harass that male rather than form a new consortship with the female. I saw comparable incidents to this: on one occasion, Major, a sub-adult male, fought ferociously to win an oestrous female early in the day, incurring a wound. An hour later he sat impassively while the female, wandering off, was appropriated by an older male after a short fracas with a third. These cases underline the fact that

immediate material rewards may come second to longer term investment in social standing.

Do these considerations suggest greater complexity for males? Some comments about female dominance should be made. Firstly, newborn infants are a source of great attraction to other members of the group (both male and female) and their mothers enjoy a temporary increase in rank (Weisbard and Goy 1976). As long as there are infants present, the hierarchy will thus suffer such perturbations.

Secondly, the existence of a strong linear hierarchy in females does not prevent frequent disputes breaking out, many of which involve the intervention of other animals. These are often kin, but the well documented phenomenon of male-female friendship also plays a role here. Such friendships have been reported in baboons (e.g. Saayman 1970; Seyfarth 1976; Smuts 1985), Japanese macaques (e.g. Takahata 1982) and rhesus macaques (Chapais 1983, 1986; Hill 1990). Typically, grooming and possibly preferential sexual access on the part of the females, is rewarded by protection (of both the female and her infant) against actual or potential aggression (e.g. Smuts 1985). Clearly such friendships can act to modulate dominance relations. In Chapter 3 it was noted that individuals invariably topped up the complexity of the system that they comprised when they were cognisant of the system themselves (particularly if this was reflected in their behaviour). With respect to the discussion at hand it is tempting to suppose that, endowed with the simplifying mechanism of a strong hierarchy, females simply generate a quantity of complexity on top of this equivalent to that which would exist without it (c.f. the unstable male hierarchy). However, this constitutes a rather idealised application of the principle and it seems likely that the rigidity of the female hierarchy does impose genuine simplifying constraints.

The general question of whether dominance (in any form) increases or decreases complexity was raised in the introduction to this chapter. My feeling is that whilst it *may reduce* unpredictability of interactions, its existence as a social structure provides a scaffold for greater organisational complexity. Such organisational complexity is that residing in the *links* between Hinde's (1976) levels of social organisation. Thus, to employ the concepts reviewed in Chapter 2, the total amount of information required to specify the system does not decrease with the appearance of a hierarchy, rather it reapporitions it from H(patterns) to H(organisation).

Finally, the reality of permanent changes in the female hierarchy must be addressed. Female baboons may be able to recognise and capitalise on 'windows of opportunity' such as the depletion of a higher ranking matriarch's kin allies. The troop fission in STT discussed earlier may have constituted one such

window. Unfortunately, detailed behavioural data is not available for this period. Thus it is difficult to know whether those who fell in rank did so because on return to the main troop, their rank status had weakened and become more 'negotiable' or whether their experimentation at living in the daughter troop was prompted by an earlier coup which had lowered their rank.

Cheney and Seyfarth (1990) go so far as to suggest that such windows of opportunity are anticipated far in advance by individuals assessing, for example, future demographic compositions based on variabilities in individual fecundity. If this is true, and females act according to this foresight (e.g. by pre-emptive affiliation to rising stars) then a hitherto unsuspected 'dynastic' social sophistication would seem to be operating. At any rate we have no basis for supposing that the slower rate of dominance turnover in females is indicative of lesser complexity at the relationship or 'strategic' level.

Troop fission may well involve dominance-based choices. As noted above, the split in STT involved the breaking off of the bottom third of the hierarchy. This respects the usual 'horizontal' nature of fission in baboon groups, but other types of fission have been observed, for example by Ron et al (1994). These authors document the 'unzipping' of a chacma baboon dominance hierarchy in which females appeared to follow the rule of 'Abandon Your Superior' (AYS) in choosing which of the daughter troops to join. Thus, with a few exceptions, females ranked 1, 3, 5, etc joined daughter troop A, whilst those ranked 2, 4, 6, etc joined daughter troop B. Ron et al note that this is a stable rule to follow since for each animal (except of course the alpha) it ensures a promotion in rank, and the rule cannot be improved upon if all others are following it.

However, since adjacently ranked females are more likely to be affiliated (e.g. Seyfarth 1977) the AYS strategy will disrupt the alliances that horizontal fission preserves. Thus the manner in which a troop splits may provide important clues as to the value of traditional (dyadic) dominance compared to that attached to affiliative bonds. STT split horizontally implying that females preferred to affiliate with their superiors than abandon them.

In summary then, female dominance hierarchies certainly present problems and opportunities for those that comprise them. Still, intuition accompanied by personal observation of the quality of interaction suggests that on a moment to moment basis, males suffer unpredictability from the absence of a strong hierarchy. The discussion above has been qualitatively based; what is required is quantitative measures of possible indices of social complexity. These follow in the remaining chapters.

Chapter 6: Troop Size and Grooming Relationships

Introduction

Grooming is a ubiquitous pastime of primates. It clearly serves an hygienic function (Rosenblum et al. 1966; Barton 1985) but early studies also identified grooming as an indicator of affinity (e.g. Carpenter 1963; Washburn and DeVore 1963) and it is now recognised as belonging to a cluster of highly correlated affiliative behaviours such as maintenance of proximity and coalition formation (e.g. Cheney 1977; Dunbar 1980). In many ways, grooming is an ideal affiliative behaviour; it provides an opportunity for individuals to sit very close to one another in a non confrontational manner (Goosen, 1981), to express affiliation by performing a service and it publically 'marks' (Strum in press) a relationship.

Grooming thus appears to serve a social function (Dunbar 1991) and although the benefits of grooming relationships may take different forms there ought to be an optimum grooming strategy for each individual. The overall amount of grooming performed by an individual is constrained by its activity budget and its choice of partners is constrained by the behaviour of other troop members. Finding this optimum grooming strategy and managing to enact it may thus constitute a problem in social complexity. This chapter concerns aspects of the frequency with which individuals groom and the size of their grooming networks. Grooming networks are defined as all individuals ever groomed in the study period: separate networks are created for scan and *ad libitum* data. The question of who grooms whom will be dealt with in the following chapter.

Methods (Data collection)

Grooming as a behaviour

Grooming is an easily identifiable and reasonably non-ambiguous behaviour. However, it is important to appreciate the distinction between grooming *as* grooming which is typically dyadic, relaxed and sustained and that of grooming as protection seeking. The latter typically occurs in the context of an agonistic polyadic interaction where the groomer (often an immature) signals its friendly relations with a powerful friend by grooming it (thus also maintaining close proximity). In this chapter the term grooming refers solely to instances of the former.

Biases

The data presented below were collected under scan and *ad libitum* protocols as described in Chapter 4. In attempting to compensate for the larger number of animals typically missed in scanning STT, that troop was scanned more often. However, this led to a slight overcompensation such that the average individual in STT was scanned 7% more often than that in MLK and the average female 14% more. To correct for this bias the mean frequency of grooming and the mean network size was increased in MLK by the appropriate percentage given above.

Ad libitum data on grooming does not support a comparison of frequencies between groups as so much greater a proportion of MLK was visible at any one time. The possibility that this bias also led to a differential estimation of the size of grooming networks in the two groups was considered. It was tested by plotting the apparent growth of mean network size over successive months, the results of which are given in Figure 6.1. As can be seen, there is not much suggestion of a levelling out of network size for animals in either troop; it is thus not possible to know how much the apparent growth of network size in later months is due to the accumulation of (and thus increased comprehensiveness of) samples and how much to real change in the networks themselves. The rate of change for both troops is similar. That STT does not appear to be 'catching up' MLK towards the end could be taken as evidence that sampling is as effective for both troops.

In consequence of these uncertainties, where scan and *ad libitum* data are not in agreement, confidence in the reality of any observed effect is lowered. Note that within-group data (e.g. concerning who is grooming whom) discussed in the next chapter suffer much less from the biases of *ad libitum* recording.

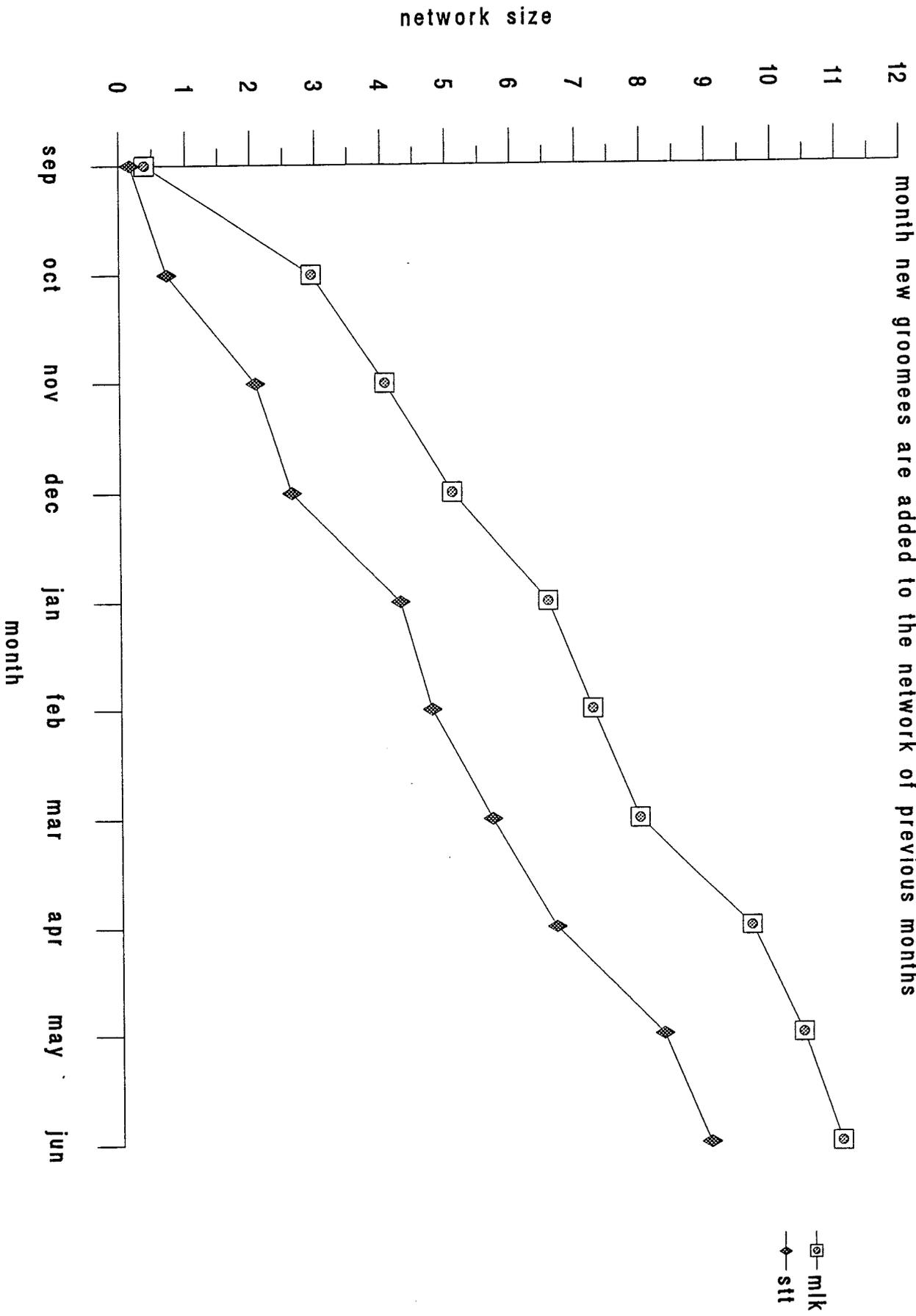
The analyses in this chapter do not use focal data, concerning as they do the behaviour of all individuals in each troop.

Methods (Analysis)

All incidents of grooming observed in the context of consorts were excluded from the analysis, whilst grooming of swollen but unconsorted females was included. Grooming performed by individuals who were not present for the entire study period has been discarded but grooming performed upon them has been retained.

Comparisons between the two groups necessarily often involved greatly unequal sample sizes. The general approach taken here is that a t-test is assumed to

Figure 6.1 Cumulative mean grooming network size of all age-sex classes (ad libitum data). Network size is the number of individuals the network holder was ever seen to groom. In each month new groomees are added to the network of previous months



be robust to this provided the variances of the groups are similar. For this reason, F-values are given where significant results are reported.

Data were analysed for whole groups and then split into the three age-sex classes of female, male and immature as described in Chapter 4. Allocation of individuals to each class was made on the basis of the animal's status at the beginning of the study period.

As the analyses become more specific and sensitive I have tended to switch to an examination of the female class only. With respect to most variables under study, this class tends to have the least statistical variance; it may be that this class is the least heterogeneous in that it is the least susceptible to age-related change. I have not been able to find a way of non-arbitrarily reducing the heterogeneity of the immature class that does not severely limit sample sizes. (The division of the class into male and female does not really affect the data, particularly since the number of immature males in MLK was very small). The high variance and low sample size for the males tends to prohibit useful general statements for that class. Another reason for concentrating on the female class is that they may show complexity at a higher level than immatures as discussed in Chapter 4.

Frequency of Grooming

The first question to be addressed is how often the study animals groomed. There is presumably a level of grooming that is socially optimal but this may be constrained by aspects of individuals' activity budgets, and depend upon their age-sex class. Dunbar (1991) has shown that, across 44 species of primate, time spent grooming correlates well with group size. Certainly, intuition might lead us to suppose that individuals would need to groom more in a large group. This might take the form of greater grooming of a set number of partners in order to keep the cohesiveness of relationships at a satisfactory level. This might result from increased *active* interference by others or, as Dunbar (1991) has suggested, simply reflect the greater need for the buffering effect of relationships required to compensate for the increased crowding found in large groups. Alternatively, we might expect greater frequency of grooming by virtue of more animals being groomed (perhaps because the optimal number of grooming partners is related to a proportion of the whole rather than an absolute number).

Table 6.1 and Figures 6.2 and 6.3 show the mean number of recorded instances of grooming for the various demographic classes in each troop.

There is a trend in each group in which females groom most, followed by

Table 6.1. Mean frequency of grooming and diversity of grooming partners in the study period (see text for details).

| | Scan | | | | <i>Ad lib</i> | | F-ratio | p |
|-------------|-------|----|-------|----|---------------|-------|---------|------|
| | MLK | n | STT | n | MLK | STT | | |
| Whole group | 14.11 | 32 | 13.91 | 75 | 30.63 | 20.92 | 1.14 | <.05 |
| Females | 21.56 | 11 | 23.62 | 21 | 43.00 | 38.33 | | |
| Immatures | 11.94 | 16 | 11.38 | 40 | 26.25 | 16.12 | 1.40 | <.05 |
| Males | 5.38 | 5 | 4.50 | 14 | 17.40 | 8.50 | | |

| | Scan | | | | <i>Ad lib</i> | | F-ratio | p |
|-------------|------|----|-------|----|---------------|-------|---------|------|
| | MLK | n | STT | n | MLK | STT | | |
| Whole group | 7.19 | 32 | 6.97 | 75 | 11.15 | 9.12 | 1.14 | <.05 |
| Females | 8.60 | 11 | 10.48 | 21 | 12.00 | 13.67 | | |
| Immatures | 7.18 | 16 | 6.40 | 40 | 11.87 | 8.25 | 1.40 | <.05 |
| Males | 3.97 | 5 | 3.36 | 14 | 7.00 | 4.79 | | |

Figure 6.2 Mean instances of grooming that individuals gave across whole 10 month study period (scan data). Standard errors shown.

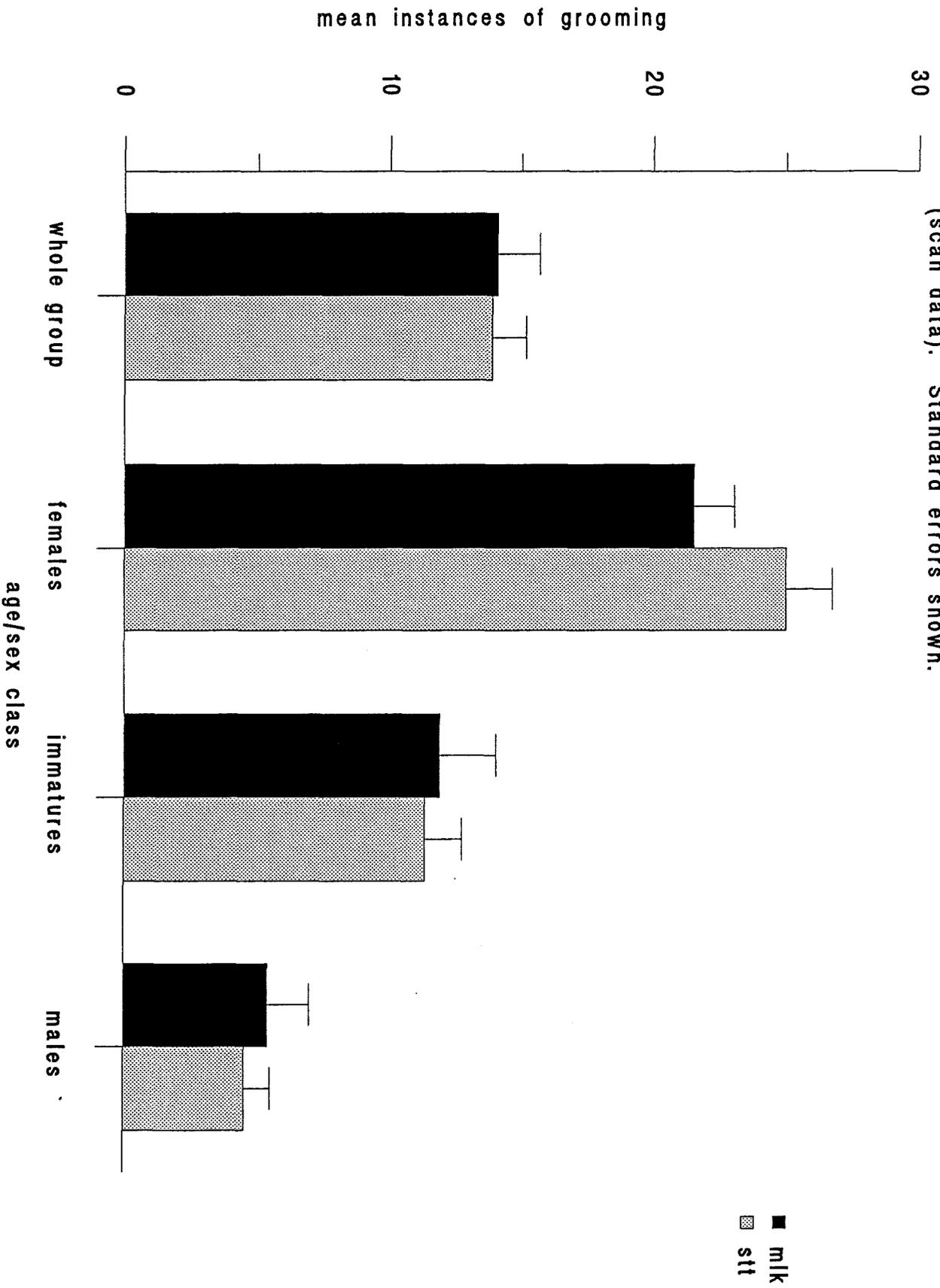
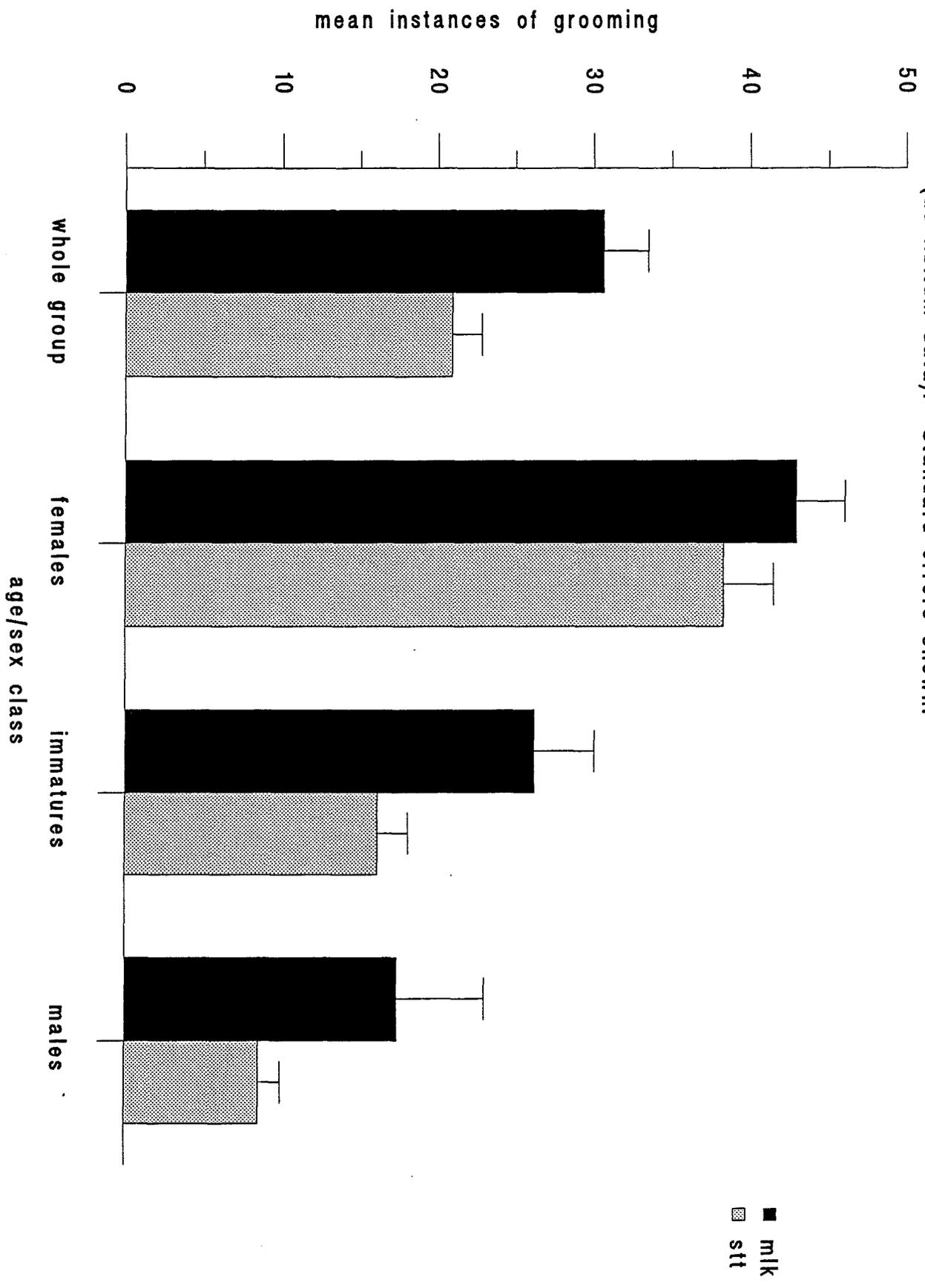


Figure 6.3 Mean instances of grooming that individuals gave over the whole 10 month study period (ad libitum data). Standard errors shown.



immatures and then males. Using t-tests, a comparison of the means of each age-sex class across troops reveals no significant differences between the troops in the scan data. The *ad libitum* data are unsuitable for such a comparison as previously discussed.

A consideration of activity budgets in the two troops should be used to qualify these data. Two-minute point samples of focal animal activity can be used to make a general statement about whole troop activity. The percentage of these samples that were of feeding/moving was calculated for each animal for each month (the activities that comprise the feeding/moving super-category are shown in Table 4.5). A t-test was used to compare these percentages and it was found that STT spent more time moving and feeding than did MLK ($t=2.62$, $N=90$, $df=87.7$, $p=0.008$). This result is shown in Figure 6.4. Large groups tend to have to devote more time to foraging since food patches are depleted more quickly (Clutton-Brock and Harvey 1977a) and this is probably reflected in the data presented here.

In consequence, we cannot be sure whether the equivalence of grooming time in the troops means that group size does not exert pressure for higher grooming rates or whether this pressure is overruled by (non-social) activity budget constraints. In other words it is difficult to know what STT baboons would 'like' to do if left to purely social devices.

Diversity of Grooming (grooming network size)

If grooming indicates affinity then the size of an individual's grooming network represents the number of others that individual currently holds a certain kind of relationship with. Is the size of grooming networks related to group size in the case of these study troops? Given the result above, this would clearly necessitate the average relationship to be weaker in so far as its strength is related to amount of grooming given. It is possible that this would be the optimal way to deal with a large group given a constraining activity budget, however.

Grooming network size was defined earlier as all individuals the network holder groomed in the study period. This clearly neglects the possibility of changes in network size and membership over time; indeed these two factors become confounded. However, since the size of the dataset does not support a breakdown into smaller time blocks and since Figure 6.1 discussed earlier shows the apparent growth of network size to occur at a similar rate in both troops, these problems are overlooked.

Table 6.1 and Figures 6.5 and 6.6 show the mean network size for the

Figure 6.4 Percentage of focal sampling time which individuals spent in feeding or moving behaviour. Data from 2 minute point samples. Standard errors shown.

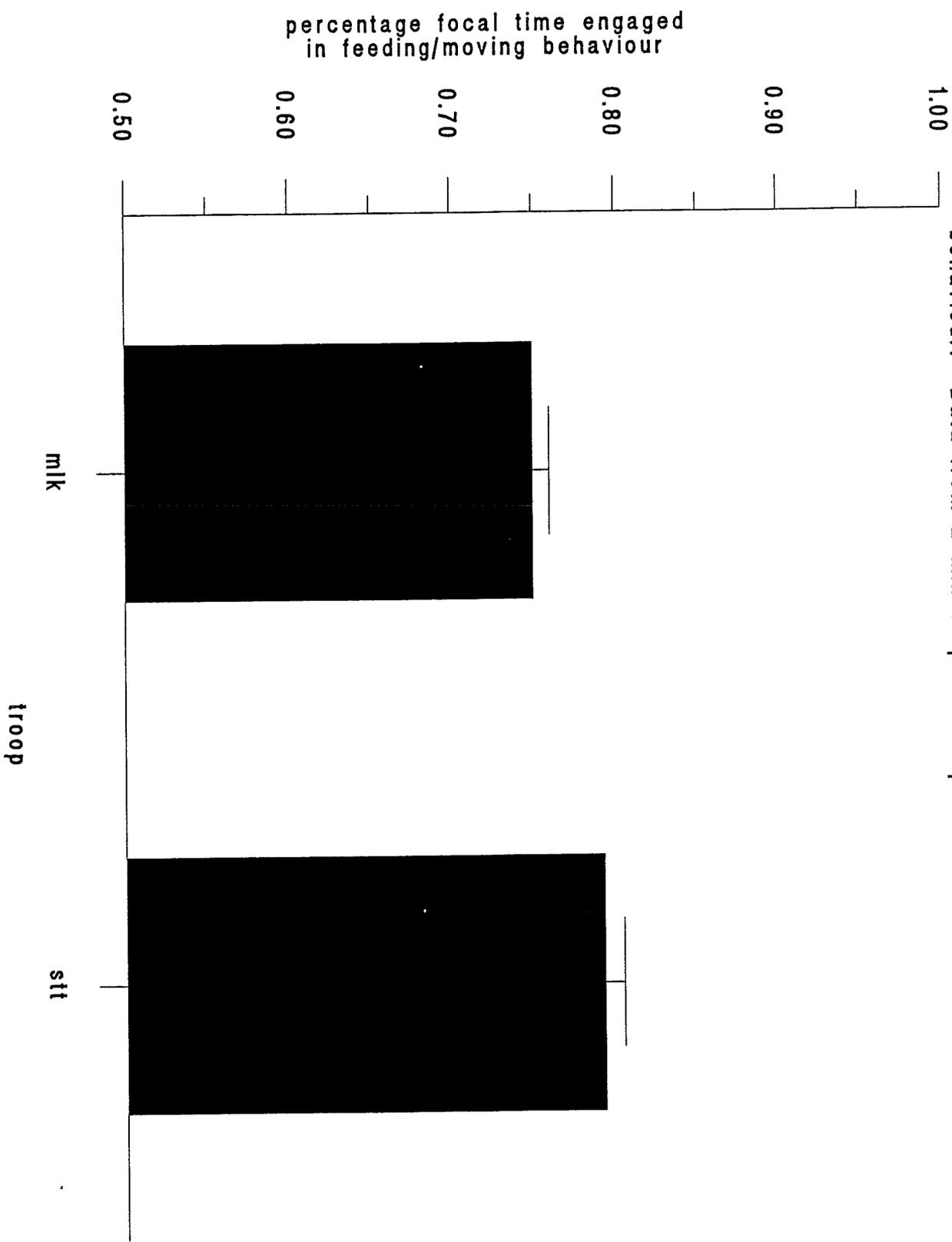
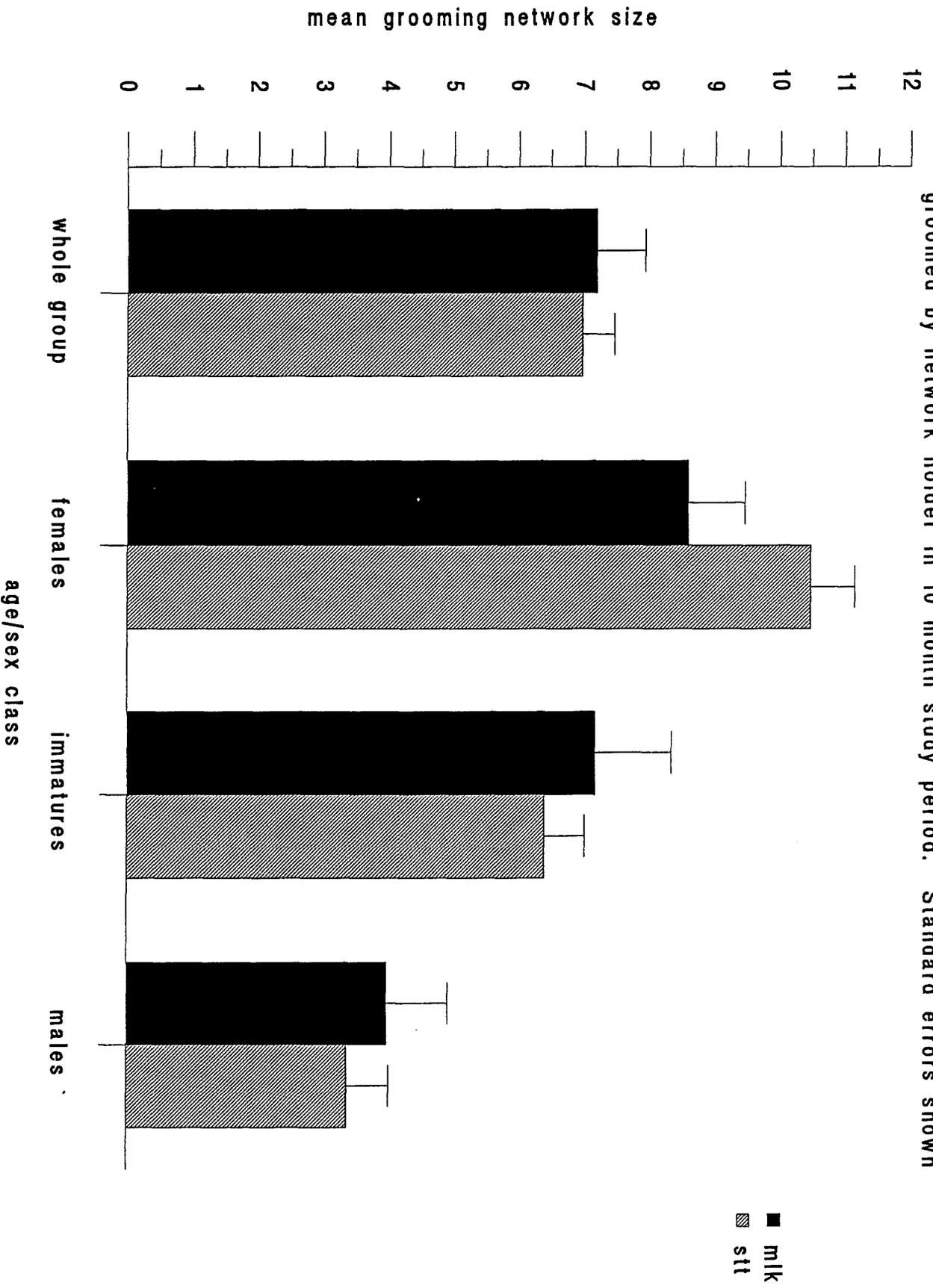
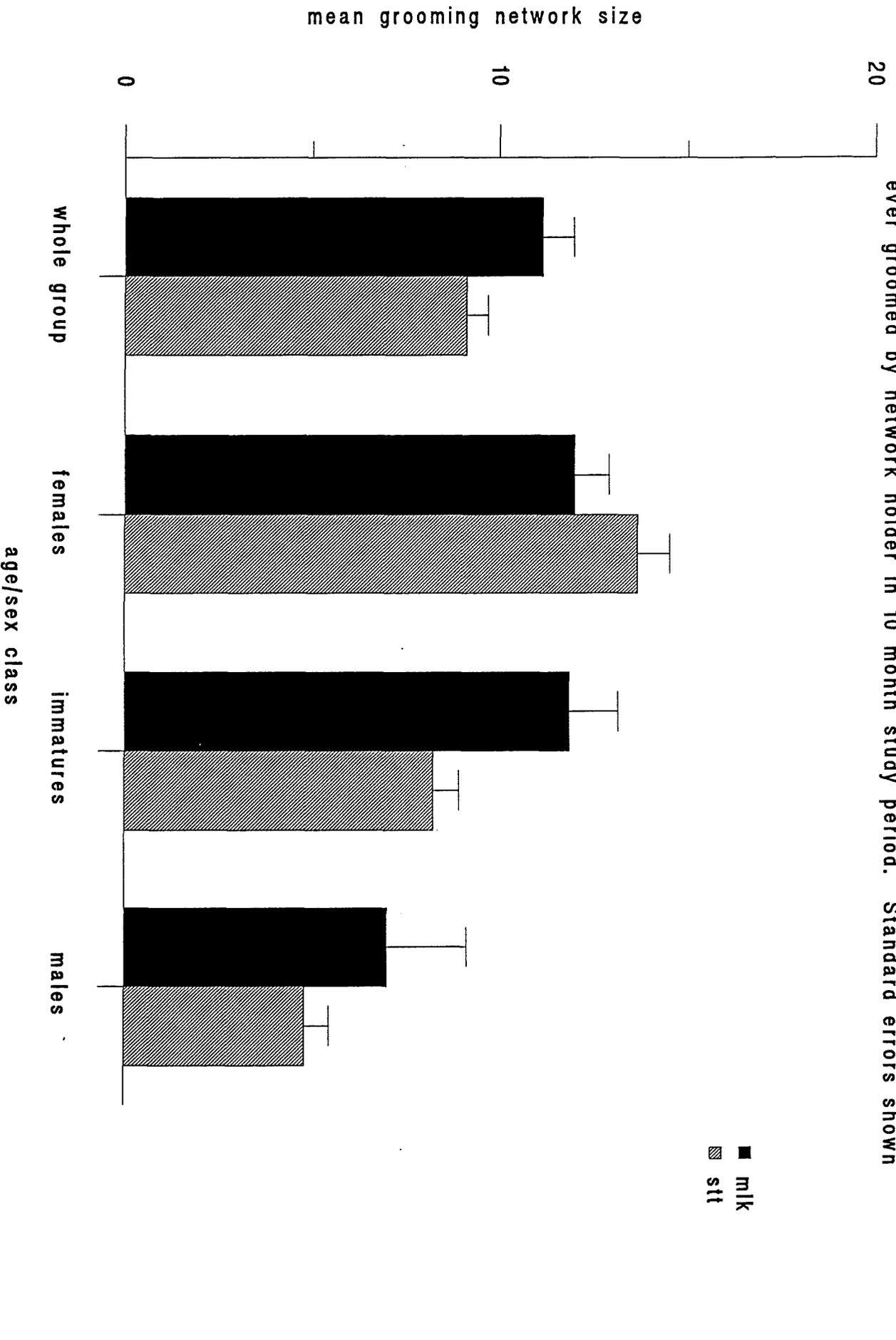


Figure 6.5 Mean grooming network size (scan data). Network size = number of individuals ever groomed by network holder in 10 month study period. Standard errors shown





various demographic classes according to the two methods of sampling. The only means which are significantly different between the troops were obtained under *ad libitum* recording and are those for the whole troop and for the immatures. (The result for the whole group is largely a consequence of the result for the immatures). This result is not supported by the scan data which is likely to be a slightly more reliable source. In contrast to immatures and males, STT females groom more partners than do MLK partners, but this difference is not significant.

Allocation of Grooming

The two troops groomed roughly the same number of individuals and groomed with roughly the same frequency. The possibility remains however, that troop size affects the allocation of an individual's grooming over its network. Thus, group size might change the relative value of strong and weak relationships. Given work such as Smuts (1985) on male-female friendships, we might expect qualitative differences in the nature and function of strong and weak relationships. For example, strong relationships may function to maintain alliances for help during contests. Weak relationships may be more in the nature of appeasement; they could prevent aggression from, and promote spatial toleration by, the particular animal with whom the weak relationship is held. The question of whether group size alters the merits of these two strategies might be reflected in grooming allocations. Certainly, such strategic decisions ought to suggest sophistication in the face of social complexity.

To investigate this, members of each individual's network were ordered by the grooming preference the individual showed towards them. The frequencies of grooming at each point in the network could then be pooled across network holders and average frequency of grooming could then be plotted as a dependent variable against partner preference. This plot is shown in Figure 6.7 for the female class with grooming of close kin (mothers and daughters) excluded. The decision to exclude close kin was based on the observation that these were by far the most preferred grooming objects of most individuals. Since individuals differed in the number of kin they held, the first three points of Figure 6.7 would conflate kin and non-kin grooming, tending to increase the overall variance. Furthermore, the age structure of matriline in the two troops was different, with a greater number of young infants in STT who were groomed excessively often by their mothers. This would affect the allocation functions.

Only scan data were used because of the difficulties of using *ad libitum*

mean instances of grooming
 across all scan sample points

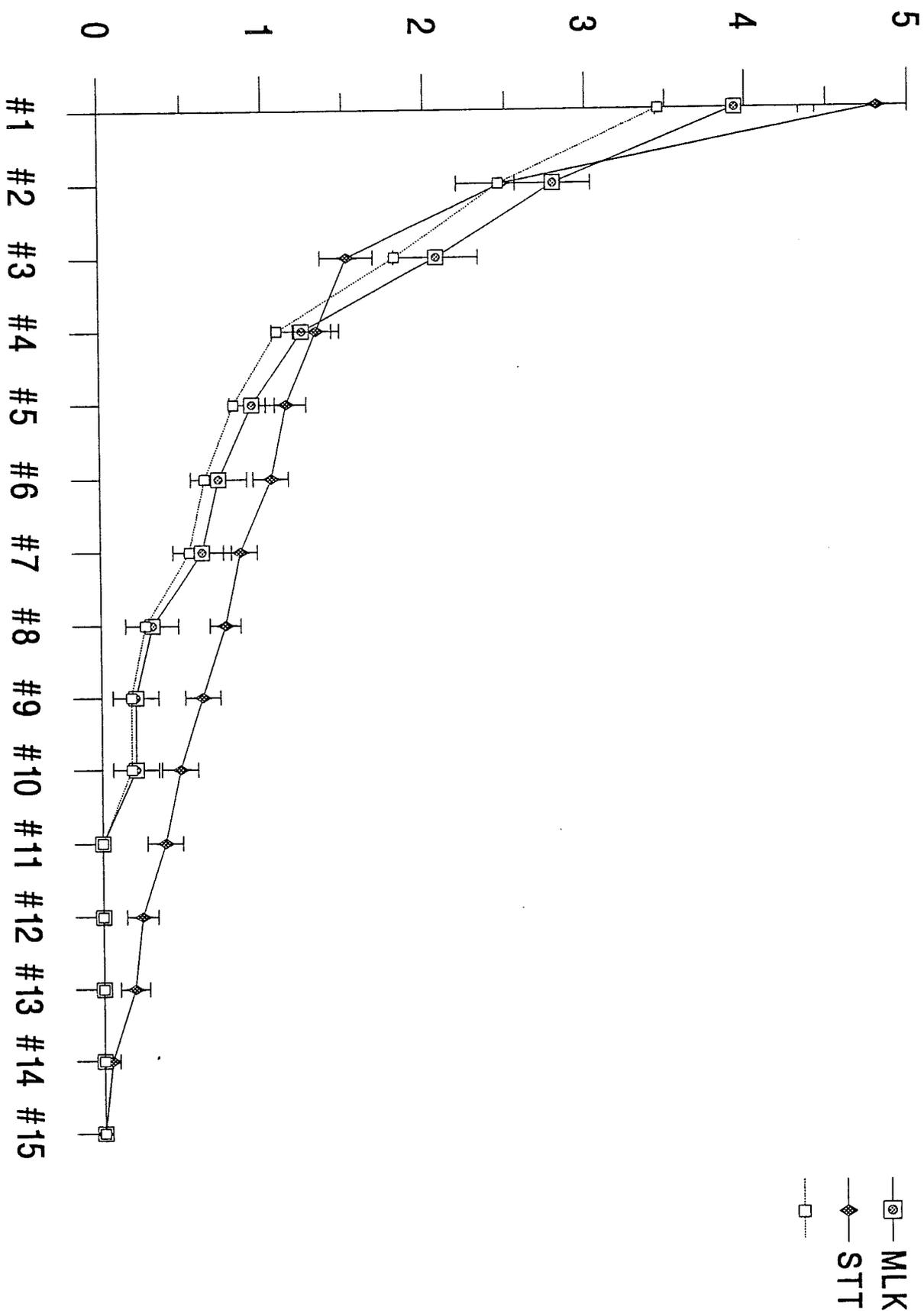


Figure 6.7 Mean female allocation of grooming across networks (scan data). Frequencies with which females groomed partners at ranked points of favour in network over 10 month period were used and means taken. Kin grooming excluded. Standard errors shown.

measures of frequency as already discussed.

An inspection of the curves in Figure 6.7 suggests that they are not the same. STT females appear to devote more time to their favoured partner and to more distantly acquainted partners at the expense of their second and third favourite partners. The statistical reality of this was tested in two ways, using analysis of variance and using a battery of ten t-tests for each of the levels of partner preference. Only the first ten levels were used since this was the maximum non-kin network size among MLK females and the points thereafter, being zero, could not be corrected for the aforementioned scan sampling bias. Also, since the compensation for this bias constitutes data manipulation on the basis of an assumed relationship (i.e. that observed incidents of grooming grow linearly with hours of observation in this study) the original uncorrected values for MLK grooming are shown in Figure 6.7 as the lower limit of certainty regarding the 'true' figures for their grooming in comparison with STT. For statistical purposes, however, compensated values are used.

A differential style of allocation by members of the two troops should be reflected in the interaction of the two factors of group and partner preference. An analysis of variance shows this interaction to be non-significant ($F=1.45$, $df=9$, $p>0.15$). The values of t for cross group comparisons at each level of partner preference are shown in Table 6.2 and prove rather disappointing.

Discussion

The broad conclusion here is that the size of the study troops does not greatly affect frequency of grooming or size of grooming network. This must be considered in the light of an activity budget that varies with group size. There is some suggestion that immatures in the small group have slightly larger grooming networks.

There is some evidence of a differential style of grooming allocation in the two groups. The one reasonably robust feature of Figure 6.7 is that more grooming is done of more distant acquaintances, thus it may be that, as troop size grows, such animals assume an increasing importance.

What can be concluded about complexity from these results? Great differences between the troops in network size or grooming frequencies are absent so these factors, in themselves, do not pose different degrees of complexity across troops. However, it would seem that by failing to extend their networks, STT individuals must find themselves cohabiting with many more animals with whom no

Table 6.2 Mean allocation of grooming across female grooming networks (adjustment for sample size has occurred: see text for details). Values of *t* refer to differences between groups in allocation at each point in the network

| Partner preference | MLK grooming frequency | STT grooming frequency | <i>t</i> | 2-tailed p |
|--------------------|------------------------|------------------------|----------|------------|
| 1 | 3.93 | 4.81 | -1.27 | 0.22 |
| 2 | 2.80 | 2.48 | 0.89 | 0.38 |
| 3 | 2.07 | 1.52 | 1.80 | 0.09 |
| 4 | 1.24 | 1.33 | -0.38 | 0.71 |
| 5 | 0.93 | 1.14 | -1.12 | 0.27 |
| 6 | 0.73 | 1.05 | -1.57 | 0.13 |
| 7 | 0.62 | 0.86 | -1.13 | 0.27 |
| 8 | 0.31 | 0.76 | -2.42 | 0.03 |
| 9 | 0.21 | 0.62 | -2.33 | 0.03 |
| 10 | 0.21 | 0.48 | -1.51 | 0.15 |

affiliative grooming bond has been established. This may be expected to increase the unpredictability of interaction outcome between dyads: a possibility examined in Chapter 11. There is a sense in which that in failing to embrace the inevitably higher 'system complexity' of a larger troop by increasing their network size or strengthening the relationships within it, individuals in STT leave this complexity at large, to be faced on a moment to moment basis.

Chapter 7: Priority of Access and Grooming Patterns

* A version of this manuscript has been accepted for publication in *Animal Behaviour*

Introduction

Hinde (1976) has proposed a model of social structure in groups, in which the patterning of interactions between animals determines their relationships and the patterning of relationships determines the group's structure. Hinde's scheme justifies the abstraction of a relationship (non-observable) from interactions (observable). It has proved to be widely applicable in the study of social behaviour and provides studies of quite different taxa with common ground to compare the expression and consequences of sociality across the animal kingdom (see Hinde 1983a,b).

An attractive aspect of Hinde's model is its formalising of the different levels at which sociality can be analysed. Whilst a relationship is emergent and dependent upon the 'lower level' interactions, it is valid to consider the top-down effect a relationship can have on its constituent interactions. This is especially so for animals who may be intelligent enough to themselves recognise such emergent relationships as rank and kinship (e.g. Dasser 1988), where such descriptions on the part of an ethologist go beyond anthropomorphisms and assume significance in the animal's underlying psychology.

Grooming can be a good global marker of the status of a relationship between two primates and it is the relationship that is of interest here, rather than the grooming *per se*. The aim of the present chapter is to distinguish several models based on different interpretations of priority of affiliative access and to test their success at predicting grooming patterns in the study troops. As grooming has been reported in a range of species as diverse as horses (Rubenstein 1981) and rats (Eisenberg 1962), the principles at stake may prove to be widely applicable. Grooming is an activity that is typical of the primates and the diversity of functions it serves in this order leads us to suspect discontinuity in its status when compared with non-primates; primate grooming (at least in Old World monkeys) appears to serve a largely social function (Dunbar 1991). However, to the extent that grooming indexes *affiliation*, the present chapter is relevant to understanding patterns of any type of affiliative behaviour which is shaped by dominance relations

within a social group.

Priority of Access Models

A priority of access model (Seyfarth 1976, 1977; Cheney & Seyfarth 1990) offers an elegant account of how the distribution of grooming amongst the females in groups of many species of Old World Monkey assumes a regular pattern with respect to rank. Seyfarth (1977) identifies two factors as being likely to influence a female cercopithecine monkey's grooming. Firstly, high ranking individuals will prove to be more attractive groomees as they offer the greatest possible support in agonistic interactions. Secondly, since grooming is primarily a dyadic activity, competition for access to these higher ranking animals will force animals to compromise. Seyfarth (1977) discusses the implementation of these assumptions in a computer simulation. In this simulation, the highest ranking animal (A) is unconstrained in her grooming and grooms according to the attractiveness of all other animals to her. The next highest ranking animal (B) is constrained only by A and so on, with low ranking animals being constrained by an increasingly large pool of individuals.

The question of precisely how attractiveness is estimated is addressed, with respect to baboons, in a different paper by Seyfarth (1976). In this he first provides a theoretical distribution of grooming based solely on attractiveness which is assumed to be a direct function of rank. An individual grooming of another (say A's grooming of B), expressed as the percentage of its total grooming is governed by the quotient;

$$AB = \{ \text{attr B} / (\text{attr B} + \text{attr C} + \text{attr D} + \text{attr E} \dots) \} * 100$$

Where 'attr' is the attractiveness of the groomee. The effect of this is to produce a grooming matrix whose rows contain cell values decreasing linearly with rank. This is reproduced in Table 7.1.

These cell values must then be modified to incorporate the *constraints* of rank. So, for example, the author holds that the constraint D suffers in accessing A (cell DA) will be determined by cells AB, AC, BA and CA. The rationale is that D will be unable to groom A when A is either grooming or receiving grooming from an animal higher ranking than D.

The implications of this state of affairs are that D will meet strong

Table 7.1 A theoretical distribution of grooming among females (taken from Seyfarth 1976). Each groomer has 100 units of grooming to distribute according to the attractiveness of groomees: this is assumed to be linearly and positively correlated with rank. There is no competition for access.

| | receiver | A | B | C | D | E | F | G | H | Total |
|---------|----------|-----|-----|-----|-----|----|----|----|----|-------|
| groomer | | | | | | | | | | |
| A | | | 25 | 21 | 18 | 14 | 11 | 7 | 4 | 100 |
| B | | 28 | | 21 | 17 | 14 | 10 | 7 | 3 | 100 |
| C | | 27 | 23 | | 17 | 13 | 10 | 7 | 3 | 100 |
| D | | 26 | 23 | 19 | | 13 | 10 | 6 | 3 | 100 |
| E | | 25 | 22 | 19 | 16 | | 9 | 6 | 3 | 100 |
| F | | 24 | 21 | 18 | 15 | 12 | | 6 | 3 | 100 |
| G | | 23 | 20 | 17 | 14 | 12 | 9 | | 3 | 100 |
| H | | 22 | 20 | 17 | 14 | 11 | 9 | 6 | | 100 |
| Total | | 175 | 154 | 132 | 111 | 89 | 68 | 45 | 22 | |

competition for access to those ranked above her (from other higher-ranked animals), but relatively little competition for access to those ranked below her (who are relatively unattractive to these higher ranking and therefore constraining animals). More specifically, individuals will groom those below them in direct relation to their ranks and those ranked above them in inverse relation to their ranks. In consequence, the interesting and central prediction is made that most grooming will occur between adjacently-ranked individuals.

However, it needs to be recognised that the statements made above concerning the expected distribution of grooming with respect to rank difference require that, for any individual, competition grows *faster* than attractiveness for those animals ranked higher and has relatively little effect on grooming of those ranked lower. If this were not the case, competition would not modify the basic pattern due to attraction. In practice, however, this relationship between competition and attractiveness need not hold, as considered later in the present chapter.

The Nature of Grooming Competition

Some observations should first be made about competition. The first interesting implication of the priority of access model as expressed by Seyfarth (1976, 1977) is that competition is expressed behaviourally, such that one animal's grooming of another may be prevented by the latter already being in a grooming dyad. To the extent that members of a group are required, temporally, to co-ordinate the elements of their daily activity budgets (e.g. Hall 1962) this may be a realistic source of competition.

However, it is important to consider the possibility that besides actively striving to acquire useful relationships for themselves, individuals strive to prevent relationships forming between others, particularly those which might undermine their own (Kummer 1975; Stambach and Kummer 1978; Stambach 1982; Silk 1982; Seyfarth 1980; Cheney & Seyfarth 1990). Kummer (1975) identified two ways in which gelada baboons intervened in incipient interactions of fellow group members. These were "interposition", in which the intervener stepped between two others, threatening one of them and "substitution", in which the intervener overtook his rival as he approached a target and proceeded to perform the rival's 'anticipated' action himself. Such social interference may have a pervasive influence on grooming. Viewing priority of access as a product of compromise in the face of interference, rather than as a result of passive obstruction, allows the model to be generalised: it would be expected that any dimension of affiliation (e.g

proximity, absence of discomfiture) would show a similar pattern of distribution across rank differences. In the general case, priority of access in grooming reflects priority of access in establishing relationships.

The second point to be made about the handling of a competition term is that we need to determine which animals can cause the competition. Several interesting questions arise at this point. They relate to the fact that the resource that causes competition may itself relate differentially towards the competitors. A food item, whilst it may have different value to competitors, remains food nevertheless and so bears a similar relation to all individuals. However, another individual, as a resource to be competed over, will occupy a different relative rank position with respect to any two potential competitors. This triadicty of relations requires a more careful assessment of competition. For example, one may predict that B does not suffer competition for access to A when the latter is being groomed by C, even though from a pure 'activity budget' perspective, A is unavailable since it is already being groomed: B should be able to displace C. But this could equally be achieved were it the case that A were grooming C, in which case A's access to C is being constrained by the lower ranking B, which runs counter to the spirit of the priority of access concept.

What emerges here is a possible divergence of the meaning of *constraint* and *competition*, hitherto used synonymously. In the case just discussed, B might, on any one occasion, have no motivation to groom either A or C, having filled its 'quota' for those individuals. Thus it would not be *competing* in an overtly behavioural sense. In any case, it should be unable to compete against A's access to C effectively because A's rank predicts it to be the better competitor. However, B might still have both the motivation and competence to *constrain* the access of both A and C to one another in a 'spiteful' fashion, by targeting C.

In this scheme of things, competition is used to refer to a specific form of constraint where both constrainer and constrained are pursuing the same goal: for example, both B and C wish to groom A at a certain point in time. This is to be distinguished from the more general case where the goals of the two individuals are incompatible, for example, where C wants to groom A and B does not wish this to happen. This would be a case of constraint, where B prevents C grooming A but does not itself attempt to groom A and is thus not directly competing with C for this goal.

These considerations relate to the identification of rank-defined alliances by Chapais (1992). In that paper, the typically close relationship between adjacently-ranked animals is proposed to function as a safeguard against rank loss for both parties. The lower-ranked of the pair would be motivated to interfere with a third,

yet lower-ranked individual's access to its partner, in order to prevent the two forming a 'bridging alliance' in which the lowest of the three rises to a position just below that of its ally. The higher-ranked of the pair would be motivated to prevent its partner gaining access to animals higher-ranked than itself for the same reason. However, it would also be motivated to interfere with its partner's association with yet lower-ranked animals to avoid a 'revolutionary alliance' in which both the lower-ranked animals rise above the target of their alliance. In the case of one-male unit social structures, a male may be able to intervene in practically *all* affiliation between the (female) low-rankers and the disruption of potential female-female alliances may well be the function of this behaviour. Kummer (1975) notes that this might be responsible for the star-shaped sociogram of hamadryas baboons. Gelada baboons appear to employ the same tactic but with more limited success, producing a chain-type sociogram and in this species females may ally to attack their male (e.g. Dunbar and Dunbar 1975 p. 41).

The Success of the Priority of Access Model.

Seyfarth (1976, 1980) and Cheney & Seyfarth (1990) provide data that consistently show that in adult female baboons and vervet monkeys, high-rankers receive more grooming and that most grooming is between adjacent pairs. Seyfarth (1976) also cites a number of other studies on different species purported to be in agreement with his model.

It is important to bear in mind that, in its purest form, the priority of access model attempts to explain the structure of grooming relationships entirely as a function of rank, without any reference to kinship. However, Seyfarth (1983) suggests that high grooming rates between adjacently-ranked animals are a cumulative effect of rank and kinship. Cheney & Seyfarth (1990) note that these effects ought to interact with one another depending on a matriline's place in the hierarchy. Since a high ranking individual's kin are also high-rankers, these animals can fulfil both grooming objectives simultaneously. Low-rankers have to apportion grooming between kin and high ranking non-kin to achieve this. Cheney & Seyfarth cite a number of studies that purport to back their claim of greater cohesiveness in high ranking matriline.

De Waal & Luttrell (1986) have provided a critique of the priority of access model on the basis of the confounding of rank and kinship. They note that both Silk (1982) and Chapais (1983) failed to find high grooming rates among adjacently-ranked but not kin-related females in Old World species. However, De

Waal (1991) has published data showing that, independently of kinship, rank distance affects social relationships more generally. De Waal & Luttrell (1986) offer a 'similarity principle' as an alternative hypothesis in which individuals are simply attracted to those similar to themselves (rank being one aspect of this similarity). This is suggested as an adaptive strategy because such coalitions offer the greatest likelihood of compatibility. Similarly, Colvin (1983) provides theoretical reasons why attraction to those of similar rank is likely as well and provides data from immature male rhesus macaques in support of this position.

Attempts to demonstrate priority of access by a direct analysis of displacements remain ambiguous. Across various species there seems to be a tendency for greater competition for access to high ranking animals (Silk 1982; Seyfarth 1980; Cheney & Seyfarth 1990). However, both de Waal & Luttrell (1986) and Silk (1982) found that the only consistent cases of competition for access in grooming concerned a displacing individual that ranked higher than *both* the groomer and groomee in an existing dyad. This is the only configuration of ranks in which the initiator of the competition can be reasonably sure of escaping aggression from both members of the existing dyad. There is thus a clear need to test more closely any predictions about the relationship of rank and grooming patterns arising from the principle of priority of access.

Models of Priority of Access Tested in this Chapter

The models presented here follow Seyfarth's (1977) lead and are designed to describe grooming in adult and sub-adult female baboons. Three alternative models of priority of access are developed. One conceives of constraint consisting in activity budgets, one in active interference and, in the third, the nature of the constraint is not specified. All three models assume that individuals attempt to give and receive a similar amount (arbitrarily 100 units) of grooming. This assumption of symmetry may not necessarily be justified by real populations. However, Seyfarth's (1977) simulations showed that very wide variations in the amount of time individuals spent in grooming interactions had only minor effects on the grooming distributions predicted by his model. The matrix plot of predicted grooming frequencies for each model for a hypothetical eight female group is provided for each case (producing the theoretical plot for each of the differently sized troops actually studied does not produce qualitative differences).

Engagement model

The title of this model reflects the nature of the constraint, namely that the desired object of grooming may already be engaged in a grooming dyad. This model essentially follows the simulation procedure of Seyfarth (1977). For n ranked animals, attractiveness is set at $(n+1) - \text{rank}$. So, for example, the predicted amount of grooming (before competition is considered) that D will give to A when there are five animals, ranked A to E is

$$DA = \{ \text{attr A} / (\text{attr A} + \text{attr B} + \text{attr C} + \text{attr E}) \} * 100 = 38$$

where the attractiveness of A is five, B is four and so on. This generates a percentage which can be considered a proportion of the groomer's total grooming effort.

The grooming of the top-ranked animal is generated first, then that of the next-ranked animal and so on down the hierarchy. An animal will fail to groom another by the amount the equation above specifies if (i) it has already filled its quota for giving grooming or (ii) the animal to whom it is directing its grooming has filled its quota for receiving grooming (this will be from animals higher-ranked than the aspirant groomer).

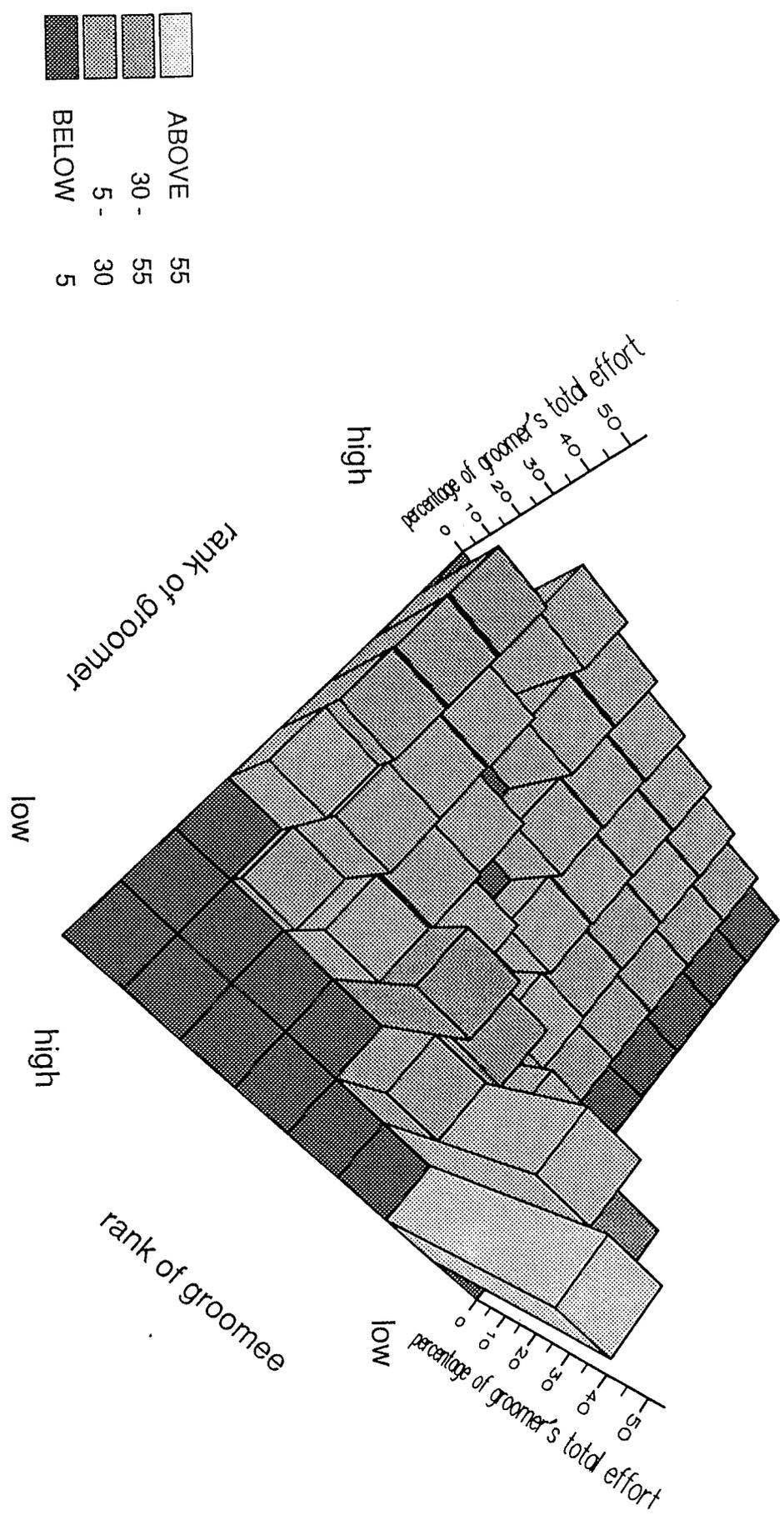
All animals were set a target of both giving and receiving 100 units of grooming. Output for the model is shown in Fig. 7.1. In this model and in the ones to follow it is typically only the lowest-ranked animal who fails to groom and be groomed with the frequency that the model stipulates to be her objective. Higher-ranked animals manage to meet their grooming budgets though not necessarily with those individuals whom they seek.

Interference model

This model assumes competition through active interference. As with the previous model, each individual wishes to give and receive 100 units of grooming and the computation begins with the same pre-competition 'attraction' matrix. This can be dubbed 'idealised attractiveness'. This is to be contrasted with 'realistic attractiveness', achieved after the competition element has been entered. Realistic attractiveness incorporates the dangers and stress of accessing higher-ranked animals.

Assume that B interferes with C's access to A in so far as B is itself attracted to A. The incompatibility of the two animals' attraction to A can be expressed as the product of each individual animal's attraction (these, remember, are fractions of B and C's total grooming effort). C's attraction to A drops by an amount corresponding to this product, not because it cannot get to A (c.f. the Engagement

Figure 7.1 Grooming distribution predicted for eight-female group (Engagement model)



model) but because B's involvement with A is ultimately antagonistic to C's. The lowered rate of grooming of A by C reflects the discrepancy between idealised and realistic attractiveness. In effect, observed grooming expresses realistic attraction. This discrepancy is computed for each potential grooming partner and predicted grooming rates reduced accordingly. Finally, these are all scaled up so that animals fulfil their grooming quota of 100 units. A worked example of this model is given in Appendix 7.1 and output is portrayed in Fig. 7.2

Fairbanks (1980) has noted that Seyfarth's assumption of attraction to high rank ignores the possible costs of defending that relationship and in keeping with this, the Interference model presented here attributes a more sophisticated decision-making process to individuals. Rather than simply being thwarted in their attempts to reach high-rankers, individuals, through prior experience, have learnt to anticipate interference and, as such, the likelihood of a relationship's being sustained. If baboons and other Old World monkeys do make such judgements then we would not expect to see great amounts of *active* interference in the form of supplants, etc. The absence of these has been suggested as incompatible with priority of access models (e.g. de Waal and Luttrell 1986) but from the present perspective it can be seen that potential, *anticipated* interference can be as active an inhibitor as if it had been overtly expressed.

One important aspect of this model is that it acknowledges that the constraint which higher-ranked animals place on those below them may itself be mitigated by the constraint they are suffering from animals higher-ranked than themselves. The effect of this is to smooth out the competition effect and so remove the somewhat abrupt emergence of competition that occurs in the Engagement model.

Rank Difference model

This model makes no attempt to explicate the competition that is implied by priority of access. It assumes simply that competition is linearly related to rank difference as a consequence of the linear increase in interveningly-ranked animals. The model starts from Table I and incorporates competition simply by dividing the cell figure by the rank difference between groomer and groomee when the latter is the higher-ranked. Cell values are then scaled up so that each individual gives and receives 100 units of grooming as in the previous models.

This model embodies a scepticism towards the possibility of modelling the actual procedure by which priority of access effects emerge. It assumes that the process is sufficiently complex that the summary variable of rank difference will be the most effective predictor. It can be seen in Fig. 7.3.

Figure 7.2 Grooming distribution predicted for eight-female group (Interference model)

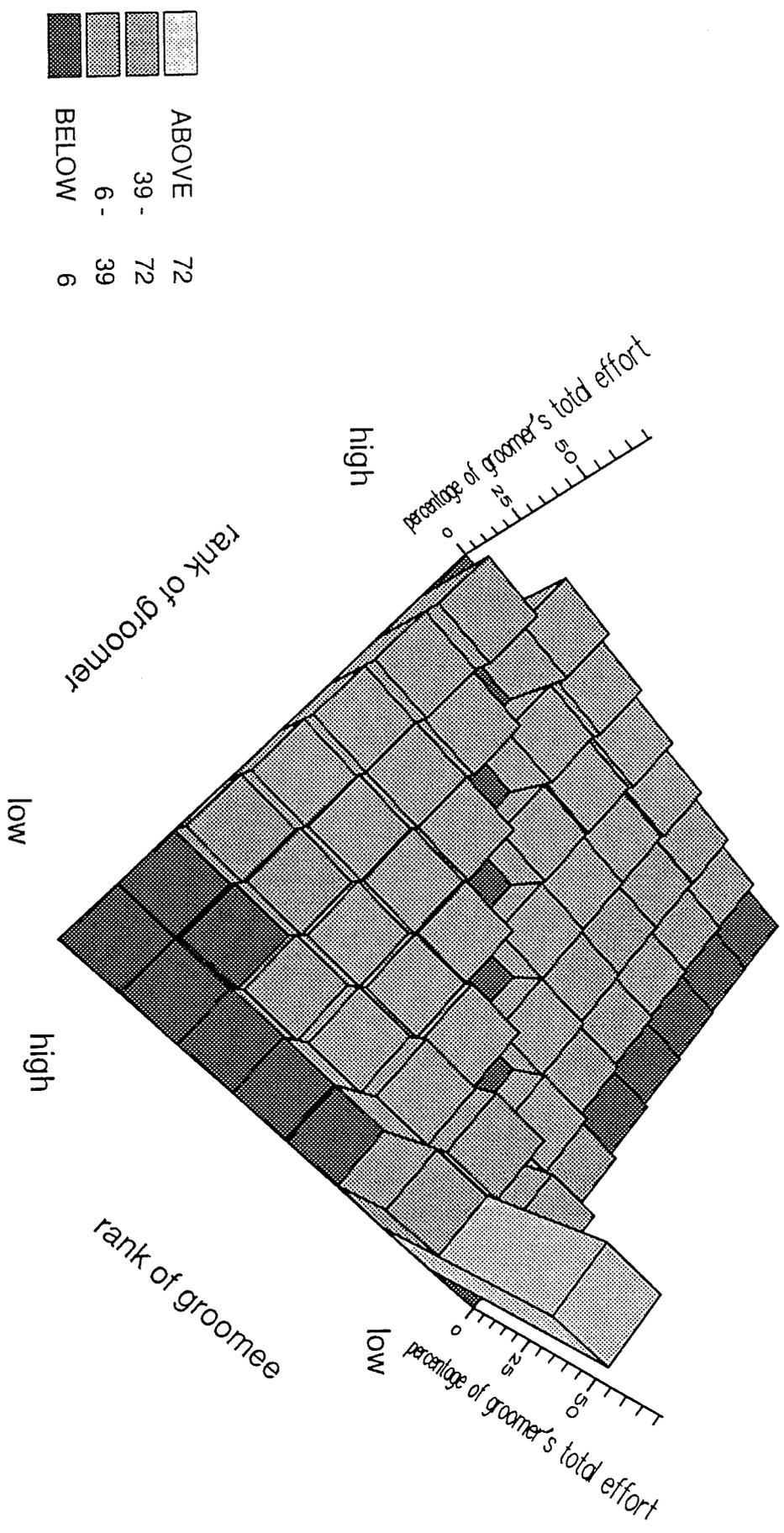
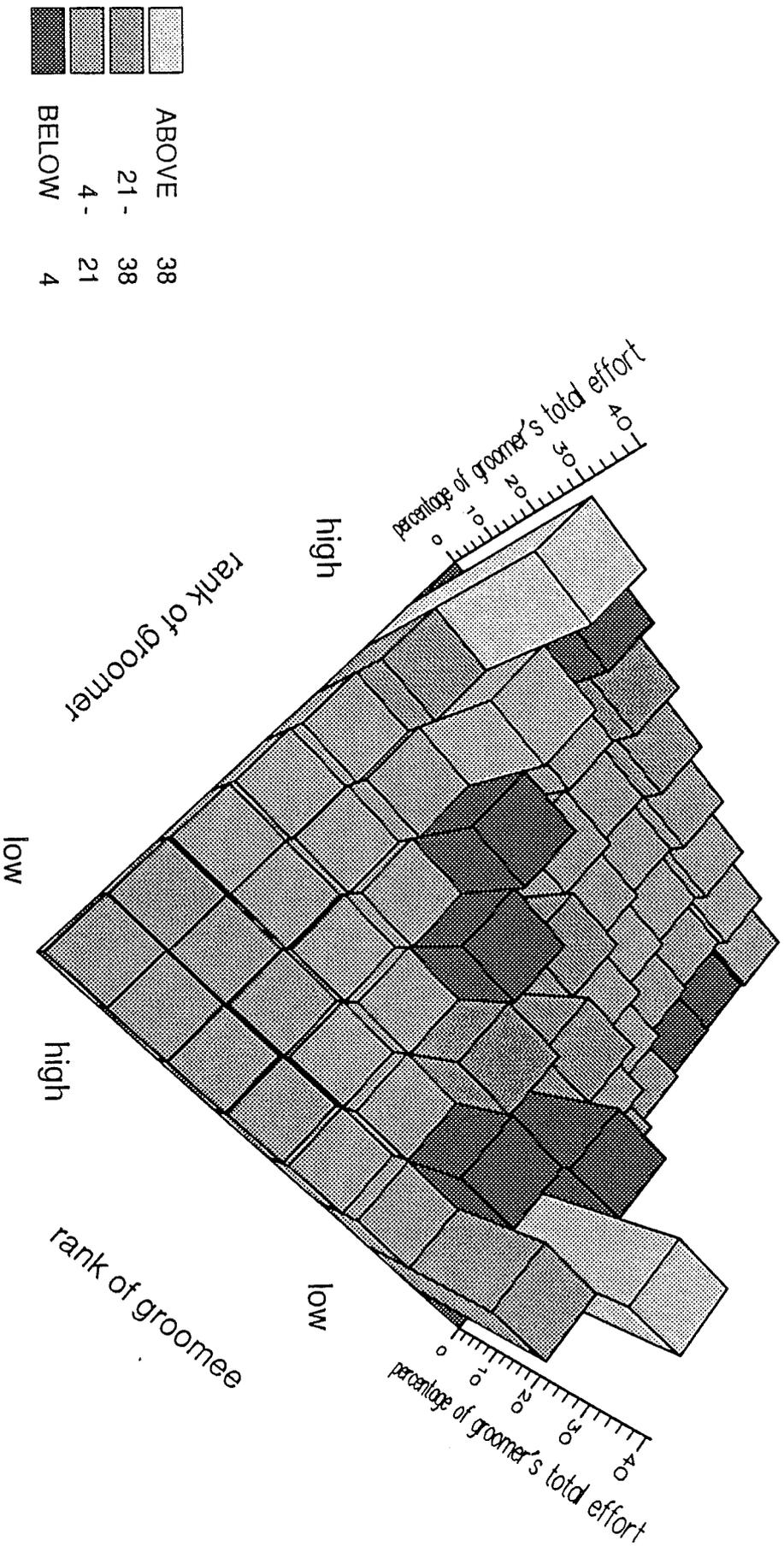


Figure 7.3 Grooming distribution predicted for eight-female group (Rank Difference model)



Notes on the Models

Priority of access models attempt to explain known aspects of cercopithecine grooming, the most notable of which is the strong grooming relationship between adjacently-ranked animals. It should be noted, however, that this phenomenon is assumed to be partly a consequence of the tendency of closely ranked animals to be close kin. Once this aspect is removed from the model then there is no guarantee that individuals will most frequently groom those ranked directly above them. As previously mentioned, it requires that the difficulty in reaching higher-ranked animals is greater than their attractiveness as grooming partners. An inspection of the matrix plots in Figs. 1-3 reveals that only the Rank Difference model shows the diagonal ridge characteristic of grooming between adjacent pairs. In the other models the effects of rank difference interact with those of absolute rank creating a surprisingly complex landscape. Seyfarth's (1977) claim is that the principles of priority of access lead to high-rankers grooming other (not necessarily adjacent) high-rankers and that competition emerges as one moves down the hierarchy such that mid-rankers must groom those adjacent to themselves. Broadly, this is the picture that emerges from the Engagement and Interference models.

Testing the Models

Notes on analysis

In keeping with previous work on priority of access modelling, the data used here are exclusively those relating to grooming between mature females. Thus ranks and rank differences are computed disregarding the juveniles in between matriarchs. For example, in MLK the rank of Desirre is 1 and the rank of Zilla (the beta female) 2, despite Desiree's three intervening children.

As noted in Chapter 6, *ad libitum* data is much less subject to bias when it concerns who is grooming whom rather than just frequencies of grooming. My tendency to be present both in the core and the periphery of the troop for the purposes of focal sampling, taken together with the relative simplicity of the grooming measure, resulted in data unlikely to show biases to which *ad libitum* protocols may be prone (Altmann 1974). To test this assumption, the scan and *ad libitum* grooming rates between kin, a large and therefore reliable data set, were examined for correlation. This measure proved to be highly significant for both the small troop ($r=0.49$, $p<.001$) and the large troop ($r=0.61$, $p<.001$). In addition, matrix correlation (see for example de Waal and Luttrell 1988; Hemelrijk 1990a,b) was used to compare the scan and *ad libitum* data presented in this chapter. Since

correlations were high for both troops (small: $Kr_{rw,av}=0.32$, $p=0.009$; large: $Kr_{rw,av}=0.35$, $p=0.001$) scan and *ad libitum* data have been pooled for analysis. Performing separate unpooled analyses on these data produces results that are consistent with those presented below but weaker.

Instances of grooming occurring in the context of agonistic interactions were excluded from this analysis. Incidents of grooming observed in the context of sexual consorts were also excluded but grooming of, or by, swollen but unconsorted females was included. Grooming in agonistic and consort contexts is not clearly an index of a stable relationship in the way that was discussed in this chapter's introduction. Grooming performed by individuals who were not present for the entire study period was excluded.

One of the most striking features of social organisation in primate groups is the great attraction that females show to new infants and the mothers of new infants. Such mothers enjoy a temporary increase in their rank (e.g. Weisbard & Goy 1976). At the commencement of the study presented here there were no infants in the troops under six months old and throughout the study period only five new infants were born. This is too small a number for a useful analysis and so, of these five mothers, three have been entirely excluded from the analysis on the basis that the rate at which they received grooming and the rank of the groomer greatly increased as a result. The remaining two mothers, alpha and beta ranked in MLK, did not show any such change and so have been retained in the interests of retaining a useful sample size. Whilst this is an inelegant solution, it constitutes the most effective use of the data available.

The inevitable confounding of kinship and dominance in female cercopithecines has already been discussed. This problem was ameliorated to some extent by the 'coup in STT, discussed in Chapter 5, and an earlier, similar coup in MLK. Grooming between the two mother-daughter pairs in each troop was excluded from the analysis on the basis of the typically strong nature of this bond (e.g. Dunbar 1984). The genealogy of the larger troop was incomplete and three pairs of adjacent females existed who could potentially be sisters. Grooming between these individuals was left in and, in possible compensation, grooming between the single sister pair in the smaller troop was also left in.

Whilst the models discussed earlier predicted grooming in many, and sometimes all, of the cells in grooming matrices, the matrices of observed grooming contained more empty cells than filled. Because of the resulting non-normality, non-parametric statistics have been used for the majority of analyses.

Results: Preliminary analyses

Before testing the data against priority of access models some preliminary analyses were performed. It has already been shown in Chapter 6 that neither network size nor grooming frequency differed significantly between troops. Those results made no reference to rank however. The mean difference in rank between groomer and groomee is shown in Fig. 7.4. Females in MLK groomed an average 2.4 ranks higher than themselves whilst in STT the figure is 0.6 ranks below. A Mann-Whitney U test proved this difference to be highly significant ($z=5.43$, $N=252$, $p<0.0001$). Note that the rank difference measure ignores the effect of absolute rank on grooming. Much of the effect results from the grooming efforts of low-rankers as can be seen in Fig. 4. Low ranking females in MLK groomed nearly five ranks above themselves whilst those in STT groomed others of roughly the same rank as themselves.

An overall picture of how grooming differed between the groups can be obtained by summing grooming incidences in each of the four quarters of the troops' respective grooming matrices. These results can be seen in Table 7.2. The behaviour of lower ranking animals discussed above is revealed in sharp contrast here. In STT they were mostly grooming those of their own rank, in MLK, those of high rank.

Results: Fit of the models

Observed grooming matrices are shown in Figs. 7.5a and 7.5b. The row-wise matrix correlations of these observed matrices with the expected matrices generated by the models is given in Table 7.3. It can be seen that the correlations tend to be greater for STT. However, the difference between correlations is not significant for any pair, even that between the Engagement model of STT and the Rank Difference model of MLK ($Z=0.63$, $N=451$, $p=0.64$).

An alternative approach to explaining grooming distributions

Alternative methods available for analysing the factors that determine grooming distributions are correlation and multiple regression. Multiple regression is a method that has been used by de Waal (1991), for example, in investigating the correlates of co-drinking and aggression in rhesus monkeys. Multiple regression

difference in rank
between groomer and
groomee

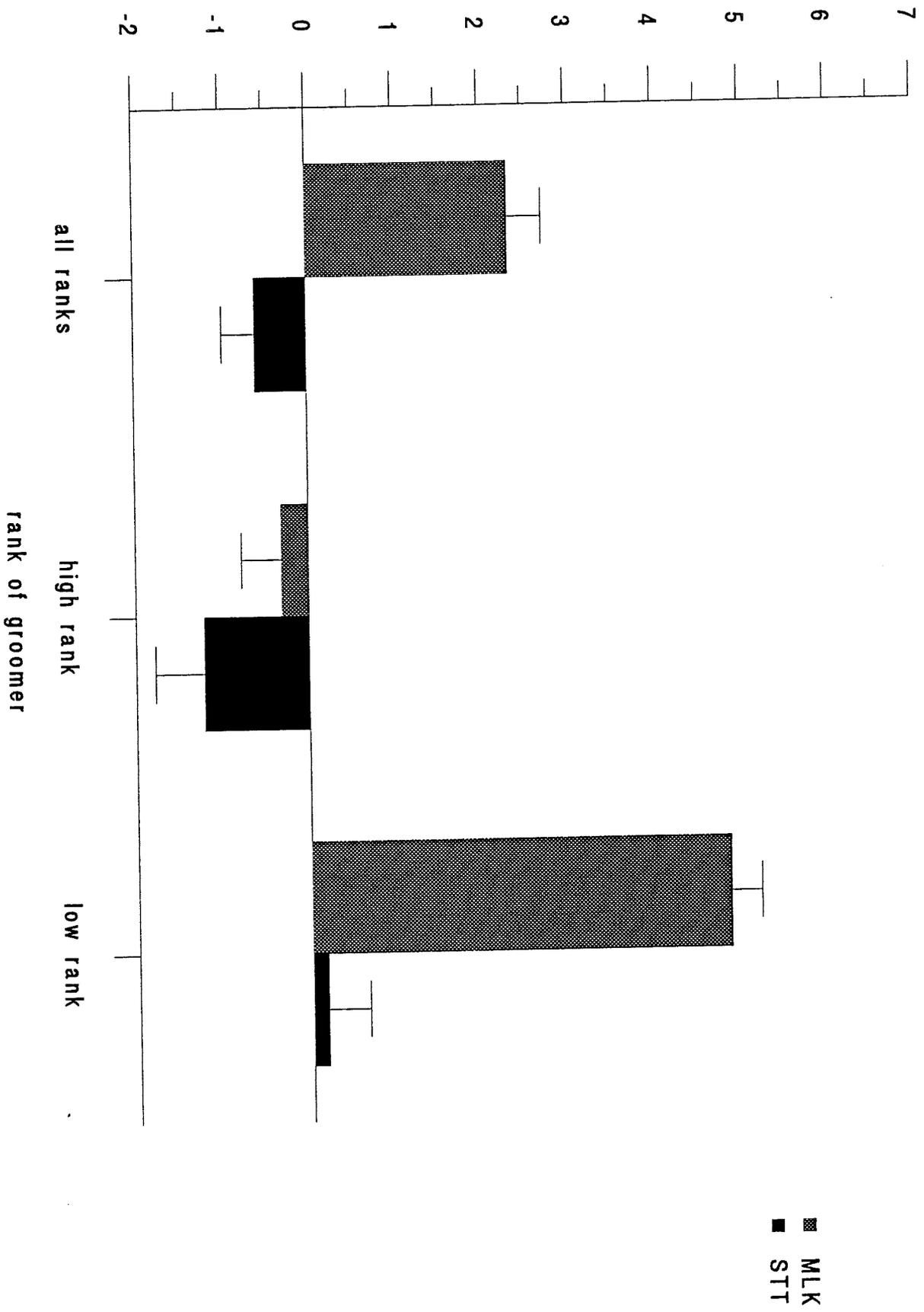


Figure 7.4 Mean difference in rank of groomer and groomee for; all ranks; top 50%; bottom 50%

Table 7.2 Grooming matrices collapsed into 4 quadrants: data are percentages of total grooming in the groups

MLK

| | | groomee's rank | |
|----------------|------|----------------|-----|
| | | high | low |
| groomer's rank | high | 39 | 11 |
| | low | 44 | 7 |

STT

| | | groomee's rank | |
|----------------|------|----------------|-----|
| | | high | low |
| groomer's rank | high | 51 | 13 |
| | low | 11 | 25 |

Figure 7.5a Grooming matrix of MLK

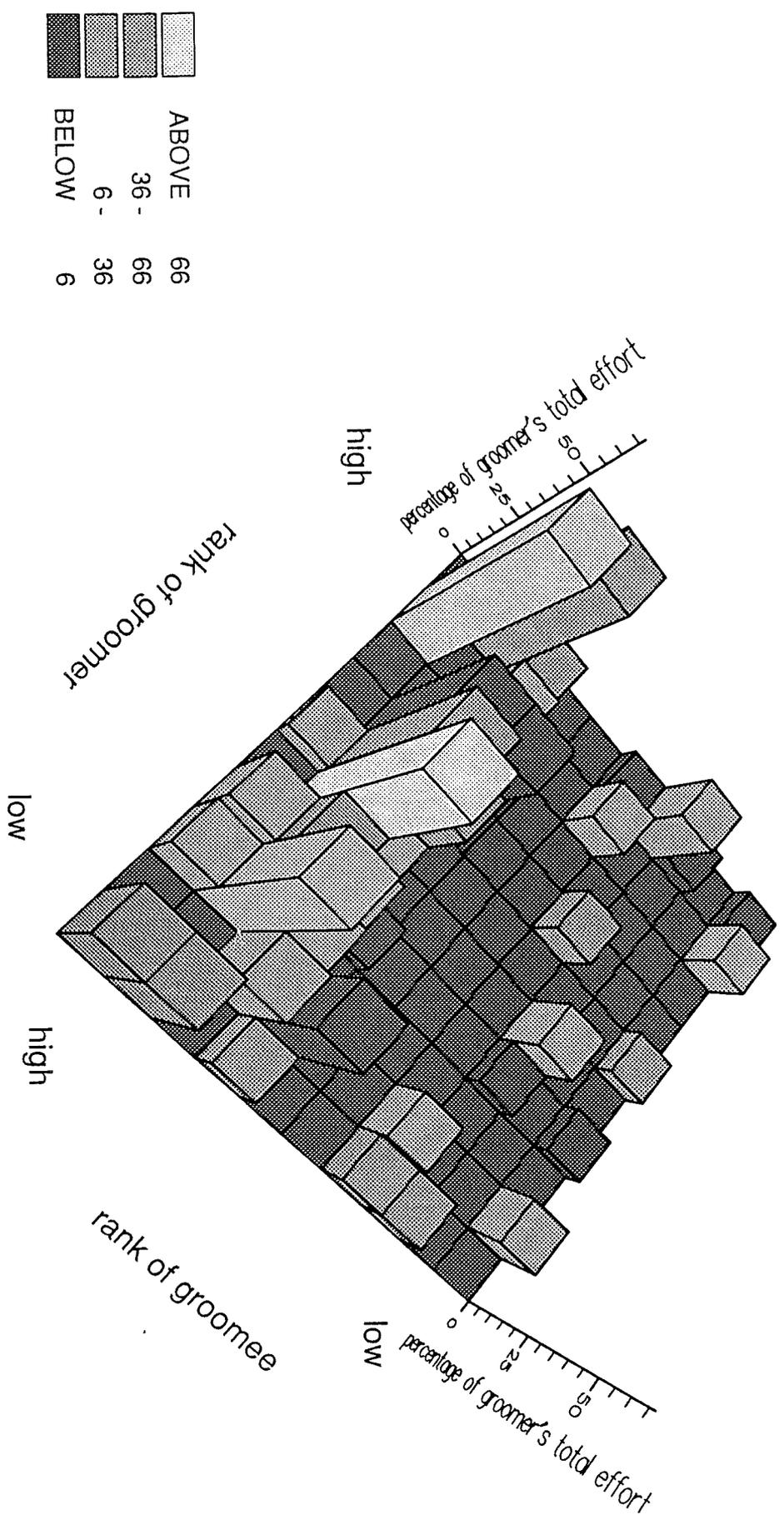
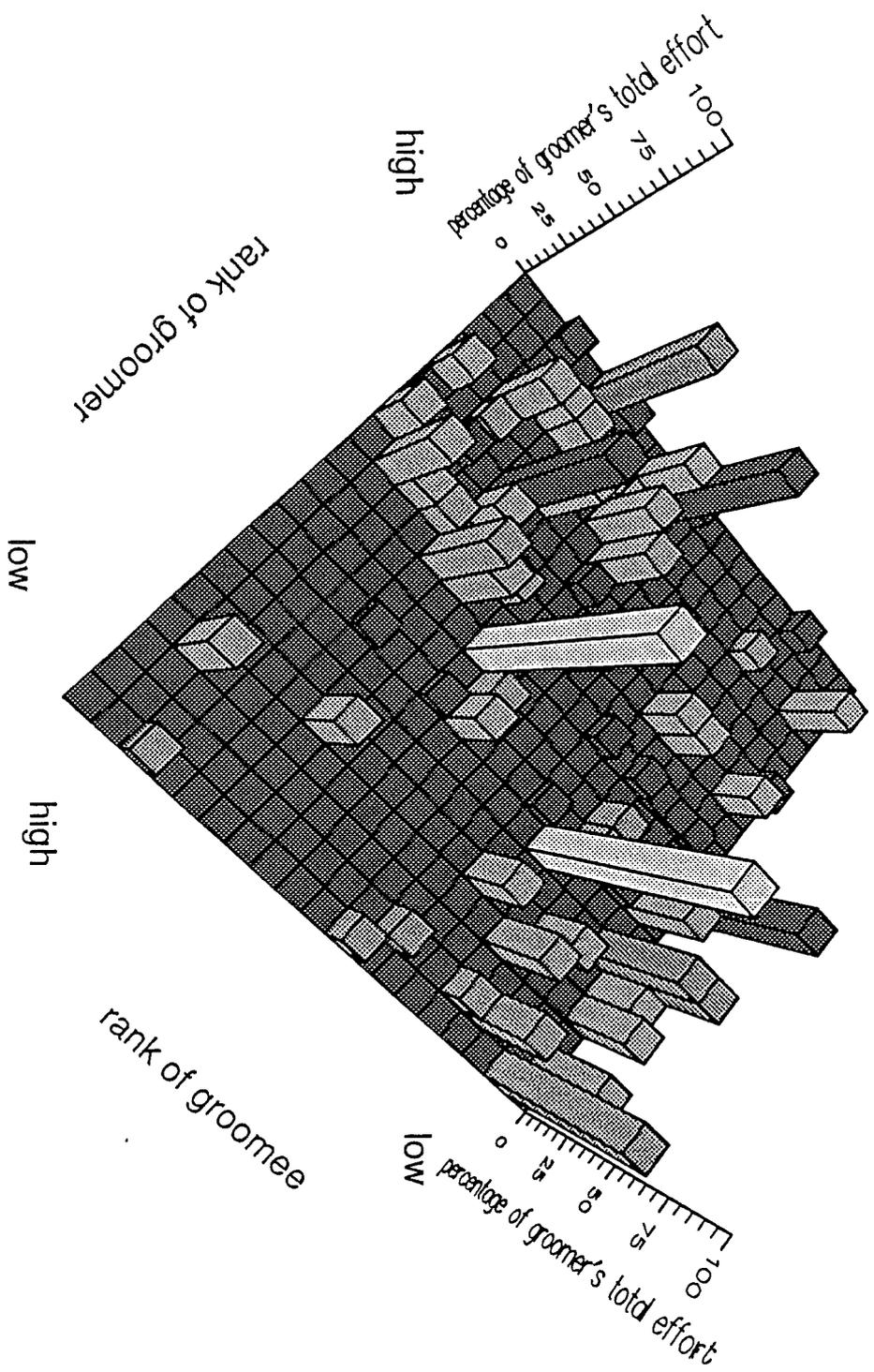


Figure 7.5b Grooming matrix of STT



| | | | |
|---------|------------|-------------|----------|
| BELOW 9 | BELOW 9-54 | ABOVE 54-99 | ABOVE 99 |
|---------|------------|-------------|----------|

Table 7.3 Matrix correlations of observed grooming matrices with those predicted under each of the three models.

| | small group | large group |
|-----------------|-------------------------------|-------------------------------|
| Engagement | $Kr_{rw,av} = 0.07$ (p=0.31) | $Kr_{rw,av} = 0.15$ (p=0.004) |
| Interference | $Kr_{rw,av} = 0.02$ (p=0.45) | $Kr_{rw,av} = 0.14$ (p=0.006) |
| Rank Difference | $Kr_{rw,av} = -0.08$ (p=0.71) | $Kr_{rw,av} = 0.09$ (p=0.050) |

can be used to investigate whether the factors that predict grooming vary between, say, a large and a small group. Furthermore, the *number* of different factors that are required to explain a given level of variance can be counted. We might conceive of this as an index of the complexity of a behaviour or system.

The non-normality of the data (many cells of the grooming matrices contained zeroes) required analysis to begin with non-parametric correlations. Both troops were examined for the effects of (i) groomer's rank and (ii) distance in rank between groomer and groomee. 'Distance' is to be distinguished from 'difference'; the former being the same as the latter but with the sign (representing grooming up, or down, the hierarchy) ignored.

The results of this analysis show that rank of groomee was a useful predictor of grooming in MLK ($r_s = -0.37$, $N=90$, $p=0.0003$), whilst distance of rank between groomer and groomee is not ($r_s = 0.14$, $N=90$, $p=0.18$). Exactly the opposite case is found in STT; rank distance is a useful predictor ($r_s = -0.21$, $N=361$, $p=0.00009$) whilst rank of groomee is not ($r_s = 0.04$, $N=361$, $p=0.46$).

In order to extend these results to a quantity more explicitly related to complexity, namely *variance explained*, a parametric analysis was required. Multiple regression assumes normality of the dependent variable and since many cells in the grooming matrix for each troop were either one or zero, blocks of cells in the matrix were collapsed to generate this normality. The criterion determining the extent of this process was that the resultant cell entries should have at least a greater than five percent chance of coming from a normally distributed population (as tested by a Kolmogorov-Smirnov test). The dimensions of the resultant matrices were five by five for both groups' data, 16 old cells being collapsed into each new one in STT, and four being collapsed in the small. This process eliminated the problem of many of the cells containing zeroes, and, whilst not ensuring normality, improved the data with regard to the assumptions of multiple regression.

The blocks of cells to be collapsed were generated from the top left corner, i.e. high-ranked groomers and groomees. In STT, cells at the right edge and bottom edge had blocks which were smaller than the others (because of the non-divisibility of a 19 by 19 matrix). The collapsed values in these were therefore scaled accordingly. Cells on the diagonal of the new matrix in each troop were also scaled up, representing the fact that they had contained the zero-cells of the cross-section of an animal's grooming row with its groomee column.

The processes described above involved the homogenising of data from different though closely-ranked animals. To ensure that spurious results did not arise from this arbitrary partitioning, non-parametric correlations were performed on these collapsed data by way of comparison with the results from the original data

Table 7.4 Multiple regression of grooming frequency using the factors of groomer's rank and rank difference between groomer and groomee

| | small group | large group |
|---------------------------------------|-------------|-------------|
| N | 25 | 25 |
| rank R | -.64 | -.17 |
| adjusted rank R ² | .41 | .03 |
| significance of rank | .0007 | .35 |
| rank distance R | .02 | -.50 |
| adjusted rank distance R ² | .0003 | .25 |
| significance of rank distance | .91 | .01 |
| total R | .64 | .53 |
| adjusted total R ² | .36 | .22 |
| significance of total R | .003 | .03 |

Figure 7.6a Correlation of grooming with rank block of groomee in MLK

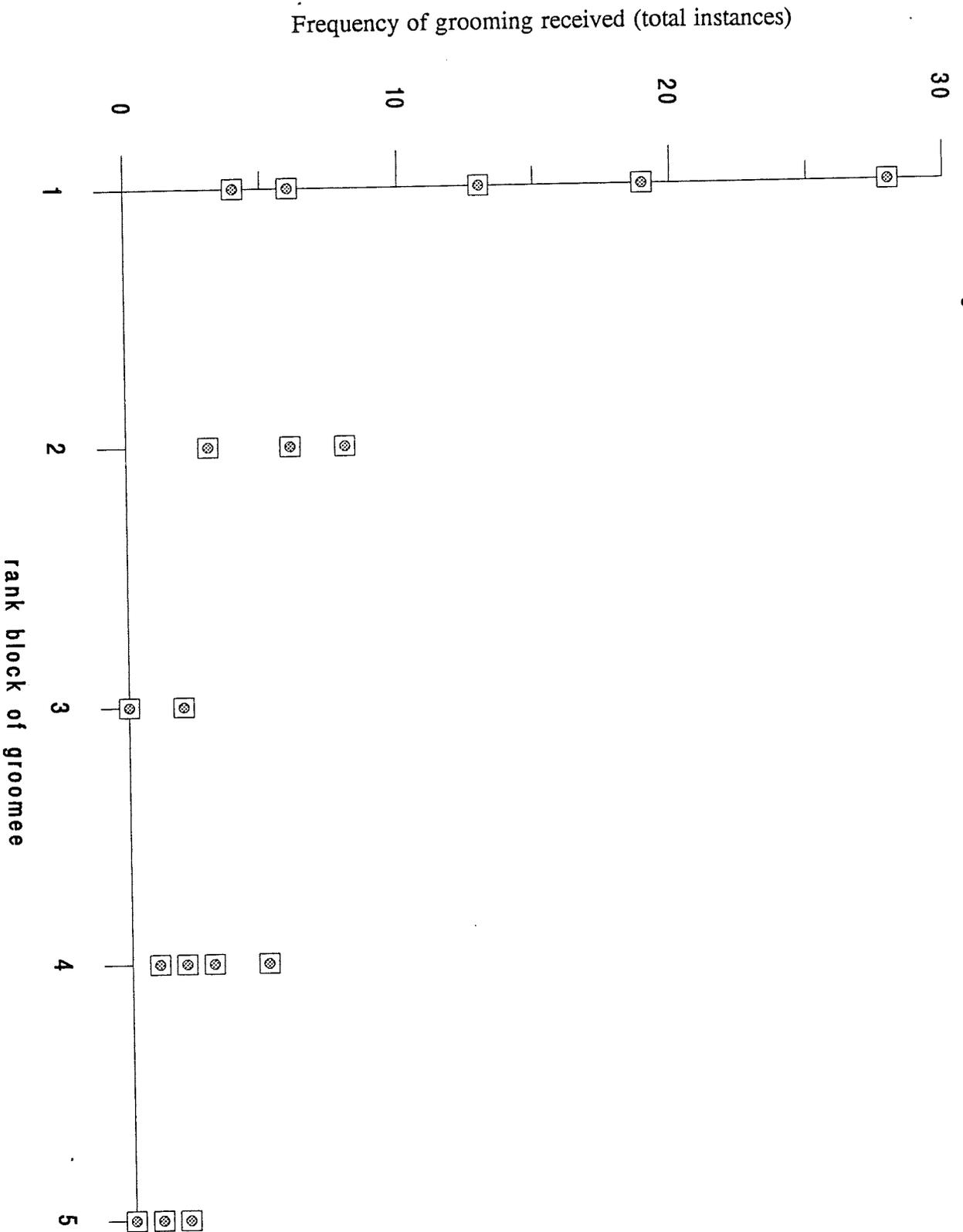


Figure 7.6b Correlation of grooming with rank block of groomee in STT

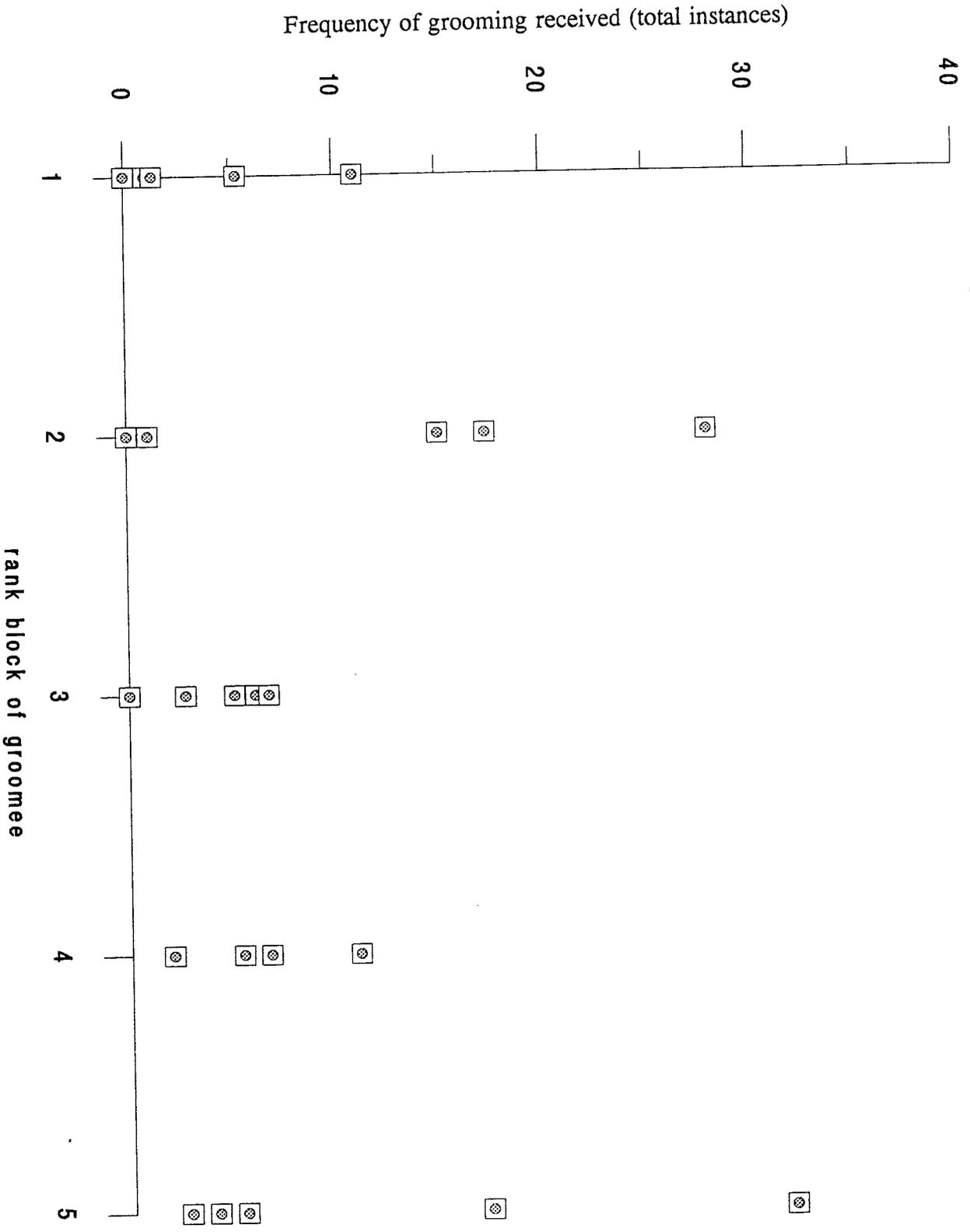
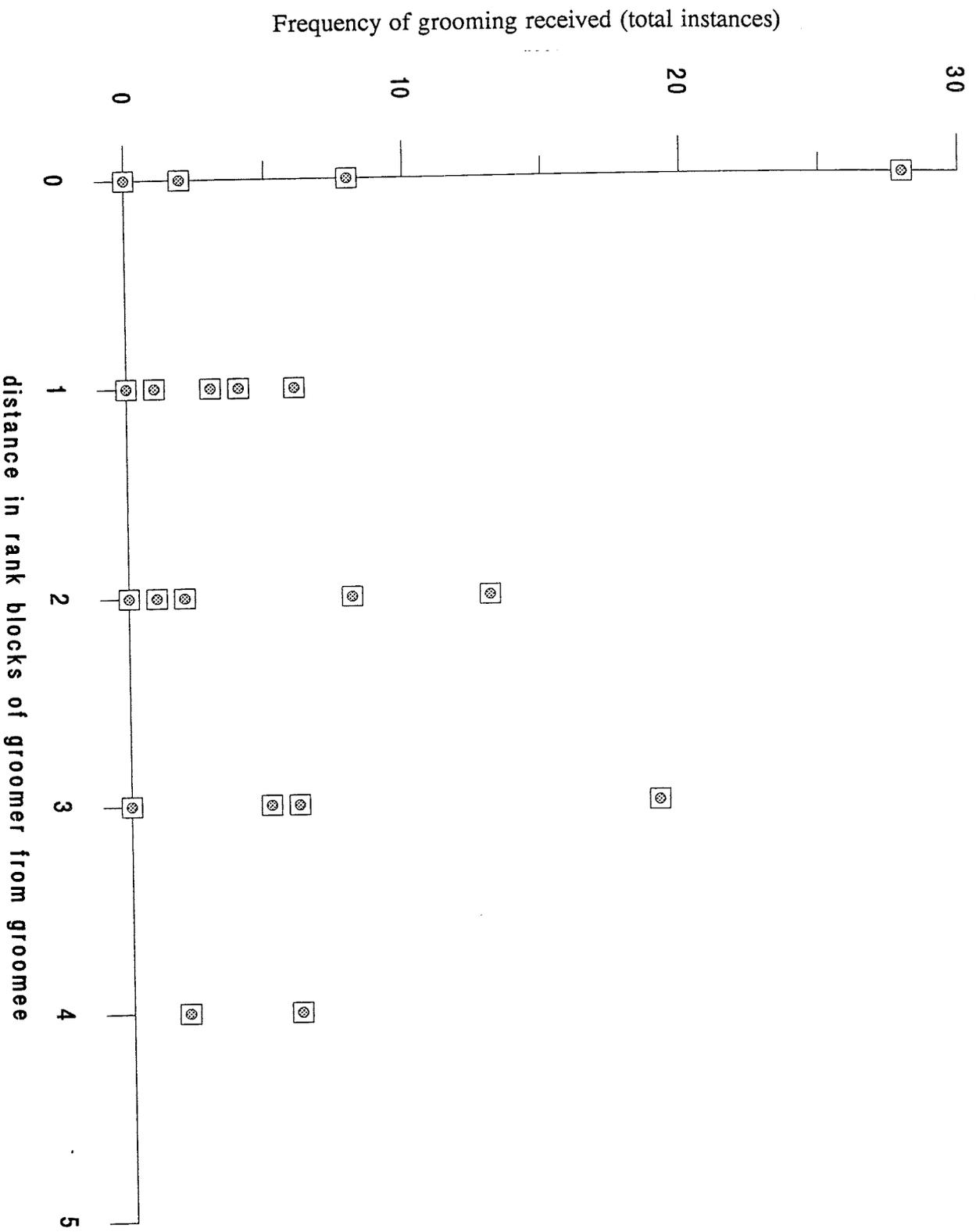


Figure 7.7a Correlation of grooming with distance in rank of groomer from groomee in MLK



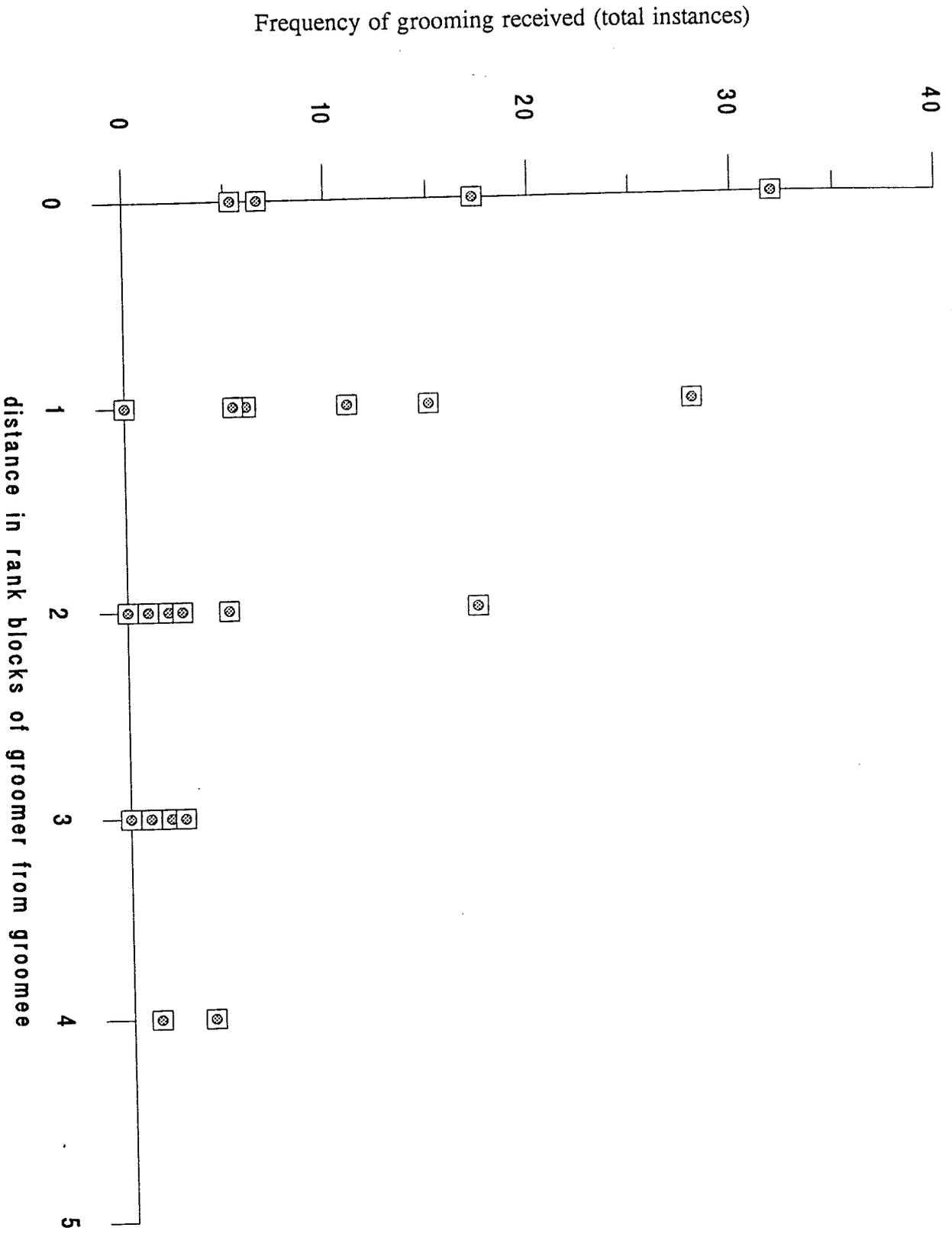


Figure 7.7b Correlation of grooming with distance in rank of groomer from groomee in STT

given above. The effect was the same as that found previously; rank of groomee was a useful predictor in MLK ($r_s = -0.67$, $N=25$, $p=0.0002$) whilst rank difference was not ($r_s = 0.10$, $N=25$, $p=0.64$), whilst in STT rank difference was a useful predictor ($r_s = -0.65$, $N=25$, $p=0.0004$) but rank of groomee was not ($r_s = 0.25$, $N=25$, $p=0.22$).

On the basis of these results, a multiple regression was performed, the results of which are presented in Table 7.4 and show support for those presented previously.

Scatterplots for the above correlations are shown in Figures 7.6a, 7.6b, 7.7a and 7.7b where the linearity of the successful predictor in each of the troops is available for inspection. It can be seen from Figure 7.6a that in MLK only the top two blocks of rank receive higher grooming. From Figure 7.7b it can be seen that in STT, differences in rank of more than three rank blocks do not seem to affect grooming rates.

Finally, it should be noted that (as Table 7.4 shows) the two factors combined explain a higher amount of the variance of grooming in MLK than in STT (though in each troop the combined effects are close or equal to the effect of the best single predictor). It is assumed that to explain the variance in STT to an equal degree to that in MLK, additional factors would have to be added to the regression equation.

Discussion

Evaluation of priority of access models

No clear picture emerges concerning the relative validity of the priority of access models since there are no significant differences in the success of the models in either of the groups. The variance of success in modelling MLK is greater than for STT. For example, the Rank Difference model performs much worse than the Engagement model with regard to MLK since the former, unlike the latter, stringently denies even mid-rankers much access to high-rankers.

Overall, it is notable that data from STT fitted all the priority of access models better than did that from MLK. With a sample size of two troops, the general applicability of this result is difficult to gauge. Differences may reflect peculiarities of the particular troops under study. Another possibility is that at any particular sample size, priority of access effects in small groups are more prone to noise generated by individual differences other than rank. The third and most interesting possibility though, is that the extent or nature of priority of access

genuinely varies according to group size.

The priority of access models do not appear to increase our understanding of grooming patterns over and above that which is evident from Fig. 7.4: low-rankers have access to high-rankers in MLK but not in the large. The ostensive advantage of priority of access models is that they incorporate the possible interaction of absolute rank and rank difference in grooming. Perhaps, however, this effect is minimal. It is possible that the effect would appear with larger sample sizes, but the present analysis suggests a limit to the precision of such models. As such, the modelling attempt has not offered much insight into the mechanism underlying the observed grooming distribution.

The application of multiple regression, however, proved extremely successful in discriminating the factors determining grooming patterns in the two troops. It is possible that this is because it is less ambitious in its precision of modelling. Seyfarth's (1977) review of female grooming in Old World Monkeys suggests that its essential features are the correlation of rank with the amount of grooming received and the high incidence of grooming between adjacently-ranked animals. Note that there is a certain amount of antagonism between these phenomena. Cheney & Seyfarth (1990) suggest that these effects are generated at different points in the dominance hierarchy, with the high-rankers generating the rank-with-grooming correlation and the mid-rankers generating the adjacency-with-grooming correlation. They present data on vervet monkeys in support of this.

High, mid and low rank are expressions relative to the size of a hierarchy. It is a characteristic of all the priority of access models presented in the current chapter that the absolute size of the grooming matrix used may affect the predicted grooming distribution non-negligibly. This, along with the clear dissociation across the troops of the two features of grooming discussed above, undermines the viability of making predictions about grooming distributions without the qualification of troop size.

It should also be noted that the quantities of rank and rank difference, though linear themselves, may not exert influence over grooming in a linear manner. Thus from Fig 7.6a it can be seen that in MLK only the top two ranks receive higher grooming. This might mean that attractiveness is not linearly related to rank and that there is a super-attractive elite at the top of the hierarchy. From Fig. 7.7b it can be seen that in STT, differences in rank of three blocks do not affect grooming rates. This might correspond to a ceiling effect of interference by higher ranked animals or a floor effect of an animal's estimation of the worth of trying to groom so high above itself.

Two methods for predicting the structure of grooming relationships have

been employed in this chapter: the priority of access models are best characterised as bottom-up causal explanations and the multiple regression analyses as top-down descriptions. Reductonist dogma holds that the lowest level of analysis practicable is always to be preferred since this offers a more comprehensive account of a phenomenon. However, in the present case it is the top-down approach that proves to be the most illuminating. Obviously, the kind of 'explanation' it provides will be unsatisfying regarding a dynamical approach to social structure; the kind exemplified by priority of access. The dynamical aspects on which models in this chapter (notably the Interference model) might have capitilised are the non-linearity of the effects of rank and rank difference and the interaction between these factors. The multiple regressions are certainly limited by their assumption of linearity since Figs. 7.6a and 7.7b suggest this is contravened. Since the dynamical approach is better placed to account for this, and yet the proposed models fail to do so, we must assume that the premises of the models are incomplete. A new generation of models is thus required.

What the current data suggest is that group size must be included as a factor in the basic premises of any model of the processes underlying grooming structure. It is difficult to see how a set of premises that does not explicitly include group size or a factor directly related to it could produce such qualitatively different grooming distributions as are found in the study troops. Factors related to group size that might be relevant include interaction rate and troop density, both of which were significantly higher in STT (see chapter 10). Ideally this study would have included several groups of variable size. Group size itself could then be entered into a multiple regression equation, its interaction with the two original factors assessed, and plausible vehicles for this interaction suggested.

Group size is so basic a characteristic of an animal's social environment that it might be expected to exert its influence pervasively through many avenues, both behavioural and demographic. It is even possible that cognitive factors come into play and that group size is a factor incorporated by baboons themselves in their grooming decisions. It is under these circumstances that the top-down approach gains validity, where complexity is great and the bottom-up dynamical approach is swamped by the number of factors needing to be accounted for, some of which may be unobservable (e.g. representations by individual animals). The study of behaviour, like biology generally, must have recourse to various levels of description because of the complexity of its subject matter. As such, the 'descriptions' generated by the multiple regression, opaque though they are to mechanism, remain valid findings: group size affects grooming relationships and thus social structure at large.

Large versus small troops

Regardless of the models' failure to illuminate differences in grooming between large and small troops, such differences clearly do exist as demonstrated by the multiple regression method. What insight does grooming behaviour give us into the social dynamics of small and large groups?

As we have seen, neither grooming network size nor frequency of grooming increase significantly in STT. This measure could be taken to imply that, behaviourally, individuals in STT are "living in a small troop" of their own construction. Such an effect would be in keeping with the (albeit temporary) 'class structure' that has been reported in macaques (de Waal 1986). In such a case, the differences in grooming distribution across troops result from the strategies that individuals decide to use rather than in the effects of group size as such.

Cognitively and socially this is extremely interesting. The equivalence of network size in STT and MLK, taken together with the tendency of individuals in STT to form relationships with those close in rank, might be taken to indicate more complexity in a troop of 80-plus baboons than an individual can deal with. At any rate we must conclude that as troop size grows, baboons find that the bonds between themselves and the majority of other troop members become, of necessity, weaker. This is expected to increase the unpredictability of interaction outcome between dyads and is thus a possible source of social complexity. Dunbar (1992) has shown that across primate genera, neocortex ratio is correlated with group size. He suggests that the cognitive complexity implied by this brain growth is an adaptation to the growth of social complexity with group size. Unpredictability of interaction outcome might well be the selector for heightened intelligence that underlay this trend. If this is so then, given that evolutionary change is driven by proximate selectors, we might expect to see such trends across differently sized groups of the same species. One advantage of the multiple regression method used here is that the overall R^2 term provides a figure for the amount of variance in a variable (in this case grooming) that a given number of factors will explain. This figure is higher in MLK. The amount of unexplained variance in either troop that is potentially predictable by factors not included in the regression equation (as opposed to variance which is 'simply noise') requires further analysis and the number of factors required for explaining a given amount of the variance can be used as an index of the complexity in that troop. It should also be noted that the factors of rank distance and absolute rank differ in their own inherent complexity, the former

being constant for any individual, the latter being particular to the dyad in which that individual is engaged.

Note that the regression technique, unlike the Engagement and Interference models, makes no attempt to model the grooming distribution by reference to the way competition is mediated (i.e. *events*) but instead uses the relatively permanent, *relational* variables of rank and rank difference as variables. Whilst a better model of how competition occurs might improve the fit to data it is clear that in the case of grooming, a useful amount of its distribution can be explained solely by reference to these factors.

This bears on the question of whether primates may be 'social psychologists' (e.g. Humphrey 1983, Whiten & Byrne 1988). If we, as observers, are able to find good predictors to explain the social world of these animals then, equally, the animals themselves may benefit from incorporating them into their decision making. Dasser (1988) has shown experimentally that macaques can use the concept of certain kinds of social relationship to obtain a reward. Using their extensive data on vervet monkeys, Cheney and Seyfarth (1990) argue that a case can be made for the representation of social relationships, *as concepts*, by these animals. One value of the kind of work presented in this chapter is that it brings the attention of cognitive ethologists to the kind of representations that we might expect our subjects to hold. If relationships allow us to best predict behavioural outcomes and we know that primates can discern such relationships, these may represent the most powerful predictors for the animals themselves. As such there may be a useful accordance between the constructs we generate to explain primate behaviour and the form we would expect primates' social cognition to take. This brings subjects and scientists into closer agreement on the kind of representations that help explain behaviour.

Chapter 8: Proximity as a Measure of Cliquishness

Introduction

Various studies have shown that, in Old World monkeys, proximity correlates well with other markers of affiliation such as grooming and support (e.g. Cheney 1977; Dunbar 1980). This chapter uses the proximity variable to cluster animals, assuming that their spatial deployment offers an indication of the overall deployment of relationships. Grooming, as an indicator of relationships, has already been considered. Like grooming, proximity indexes affiliation but there are important differences. One is that many animals can be proximal to another at once which might lessen the kind of priority of access effects already discussed. Another is that proximity is a *graded* state: an animal can keep a distance between it and its desired object of affiliation that is commensurate with either its attraction or fear: this contrasts with the all or nothing character of grooming. A third important difference is that animals can associate together in this way without interrupting feeding or moving.

The problem with using proximity as an index of affiliation is that it is a noisy variable, influenced by a lot of 'incidental' proximity. The analyses performed here address the global aspects of troop spatial deployment rather than the specific relationships of individuals.

The aim of this chapter is to explore the possibility of sub-structure in the two troops. In Chapter 7 the possibility was advanced that STT individuals might be 'living in a MLK-sized troop of their own making'. Whilst individuals clearly have networks of affiliates, if these are peculiar to each individual then no sub-trooping would appear at the group level since the networks would all overlap. However, cliquishness, in which a set of animals all share the same network, thereby producing a clear demarcation between those in or out of the clique, might well show up in the troop spatial structure. The quantitative analysis of cliquishness in grooming is an issue that has been explored in depth by Sade (1972). The general point to be made here, however, is that clique formation could reduce complexity because in a clique all animals are mutual friends and an individual interacting with a friend is less likely to have to interact with 'friends of friends'. Like rank hierarchies, cliquishness is a group level phenomenon that can result from the purely personal goals of individuals working at a local level.

I have chosen to concentrate on natal (i.e. female and immature) group members only, since one plausible existing structure upon which cliquishness might

form is the existing matrilineal dominance hierarchy.

Sampling Methods

All data used in this analysis were collected under the scan protocol previously discussed. To recap: four grades of proximity were recognised; contact, arms reach, within five metres and nearest. The first three grades, being measures of absolute distance, do not need further explanation. For the purposes of this chapter 'nearest' data is disregarded so as not to mix absolute and relative measures of distance.

Analysis Methods

For ease of analysis, a compound of the various proximity grades was sought in which the salience of the more proximal grades was recognised by weighting. The weighting chosen is based on an inverse relationship with the areas of space which each proximity grade specifies. The rationale underlying this is that the proximity grades specify a set of concentric bands around a focal of increasing area. As the area increases, so does the probability that an apparently associating animal is merely proximal to a focal through chance alone (e.g. it is on its way to a food patch).

This measure departs somewhat from that used by Smuts (1985), who used distances rather than areas. There is a certain amount of arbitrariness in the method used in any case since distance, area, etc doubtless relate to the more complex construct of affiliation in complex ways. An earlier analysis undertaken of the data presented here used the inverse of the frequencies with which animals were found within the various grades to determine weighting. This method proved to be methodologically unsound but is mentioned here since the much more moderate weighting that resulted (14: 2.2: 1) produced results that were not significantly different from those presented below. Smuts' (1985) method produces weights between these two ranges and so we can assume that for the purposes of these data the weighting method is not crucial.

Weighting was calculated as follows. Baboons were conventionally assumed to be 0.5m diameter and to have an arms reach of 0.5m. For each proximity grade, the area in which a proximal baboon's midpoint could be in to achieve that proximity grade was calculated. Thus, to be in contact with the focal, a proximal

baboon's midpoint would have to be within 0.5m of the midpoint of the focal. This describes a circle of 0.5m radius and therefore 0.79m^2 area (area = $\pi \cdot r^2$).

The grade of arms reach describes a circle of 1m radius and therefore 3.14m^2 . Since this grade further stipulates that the animal is not in contact, the resulting ring has an area of $3.14 - 0.79 = 2.36\text{m}^2$. Likewise the grade of 5m between animals describes a circle between their midpoints of 5.5m radius resulting in a ring of 91.89m^2 . These calculations are illustrated pictorially below.

The ratio of these areas is 1 : 2.98 : 116.32. Weights for the salience of each grade in affiliative terms are simply the inverse of these, thus, five metres weight = 1.0, arms reach weight = 39.0, contact weight = 116.3.

As a test of the validity of combining data from the three grades, the frequencies of instances of the grades were correlated for dyads of all animals. The correlation matrix for the grades is presented in Table 8.1. Only dyads for which there are data from both grades were entered into correlations.

Cluster Analysis

Proximity matrices were subjected to several clustering techniques. The first of these was an agglomerative clustering process using an average linkage criterion. This process is a simple one in which a number of individual elements (baboons in this case) are agglomerated in a number of steps equal to the number of elements. The algorithm searches for the two elements which are most similar (most proximal in this case) and agglomerates them into a cluster. The process is then repeated for the next most similar dyad (with the cluster formed previously being treated as a single element). The average link criterion bears on the question of how to treat the multiple differences in similarity between points in one cluster and another. The average link criterion resolves this by taking the average distance between all cross-cluster dyads.

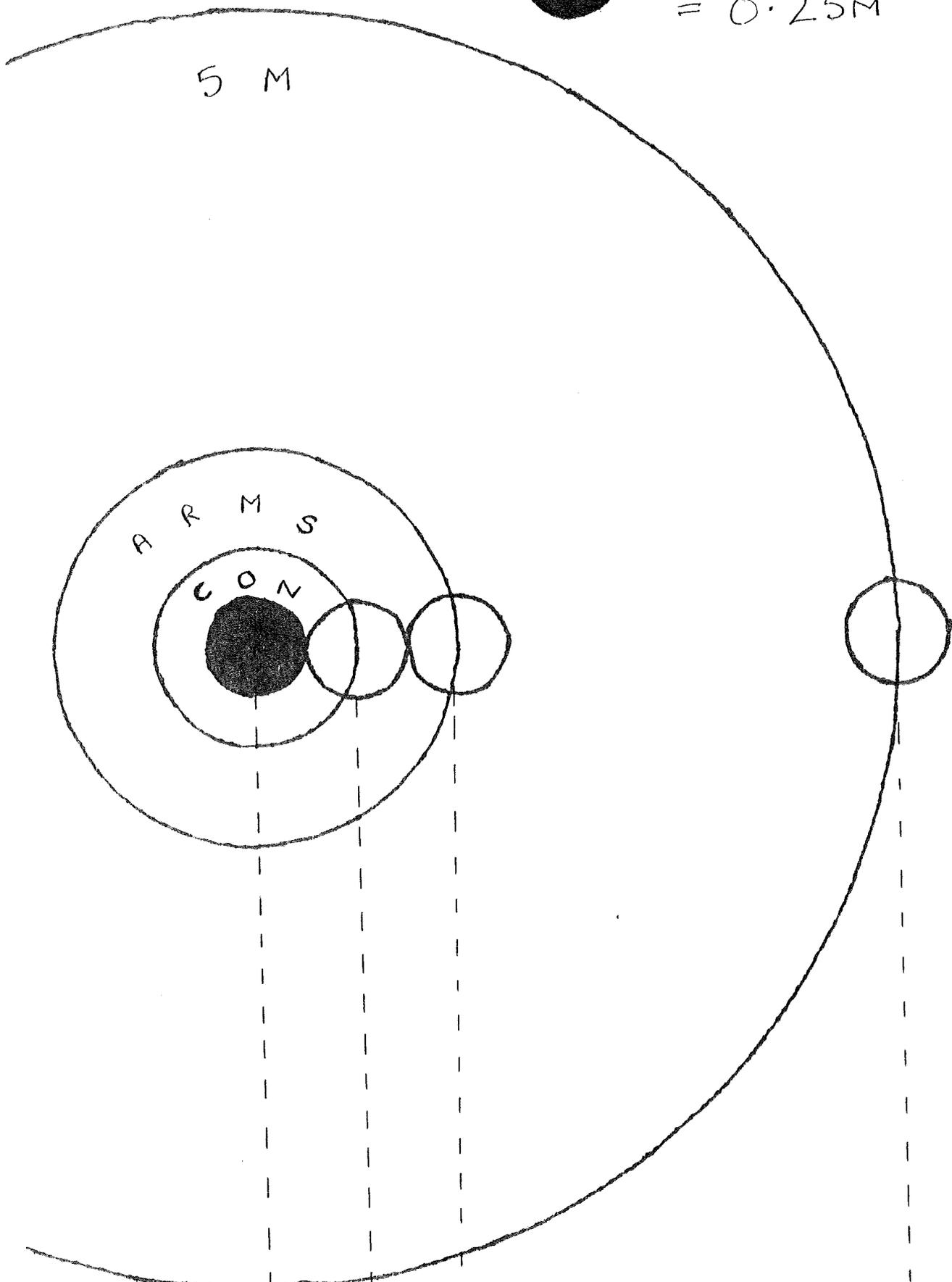
The results of this cluster analysis, using natural logarithms of similarities, are presented as dendrograms in Figures 8.1a-b. Inspection of these does not suggest any clear differences in structure between the groups.

Principal Co-ordinates Analysis

Principal co-ordinates analysis (PCA) allows similarities between individuals to be represented in a more overtly spatial way. In essence, it seeks to configure

BABOON RADIUS (r)

= 0.25M



5 M

A R M S
C O N T

CONTACT ZONE (r=0.5)

ARMS REACH (r=1.0)

5M (r=5.5)

Table 8.1 Correlations of data from each proximity grade for dyads (data are frequencies)

MLK

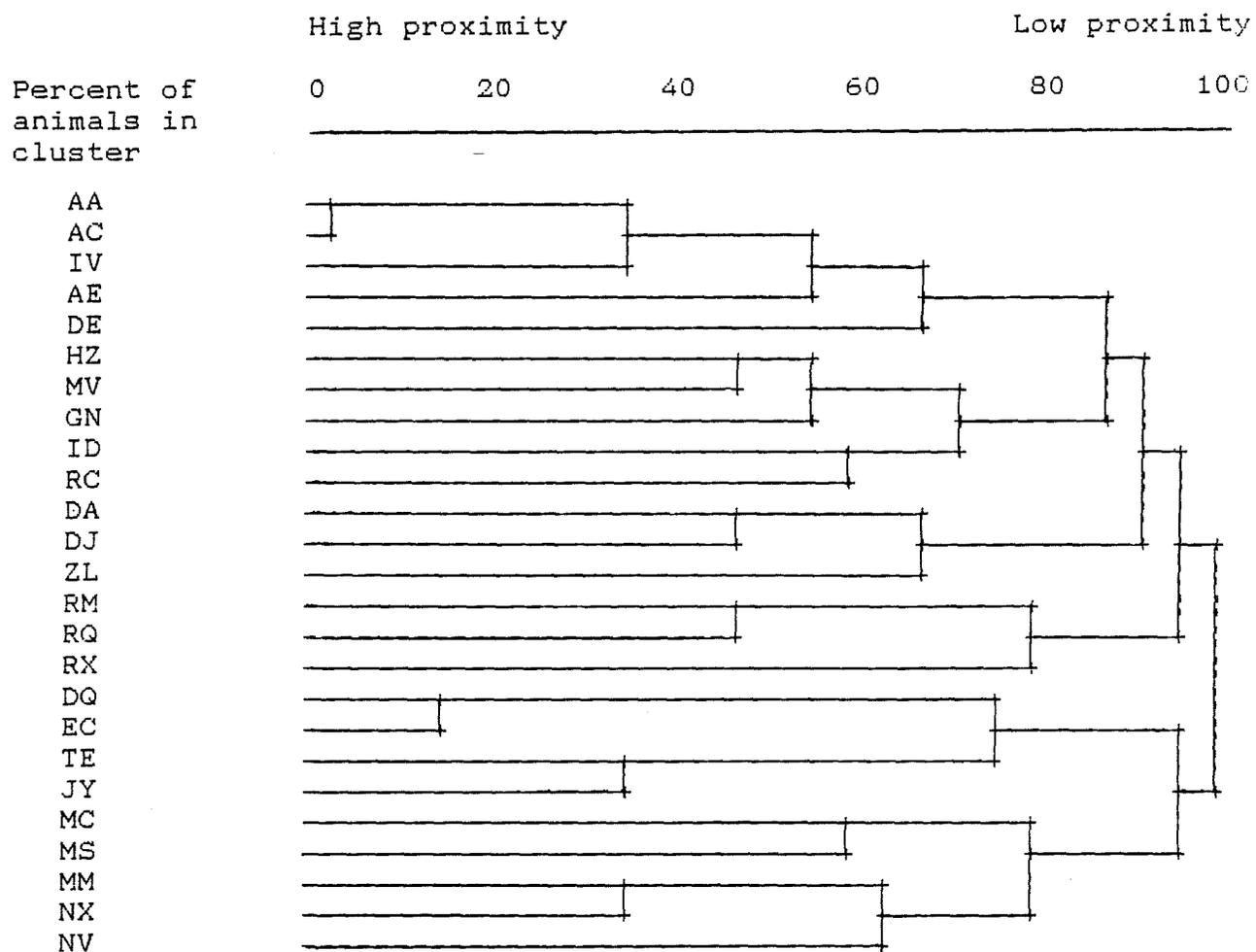
| | contact | arm's reach | 5 metres |
|-------------|---------|-------------|----------|
| contact | - | | |
| arm's reach | -.11 | - | |
| 5 metres | .30* | .36* | - |
| nearest | .26* | .16* | .26* |

STT

| | contact | arm's reach | 5 metres |
|-------------|---------|-------------|----------|
| contact | - | | |
| arm's reach | .17 | - | |
| 5 metres | .38*** | .47*** | - |
| nearest | .23** | .25*** | .41*** |

* p<0.05
 ** p<0.005
 *** p<0.0005

Figure 8.1a Dendrogram showing clustering of individuals in MLK as measured by proximity samples.



points that exist in a large number of dimensions (in this case the spatial deployment of animals across many time frames) in fewer dimensions without significantly altering the distances between the points in the true multidimensional space. As our objective at this stage is a graphical one, this amounts to an attempted representation in two dimensions.

Principal co-ordinates analysis requires firstly that relations between objects be expressed as dissimilarities rather than similarities. For the purposes of the data at hand, the obvious way to achieve this would be to take the difference between each cell value and the largest cell value in the matrix. However, PCA can run into difficulties when there are dissimilarity values that are close to zero (the dissimilarity of an object with itself). In consequence, the data were manipulated in the following manner. Similarities, the original cell entries, were expressed as a function of the average animal's 'self similarity'; this technical term refers to the minimum dissimilarity value permissible in the matrix. This figure was set as the sum of an individual's cell entries along a row, this being the total amount of proximity, or similarity, it evinced towards all other animals in the study period. The mean of the sum of each individual's cell entries was then calculated to obtain an average self similarity. This final procedure was necessary in order to preserve a symmetrical matrix. Cell entries were subtracted from this figure, and the sign of the result reversed to give a dissimilarity measure. This procedure, in summary was:

$$\text{cell value} = - (\text{cell value} - \text{avg self similarity})$$

The dissimilarity matrices were then subjected to principal co-ordinates analysis. The results are given in Figures 8.2a-d. The axes are arbitrary in these figures, as is the scale: their function is simply to show the clusteredness of elements.

There is a suggestion in the case of natal MLK animals that the majority fall into two separate clusters. However, it should be noted that this data proved difficult to plot in two dimensions: in the current context this means that spatial configurations were not consistent over time. The accuracy of the representation is given by the ratio of the sum of the eigenvalues associated with the two given dimensions to the sum of eigenvalues for all dimensions. For each of the four cases this is:

| | |
|-----------|-------|
| MLK natal | 12.5% |
| STT natal | 4.9% |

Figure 8.2a Clustering of spatial association in MLK (all natal animals). Data from 10 month study period subjected to principal co-ordinates analysis (see text for details)

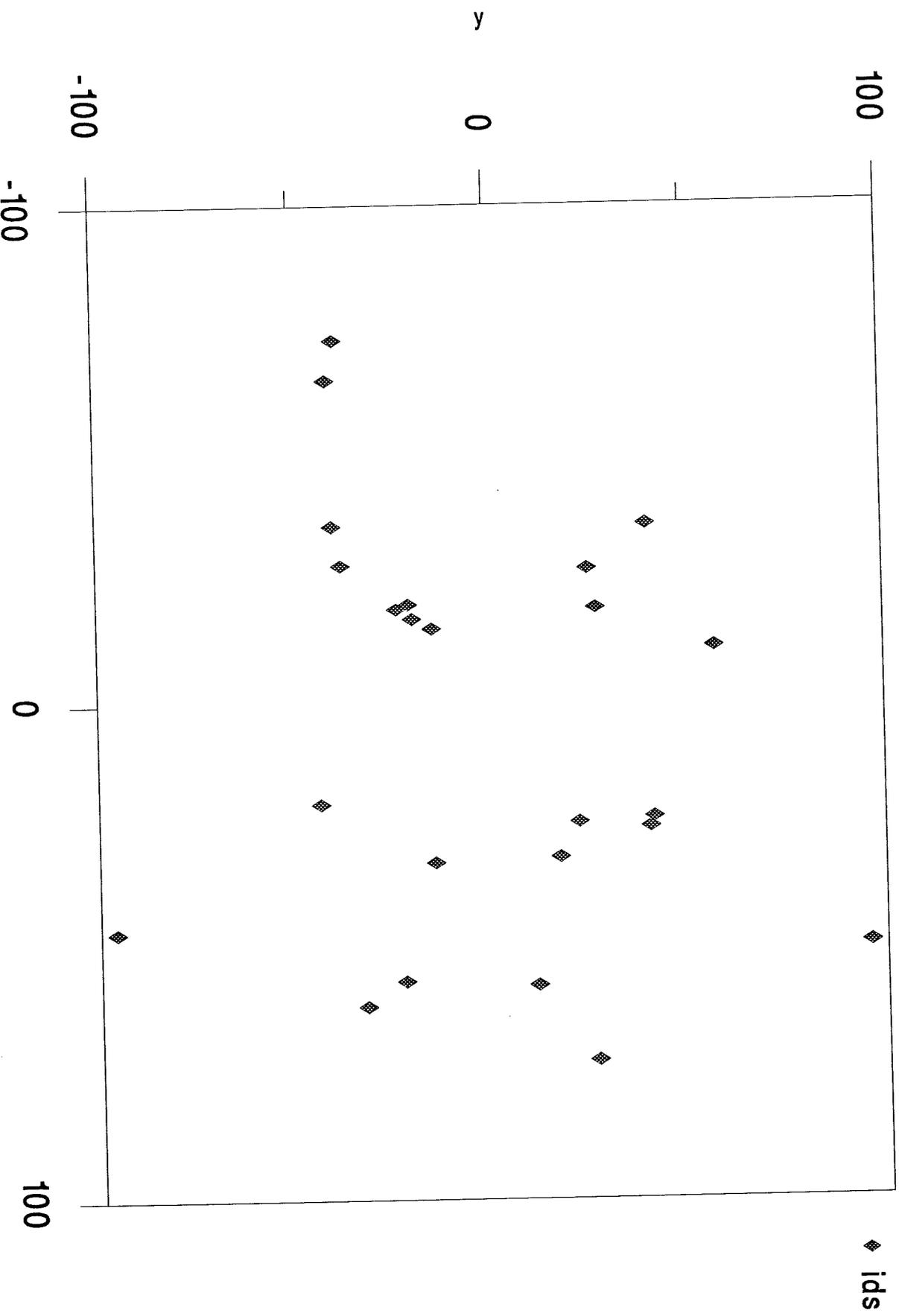


Figure 8.2b Clustering of spatial association in STT (all natal animals). Data from 10 month study period subjected to principal co-ordinates analysis (see text for details).

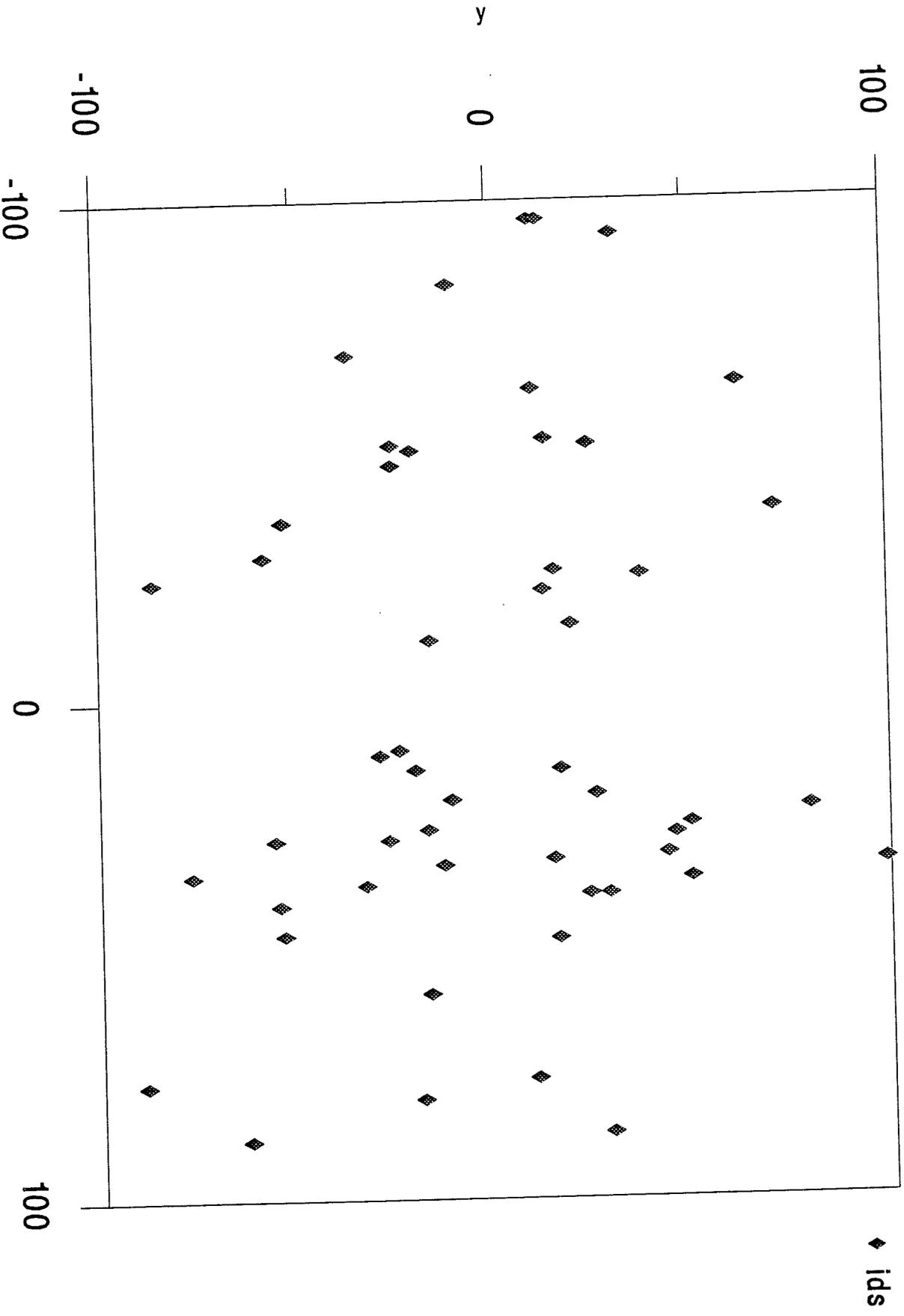


Figure 8.2c Clustering of spatial association in STT (all natal animals). Data from 10 month study period subjected to principal co-ordinates analysis (see text for details)

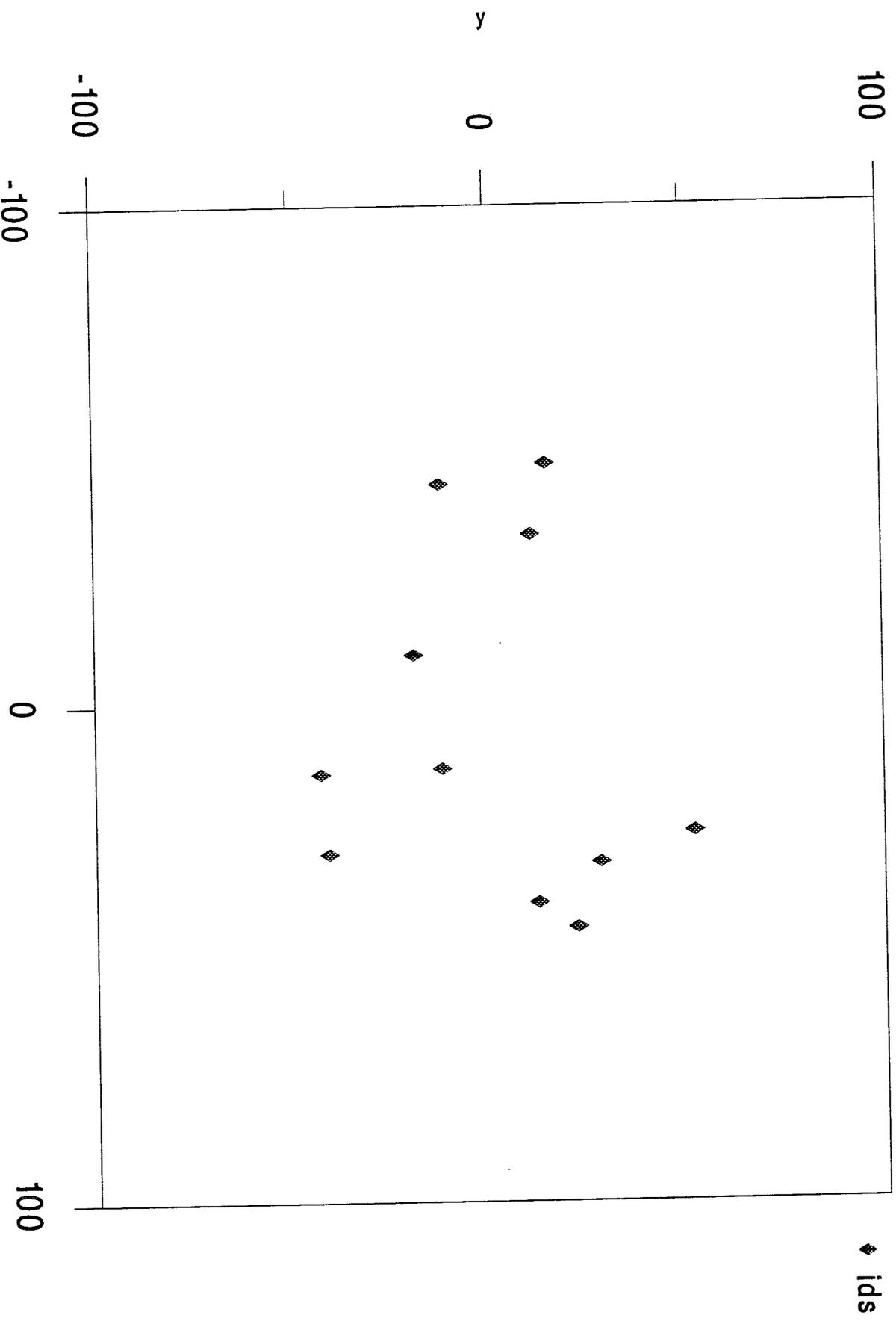
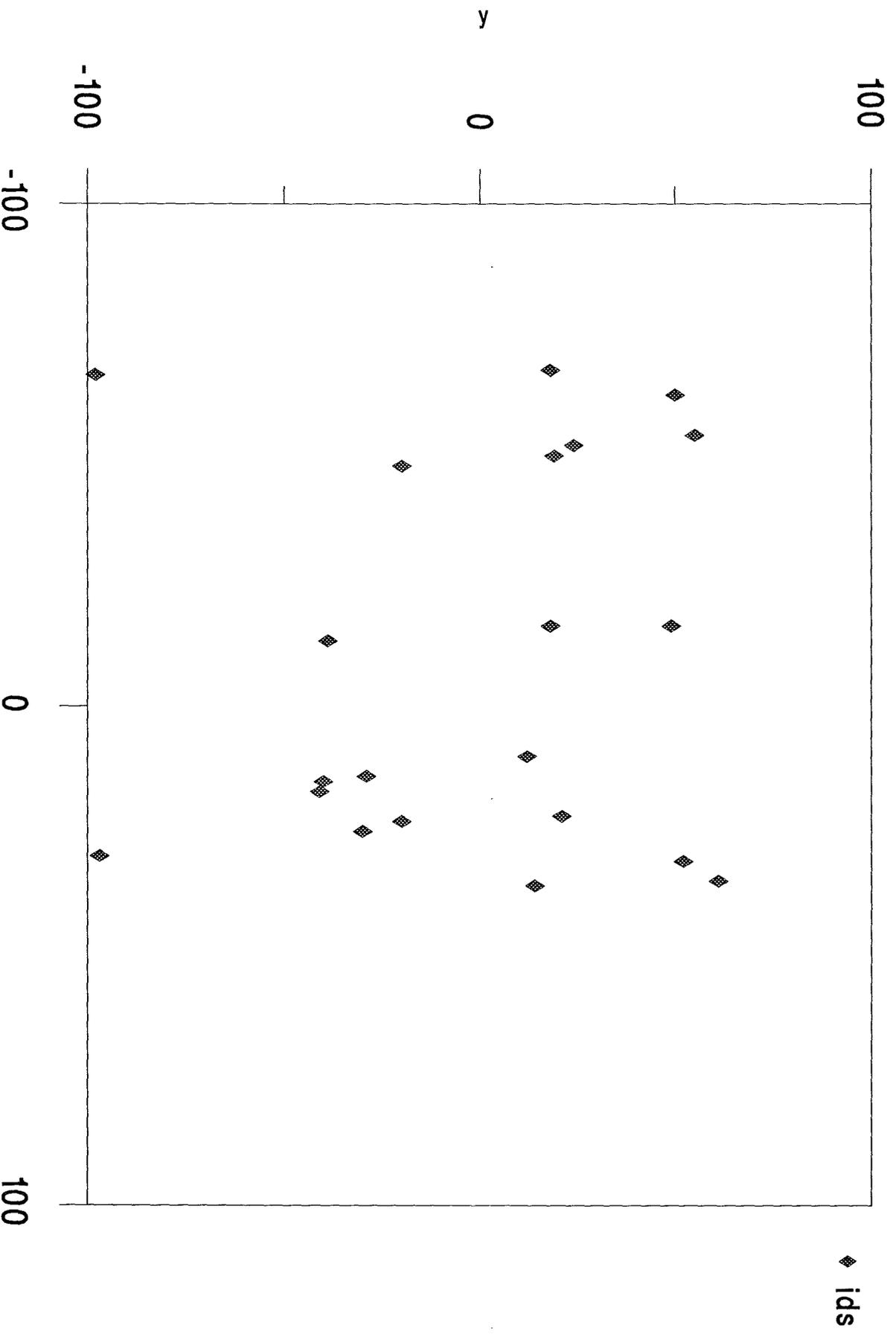


Figure 8.2d Clustering of spatial association in STT (females only) Data from 10 month study period subjected to principal co-ordinates analysis (see text for details)



| | |
|-------------|-------|
| MLK females | 27.0% |
| STT females | 13.1% |

Thus, whilst there may be a suggestion of clustering, we cannot be sure that in the remaining dimensions the clusters remain separate. The following analysis investigates this.

Frequency analysis

If there is a real division of troops into two clusters then this ought to be apparent in the distribution of dissimilarities. Specifically, we would expect a large number of low dissimilarities (existing between members of a cluster), a large number of high dissimilarities (existing between members of different clusters) and little else between. This will appear as a U-shaped distribution.

These distributions, expressed as histograms, are given in Figures 3a-d. The absolute values of dissimilarity along the x axis are unimportant, as is the fact that they differ between figures: it is the shape of the distribution that is important.

The figures, particularly those where all natal animals have been used, do seem to show bimodality. However, there is an artifact at work here, resulting from the weightings. By virtue of the weightings used (and discussed above), the proximity grade of contact is weighted to produce a hundred times the association that 5 metres proximity indicates. Contact was rare amongst the focal animals and so where just one incident was recorded this generated a large gap in the apparent distribution of an individual's allocation of spatial association. This artifact does not undermine the potential efficacy of this approach to identifying clustering. Had the two modes in these bimodal distributions been the peaks of two sub-distributions that appeared relatively normal then evidence of clustering could have been claimed. As it is however, the left-most mode of figures 8.3a and 8.3b is actually in the tail of that sub-distribution in both cases, suggesting that it is best attributed to the artifact noted above rather than to a natural phenomenon.

The figures thus show no clear pattern of clustering in the troops. It is possible that, were data sufficient, a month by month analysis might produce a clearer picture.

Discussion

Using three measures, there appears to be no difference in the spatial

Figure 8.3a Distribution of dissimilarities in spatial association (distances) of natal animals in MLK. Data from 2 minute point samples, taken over 10 month study period

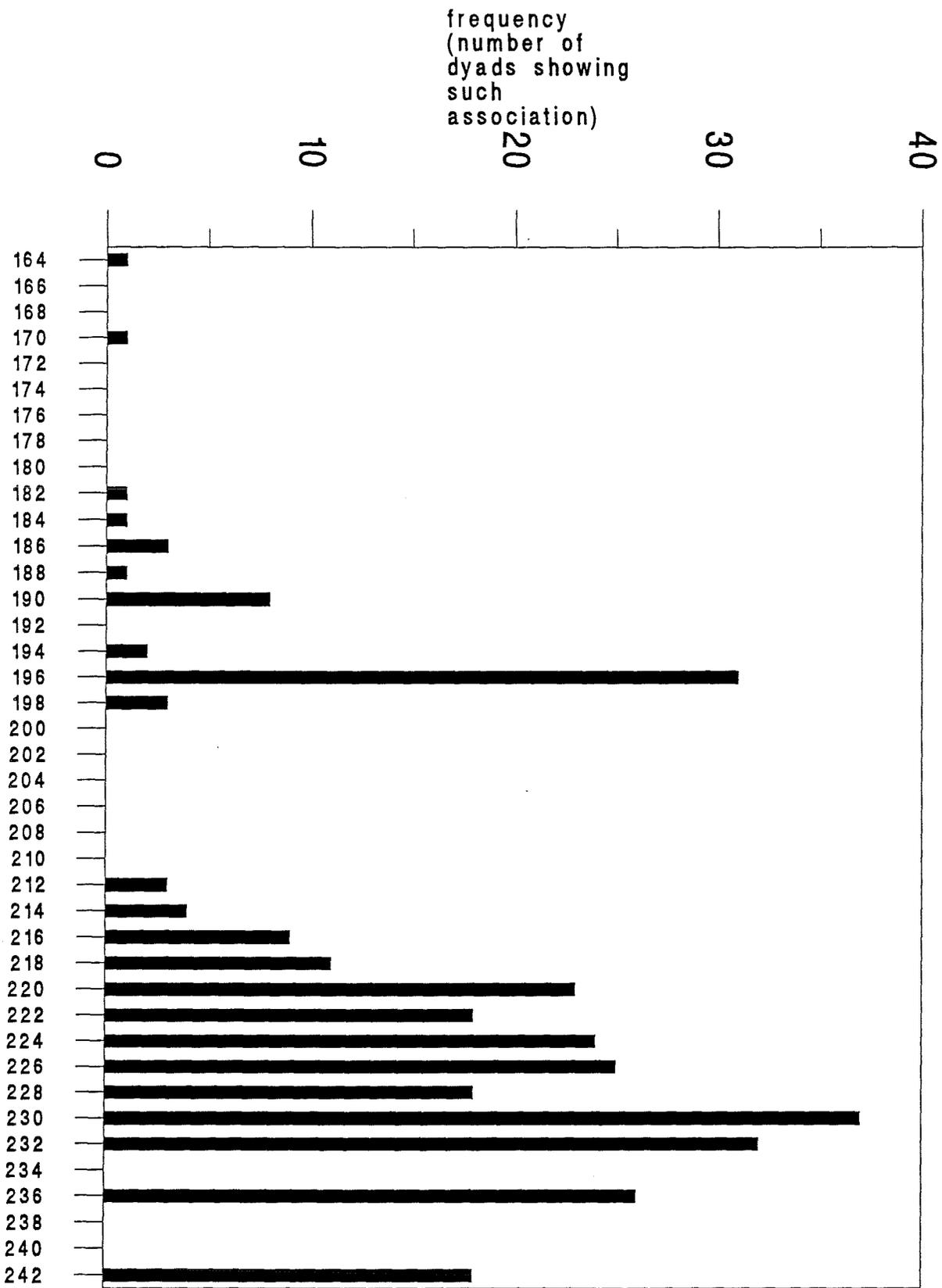
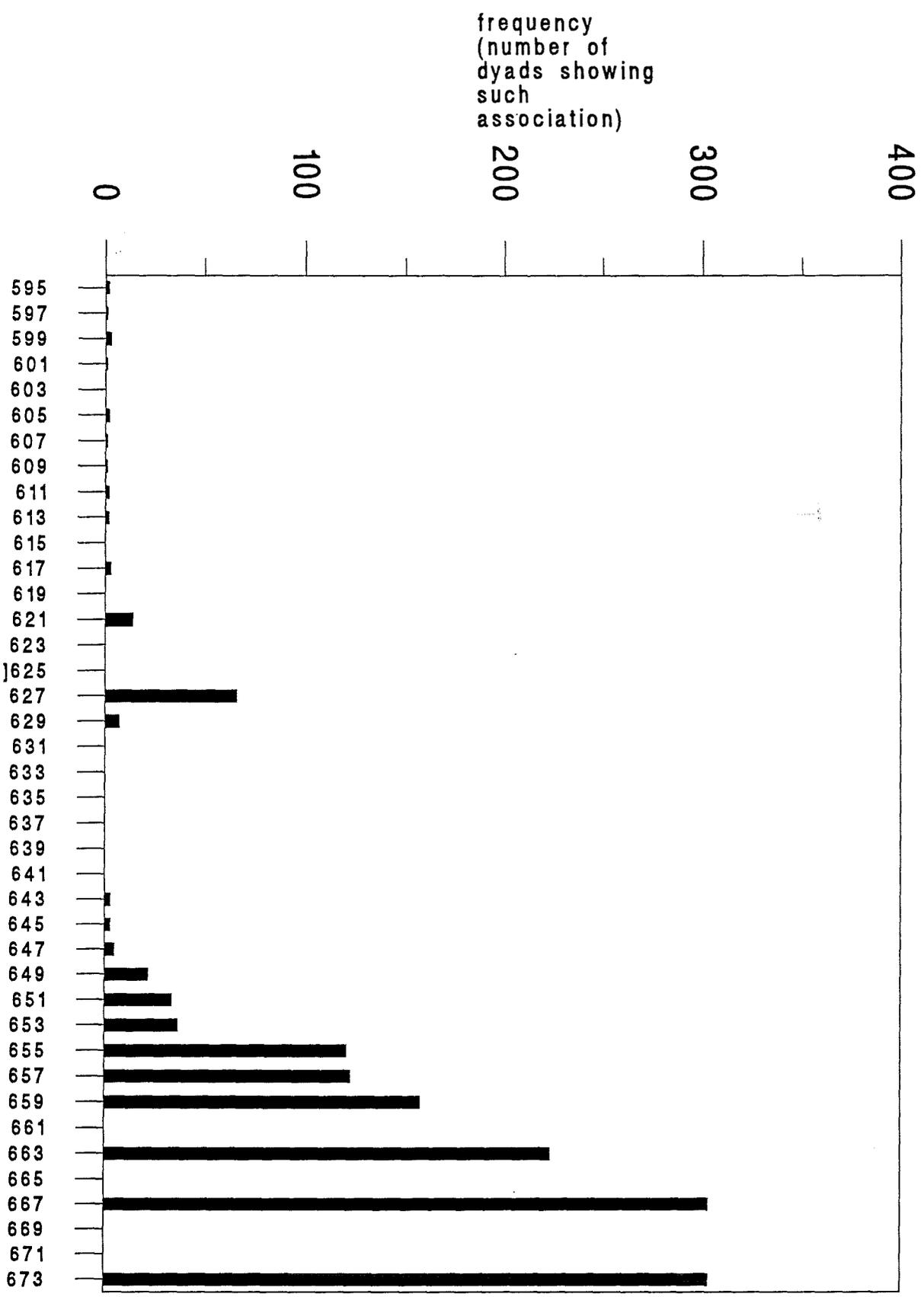


Figure 8.3b Distribution of dissimilarities in spatial association (distances) in natal animals in STT. Data taken from 2 minute point samples over 10 month study period.



frequency
(number of
dyads showing
such
association)

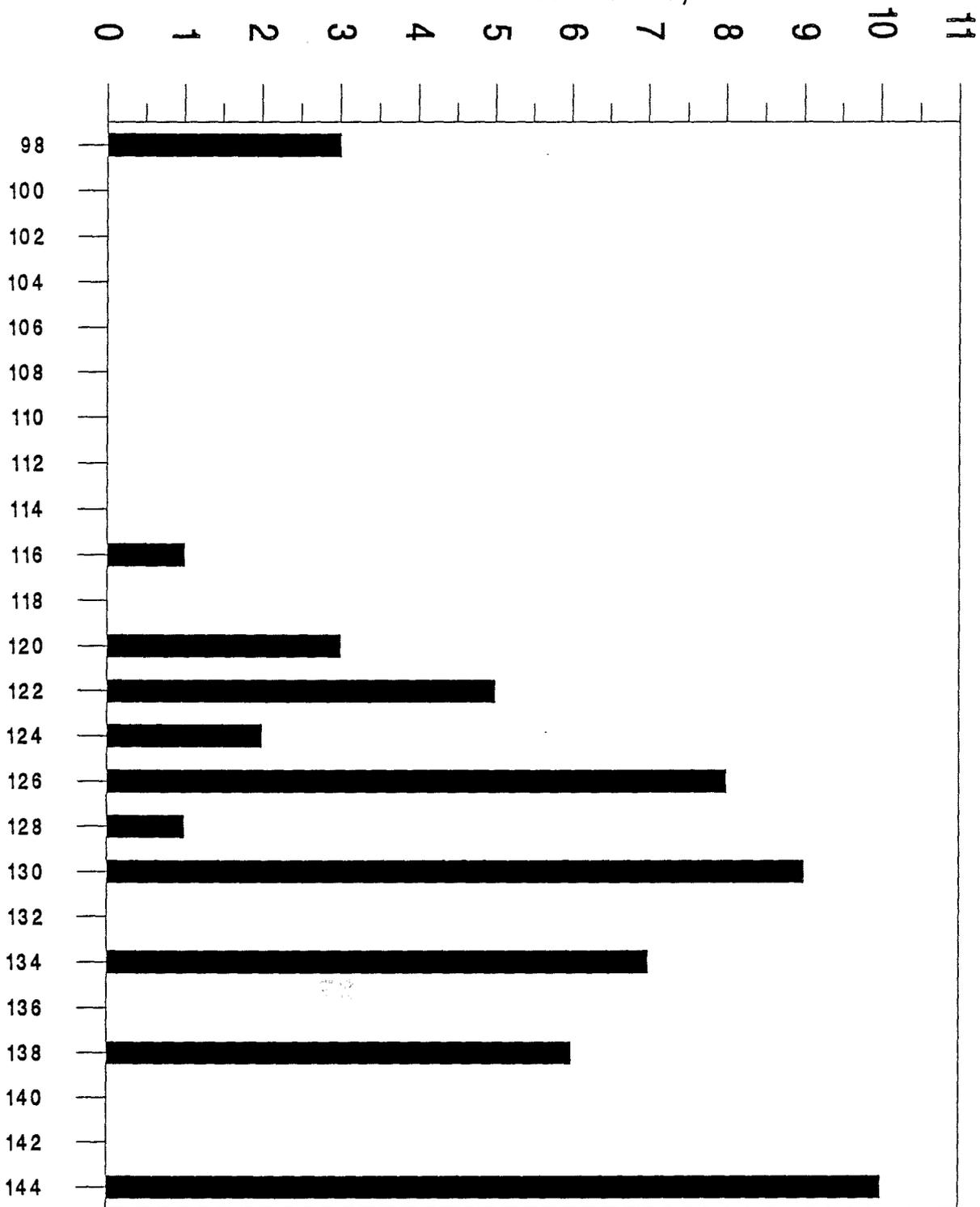
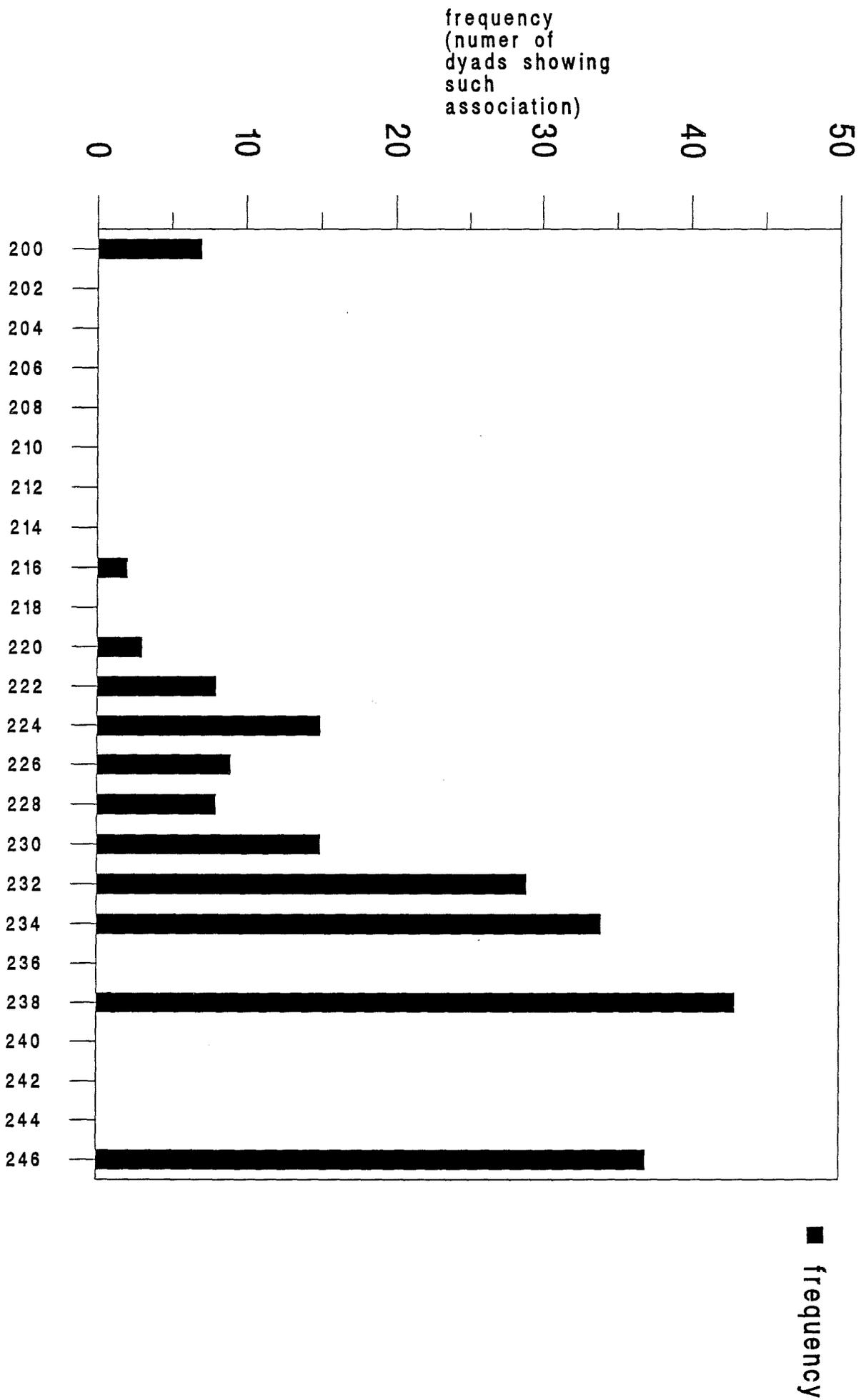


Figure 8.3c Distribution of dissimilarities in spatial association (distances) of females in MLK. Data taken from 2 minute point samples across 10 month study period.

Figure 8.3d Distribution of dissimilarities in spatial association (distances) of females in STT. Data taken from 2 minute point samples across 10 month study period



deployment of natal individuals in the two troops. Cliquishness of the variety described in this chapter's introduction, if it exists, does not manifest itself in any marked way in these proximity relations. Null results, in the case of so general an analysis, provide virtually no basis for concluding anything beyond the absence of the effect under question. Thus, regarding the question of complexity, all that can really be said here is that individuals do not seem to resort to cliquishness to combat the uncertainties involved in 'incidentally' associating with non-affiliates when trying to reach affiliates.

The analyses have ignored the possible role of male friends as 'nuclei' for female sub-groupings, the effect of which might be to disrupt female cliquishness. Byrne et al. (1990) have suggested that cross-sex bonding plays an important role in baboon social structure, a possibility reviewed in greater detail in the following chapter. This is thus a topic for further investigation.

Chapter 9: Friendship

Introduction

'Friendships' between adult male and female baboons are now a well documented phenomenon (e.g. Ransom and Ransom 1971; Seyfarth 1978a,b; Altmann 1980; Smuts 1985). These relationships are characterised by high rates of grooming (typically of the male friend by the female) and a tendency towards spatial proximity to which both partners contribute (Smuts 1985). Both males and females are assumed to benefit from such relationships. Males have been shown to selectively protect their female friends against aggression (Smuts 1985) and also their friends' infants (e.g. Altmann 1980; Stein 1981). In return, females have been shown to preferentially consort with males with whom they had friendships during their anoestrous phase (Smuts 1985) and to be more cooperative towards consorting males with whom they have been associating whilst cycling (e.g. Rasmussen 1980, 1983). Male baboons also use infants to 'buffer' the agonism of other males (e.g. Popp 1978; Packer 1980; Stein 1981; Collins 1981; Strum 1984). In Smuts' (1985) study nearly all buffering was done with a friend's infant, possibly suggesting that cooperation by infant and mother is more likely in these circumstances. Only one unequivocal incident of buffering was observed in the study presented here but given the suggestion above it is worth relating.

Westland, an adult male is sitting in a grooming clique when Goliath, a large sub-adult male, begins circling the group, yawning and molar-grinding. Visibly alarmed, Westland begins grooming Keino: the nearest infant but not the offspring of a friend. When Goliath closes down the distance between himself and Westland and threatens him with eyeflashes and headbobs, Westland lifts up Keino as a buffer. Keino screams and writhes in the grasp of Westland who drops him. Westland moves off a few feet and begins grooming Wizard, the infant daughter of his friend, Withania. Whilst most nearby troop members seem alarmed by Goliath's aggression, Wizard is remarkably calm. His mother does not interfere. Goliath moves off and threatens a different male outside the grooming clique.

This single example may illustrate the general point that buffering is only an

option if you have a female friend. These hypotheses concerning the value of friendship seem backed up by the prevalence of the phenomenon: in Smuts' (1985) study all but one of her 31 females had male friends.

Friendship and complexity

What can be said of the role of friendship in social complexity? The discussion above concentrated on the services that friends provided for each other. There is an implicit assumption here that friendship can occur because the costs of the services provided are outweighed by the benefits of those received. This approach can be extended to baboons' attempts to deal with social complexity. Clearly, initiating, maintaining and terminating relationships poses a 'cost' in complexity. What individuals may hope to gain, however, is predictability (and hence a 'saving' in complexity) *within* the relationship. Hinde's (1976) characterisation of relationships was that they were *patterns* of interactions. If the primary function of relationships is to reduce complexity (rather than provide resources as is usually assumed) then a clear prediction follows. As the complexity of interactions rises (i.e. as the rules for predicting their outcome lose power) then the likelihood of relationships forming should increase. At a phylogenetic level this seems plausible; primates, for example, are behaviourally complex and also notable for forming durable non-kin relationships.

As in Chapter 5, in which dominance was considered, we are thus led to suspect that complexity may be shunted out of interactions and into relationships. This gives the complexity greater organisation. It may also widen the scope for growth of further cognitive strategies for dealing with social complexity, both developmentally and phylogenetically. It seems reasonable to suppose that an individual must first understand (at some level) that it is in a relationship before it can plan (again, at some level) how best to exploit that relationship.

The aims of this chapter are modest. Firstly, I examine the extent of male-female association and the possibility that this is related to the female's rank, matriline size or group size. Secondly, I test for the existence of specific friendships and, thirdly, examine the stability of these.

Cross-sex association

Introduction

Byrne et al. (1990) have shown that in a mountain habitat, savannah baboons

can assume a social structure that closely resembles hamadryas baboons. In their study, grooming was focussed on males, producing a radially patterned sociogram and thus showing an essentially male-female bonded society. The authors note a confusion in the literature between matrilocality (female residence and male transfer) with female-bondedness (close affiliative links with females) and go so far as to suggest that cross-sex bonding is the norm for savannah baboons. Their study underlined the flexibility of baboon social orientation. It thus becomes valid to ask whether, under more typical savannah conditions, female baboons choose the degree of male association that best suits their social niche within their group. At one end of the continuum, females need not associate with males at all, except for the purposes of sex. At the other, males could provide the majority of social services that females require.

The effect of three factors on cross-sex association is considered. The first factor is group size, the effects of which are difficult to guess. Although social complexity might be supposed to highlight the need for friends, it seems likely that this pressure would kick in quite early, certainly by the time a group reached the size of MLK. The effect of female rank is similarly uncertain. We might expect a greater need for male friends on the part of low-rankers since agonistic disputes will tend to be settled against them. However, this need for protection ought to imply that males would prefer to be friends with high-rankers since they would then less often need to oppose the momentum of dominance in providing useful aid. Smuts (1985) found no significant difference in the number of friendships held by high and low-ranking females. Finally, the effect of matriline size is considered. A clear expectation presents itself here: females with few or no offspring ought to gain most by the protection afforded by friendship with males.

Methods

In keeping with previous chapters, grooming is assumed to be a valid indicator of the degree of bondedness between two animals. Collapsed scan and *ad libitum* data were used as in Chapter 7 and, as previously, grooming in consorts and agonistic interactions was excluded. The dependent measure was the percentage of a female's total grooming effort directed at adult and sub-adult males and immigrant male juveniles (usually large enough to constitute an effective potential ally). For testing the effects of rank, troops were separated at the middle of the hierarchy into a high and low group. Matriline size was a more difficult variable since, as discussed already, the possibility of sisterhood could not be resolved for some STT dyads. However, all mother-daughter pairs were plausibly known and this is typically the strongest of kin-bonds (Dunbar 1984). The size of an individual's

matriline was thus defined as the number of its offspring plus its mother if still living. The range of this variable was 0 to 4, with few cases of the two extremes, and so it was collapsed into two blocks: zero/one versus two or more (resulting in equal sample sizes). Since the average matriline size was the same in each group there was no confounding of this factor with group size.

Results

T-tests were performed with all three independent variables tested against percentage of grooming effort directed at males. The effect of group size was non-significant ($X_{mlk}=0.34$, $X_{stt}=0.31$, $N=32$, $t=0.67$, $p=0.51$) as was matriline size ($X_{small}=0.34$, $X_{large}=0.31$, $N_{large}=0.31$, $N=32$, $t=0.85$, $p=0.40$). The amount of effort high-rankers devoted to grooming males was close to being significantly more than low-rankers ($X_{high}=0.36$, $X_{low}=0.28$, $N=32$, $t=2.02$, $p=0.053$).

Means (collapsed across groups) were also calculated for the percentage of females' grooming effort directed at the three classes of: own matriline; other females and juveniles in the group; males. These were respectively: 0.39; 0.29; 0.32

Discussion

The first observation to be made is that Byrne et al.'s (1990) case for crediting the importance of cross-sex bonding receives justification from the results of the above paragraph: males are actually groomed more than unrelated females.

The absence of effects in the t-tests is hard to draw conclusions from. The measure, grooming directed at males, does not necessarily index friendship since that grooming may be allocated very widely. However, we would still have expected effects to show up had there been gross differences in the extent to which the groups were cross-sex bonded.

Friendship in the study troops

Introduction

It is a feature of Smuts' (1985) study, that the affiliative behaviours females showed towards males were highly discontinuous across the troop's male membership. Of 18 possible partners in her study troop, the average female devoted 66% of her grooming time to one partner, and 86% to either of two partners. This enabled Smuts to identify a genuine category of friendship for most females in her study. Such friendships are sought in this study and Smuts' methods

are followed closely for purposes of comparison. The effect on friendship of the factors of group size and reproductive state is then tested for.

Methods

All analyses below use data from focal females. Data were separated into five 2-month time blocks, reflecting the unlikelihood that all friendships would remain stable over the entire study period. Smuts (1985) noted that the strength of friendships diminished when a female began cycling. In consequence, this distinction is respected in the data presented here (fortunately the transition between the two sexual states, oestrous and anoestrous, coincided closely with transition across time blocks for each focal female). As usual, incidents of grooming between members of a consort or in the context of an agonistic interaction were not included in the analysis.

In identifying a focal female's friends, no data from focal males was used. This would obviously bias the results towards an apparent association between focal males and focal females.

Following Smuts (1985), two variables were used to assess friendship

(1) Grooming episodes: the total number of days on which grooming occurred between focal female and another male (scan and adlib data were used to augment focal data)

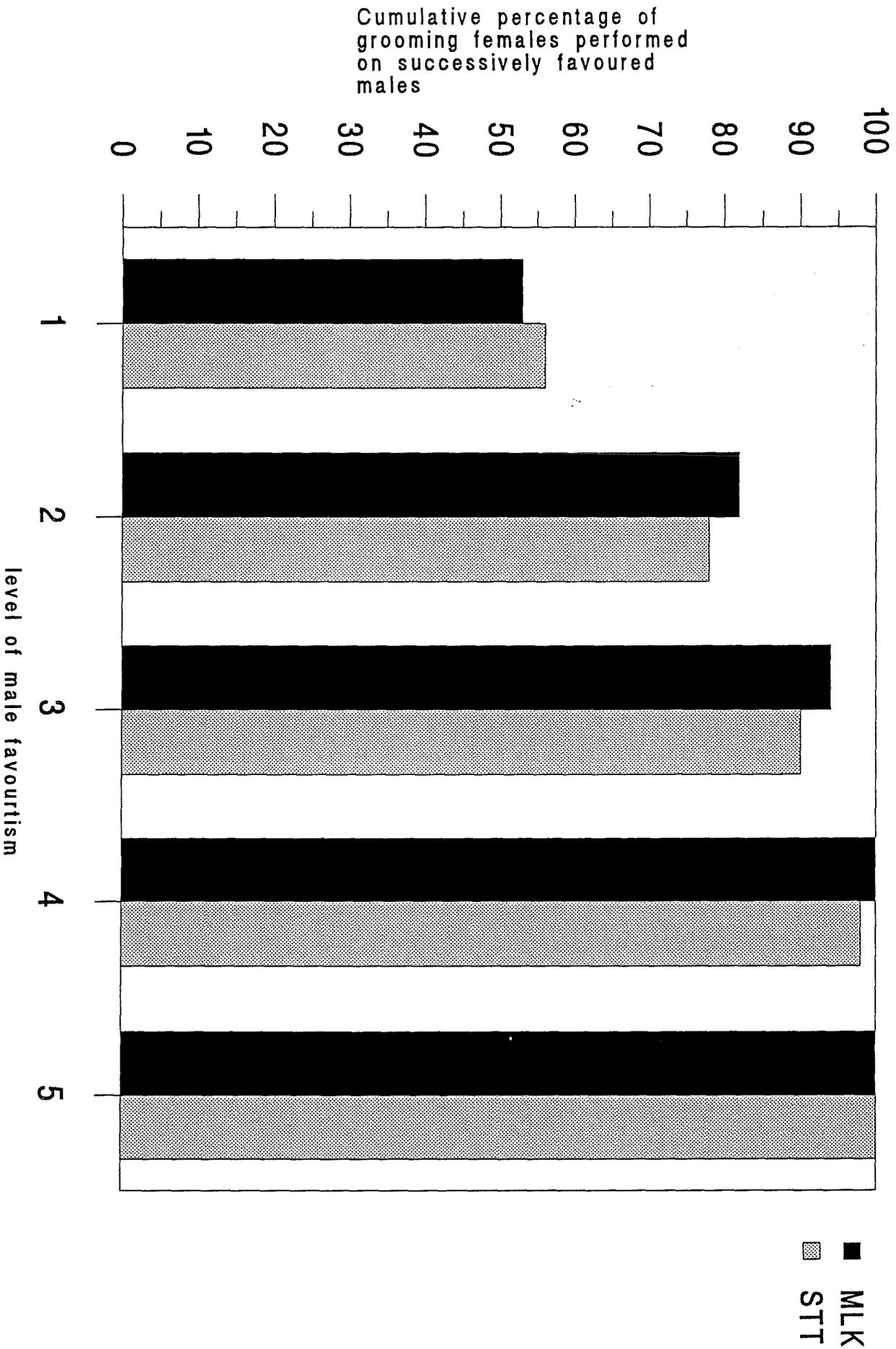
(2) Proximity: two minute instantaneous samples were made of animals proximal to the focal female as described in Chapter 4. For each time block, these were then collapsed into a composite proximity score for each animal as detailed in Chapter 8.

Results

Figures 9.1 and 9.2 serve largely as a comparison with Smuts' (1985 p.42-44) data and both clearly show that females do not allocate grooming evenly across males in their troop. We are thus able to identify the existence of friendships in the study troops.

Figure 9.1 presents data on female grooming allocation compared across group size and little difference is apparent in comparing the troops. In Figure 9.2, comparing grooming allocation in cycling and anoestrous females, there is a more pronounced difference with anoestrous females allocating a higher proportion of their grooming to their first two favoured males. Smuts (1985) found that anoestrous females devoted 66% of their grooming to one male and 86% to one of two males; in this study those respective values are 66% and 88%. In comparison, Smuts found that cycling females devoted only 47% of their grooming to their

Figure 9.1 Cumulative proportion of grooming effort females devoted to successively favoured males (1,2,..,etc): comparison across group size. Scan, ad libitum and focal data used over 10 month study, N=244 grooming instances



cumulative percentage of grooming females performed on successively favoured males

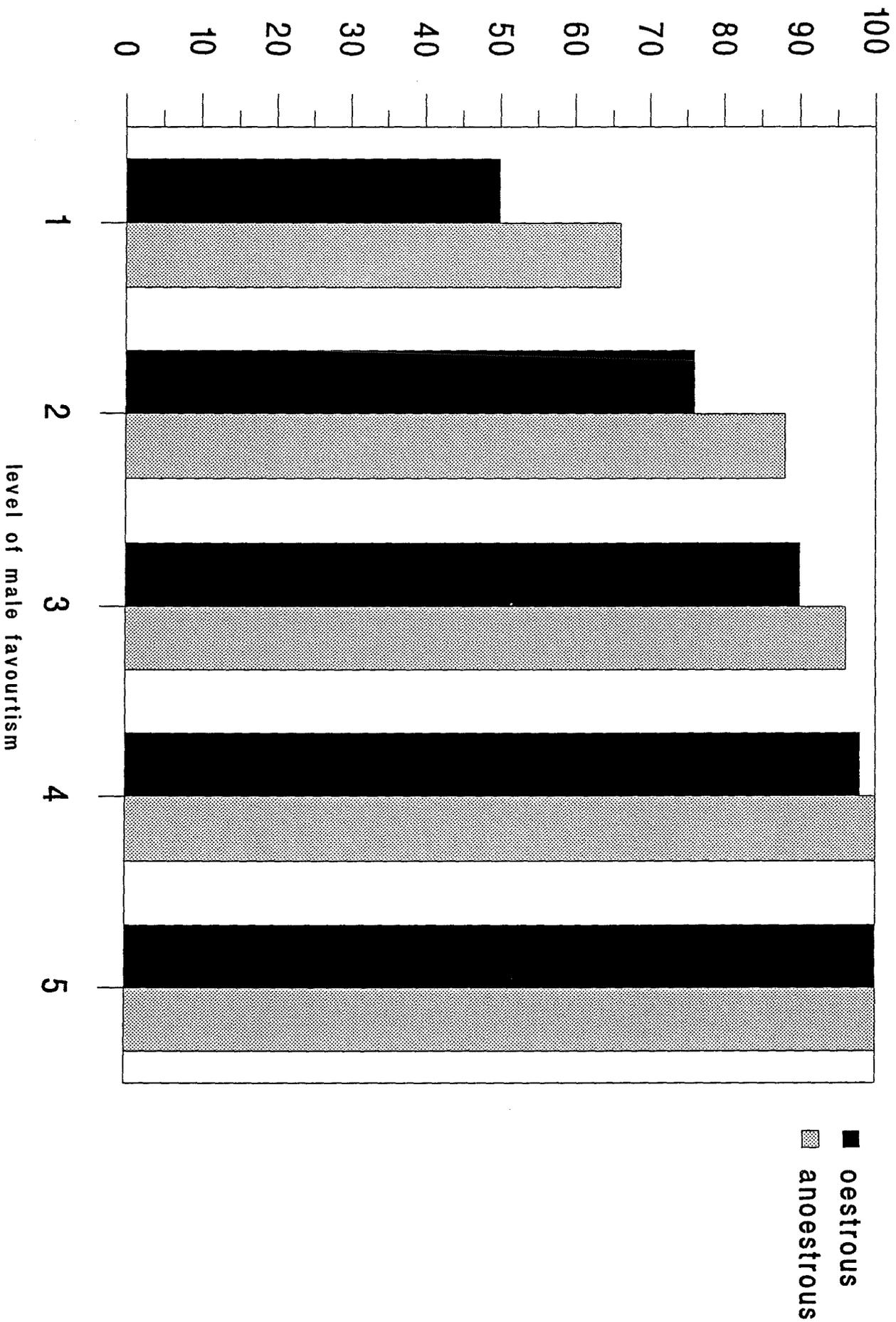


Figure 9.2 Cumulative proportion of grooming effort females devoted to successively favoured males (1,2,,etc): comparison across reproductive state. Scan,ad libitum and focal data used over 10 month study, N=244 instances of grooming.

favoured male and only 65% to either of their two favoured males; in this study those values are 50% and 76%. Thus, comparing Smuts' and this study, we find both that the general trend and the actual allocation figures are comparable. Spatial association tells a similar story as can be seen below.

The reality of any differences in the 'allocation' of friendship as a result of troop size or reproductive state was tested by observing the interaction between these factors and the dimension of favour shown to males ('friendship levels'). The following two-way analyses of variance were performed: effect of troop size and friendship level on grooming; effect of reproductive state and friendship level on grooming; effect of troop size and friendship level on proximity; effect of reproductive state and friendship level on proximity. The mean number of instances that females groomed males at each friendship level (calculated across focal females) comprises the data on which these tests are based and these data are shown in Figures 9.3 and 9.4. Only four levels of friendship are used since there were no instances of anoestrous females or MLK females grooming more than four males in a bimonthly period (see Figures 9.1 and 9.2). Corresponding graphs showing how spatial association was 'allocated' are shown in Figures 9.5 and 9.6.

Using grooming data, the interaction of troop size and friendship level proved non-existent ($F=0.01$, $df=3$, $p=1.00$) and the interaction of reproductive state and friendship level highly non-significant ($F=0.45$, $df=3$, $p=0.72$)

Using proximity data a similar absence of effects was apparent. There was no significant interaction of troop size and friendship level ($F=1.33$, $df=3$, $p=0.27$), nor reproductive state and friendship level ($F=0.14$, $df=3$, $p=0.94$).

Discussion

The plots in all the figures clearly show that the degree of friendship was not evenly distributed across males and so we can conclude that females in both study troops did have friends. However, the distinction between friend and non-friend is blurred somewhat by the absence of consistent, sharp discontinuities in grooming or association. Using the non-overlap of error bars in Figures 9.3-9.6 as an indicator of discontinuity, MLK females have two friends or one, depending on whether the grooming or proximity is to be preferred, and, using the same distinction, STT females have either two friends or no clear distinction between friend and non-friend. With regard to reproductive state, cycling females appear to have two or three friends (again, depending on choice of grooming or association as the index), and anoestrous females, one. Clearly these are approximate indications, however, and not quantitatively established by the analyses of variance.

Mean number of instances of grooming of male by focal female in bimonthly period

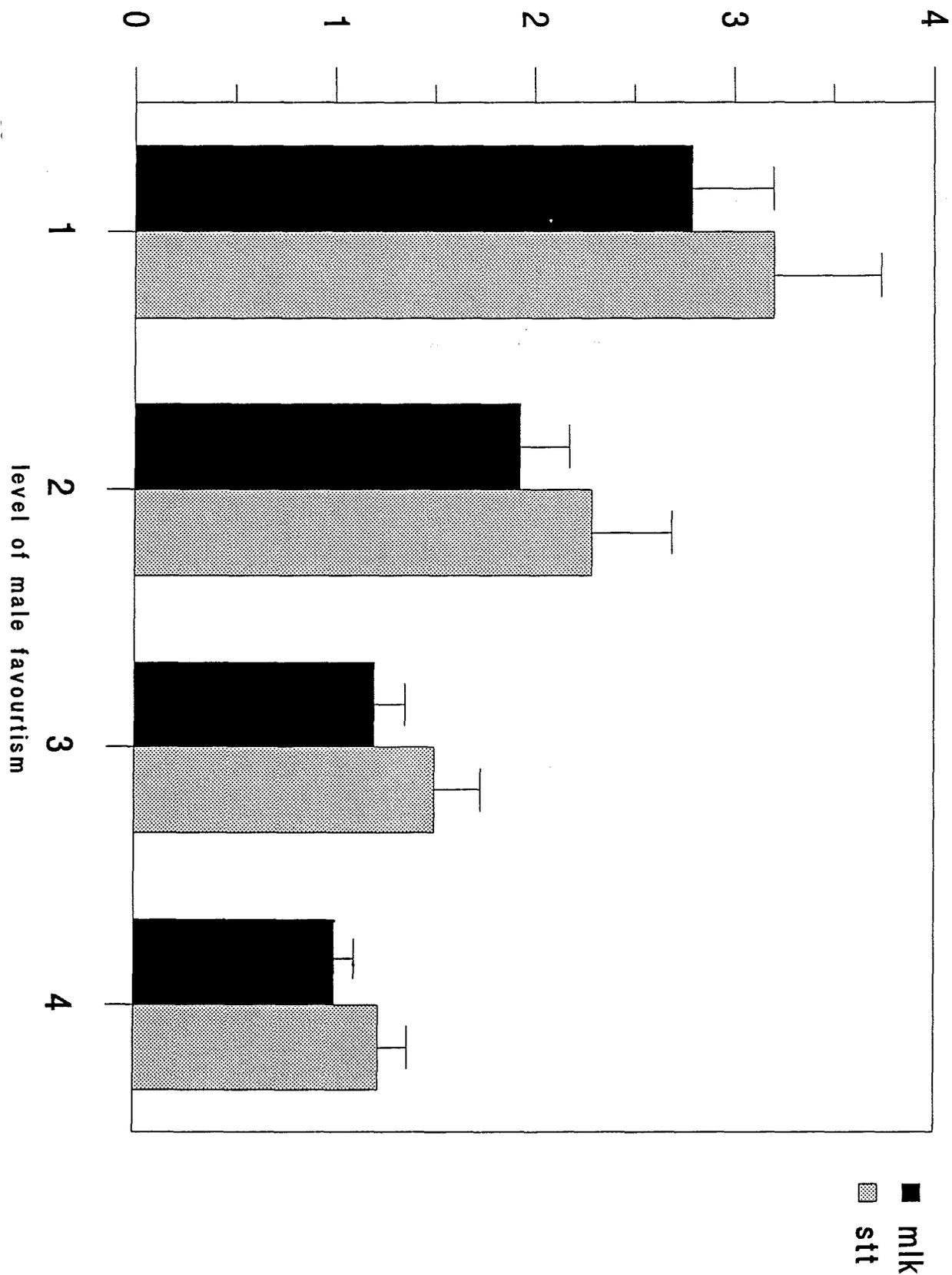


Figure 9.3 Mean instances of grooming females devoted to successively favoured males (1,2,..,etc) in 5 bimonthly periods: comparison across group size. Scan, ad libitum and focal data used from 10 month study. Standard errors shown.

Mean number of instances of grooming of male by focal female in bimonthly period

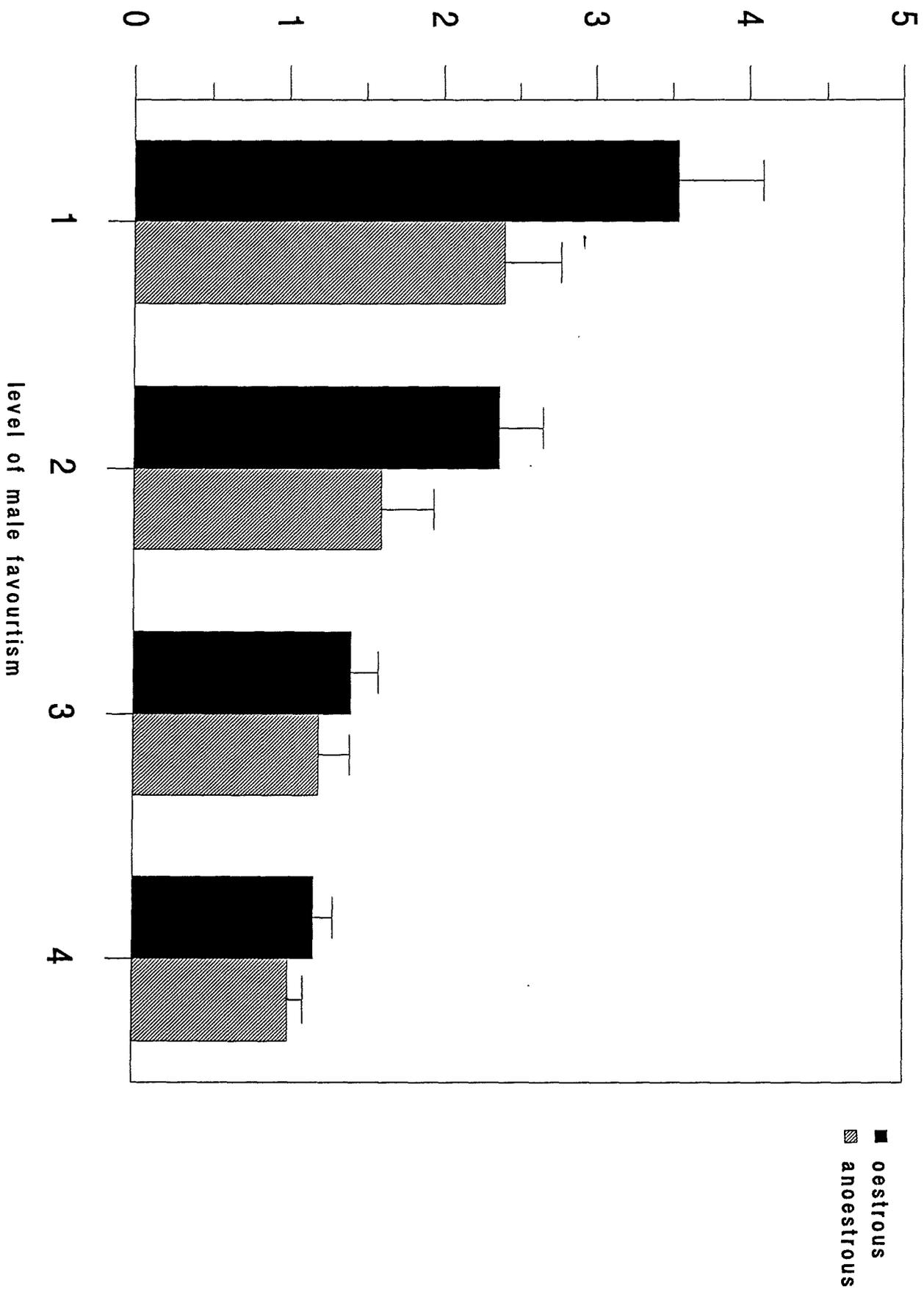


Figure 9.4 Mean instances of grooming females devoted to successively favoured males (1,2,..,etc) in 5 bimonthly periods: comparison across reproductive state. Scan, focal and ad libitum data used from 10 month study. Standard errors shown.

Figure 9.5 Mean composite proximity females devoted to successively favoured males (1,2,..etc) in 5 bimonthly periods: comparison across group size. Focal data used from 10 month study. Standard errors shown.

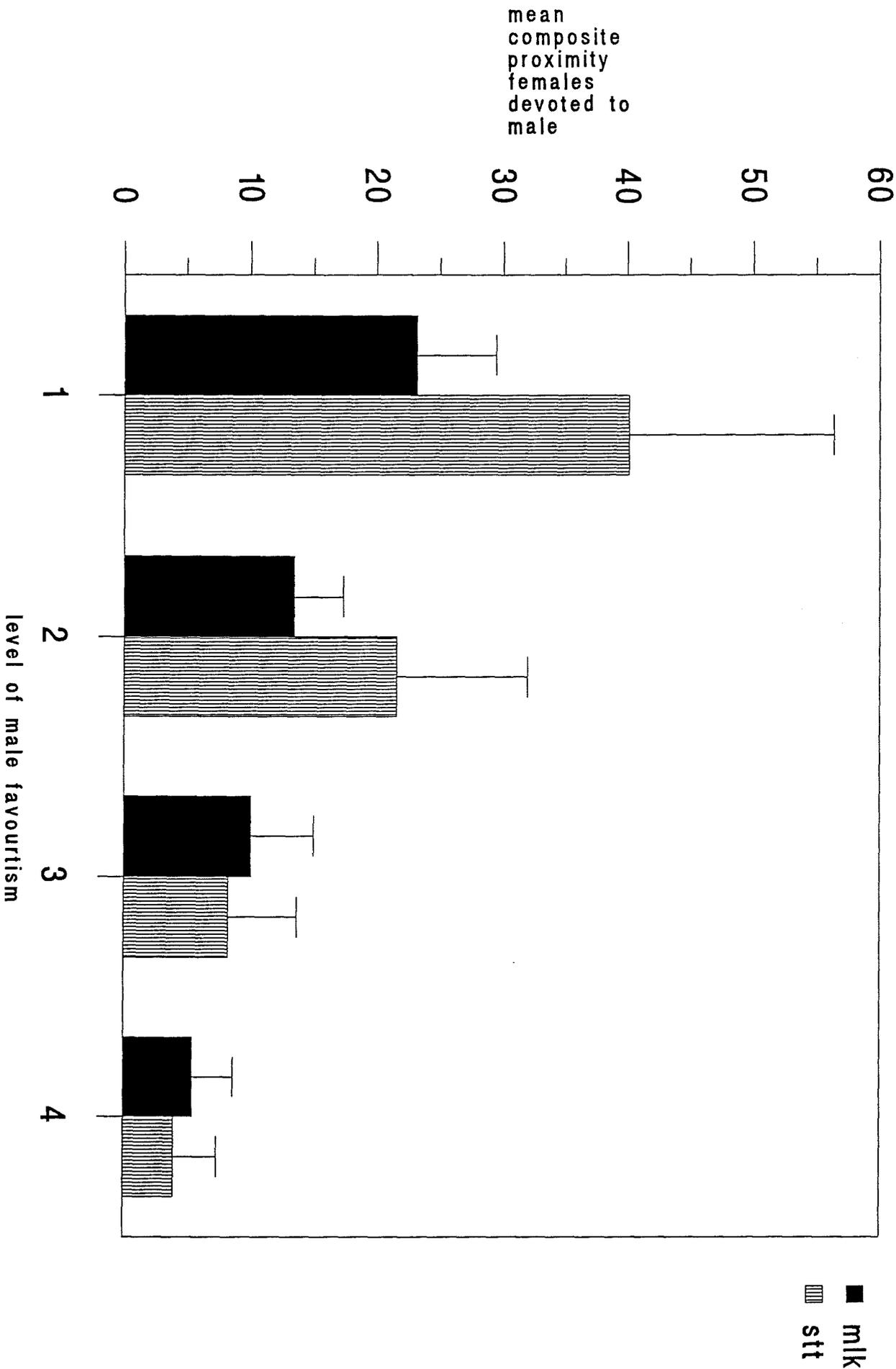
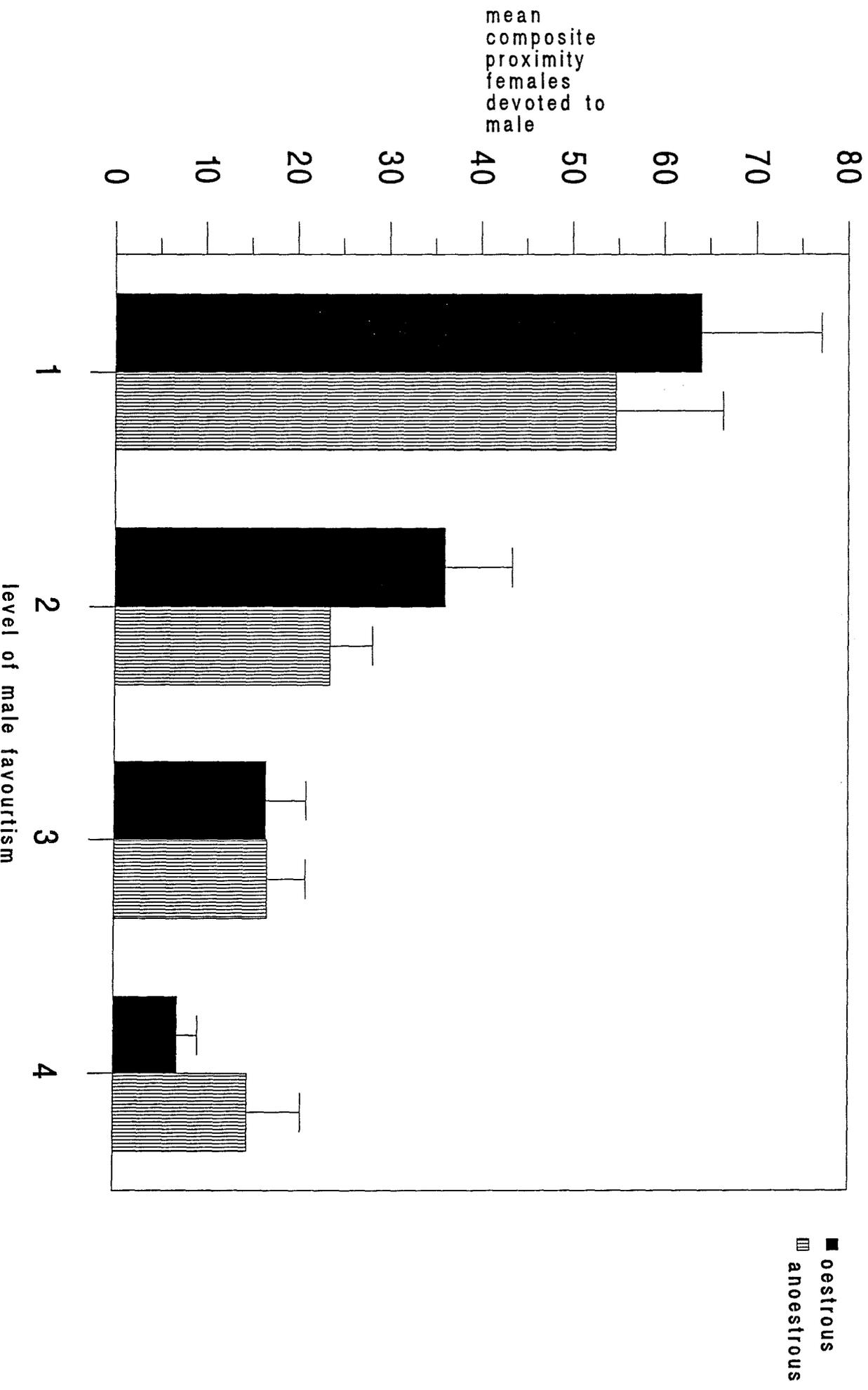


Figure 9.6 Mean composite proximity females devoted to successively favoured males (1,2,..etc) in 5 bimonthly periods: comparison across reproductive state. Focal data used from 10 month study. Standard errors shown.



Stability of friendship

Introduction

The stability of relationships is not a question addressed in Smuts (1985) influential study. It was identified in Chapter 3 of this thesis as a plausible measure of social complexity, however. Whilst a difference in the rate of change of relationships ought to *constitute* complexity it is difficult to make predictions concerning whether it will *result* from complexity. Greater social complexity might plausibly be supposed to put stress on relationships, but then, equally, the desire to maintain these relationships might rise in tandem (see section on friendship and complexity above). No predictions are made therefore, and the analyses are left to speak for themselves.

The question of whether social complexity for female baboons may vary according to their reproductive status has not yet been touched upon in this work. Smuts (1985) showed that grooming by females was distributed more widely when they were cycling, i.e. that friendship became less marked. The extent of this effect is examined in the present data.

Methods

An assessment of stability requires that each focal female's friends are identified. The criterion used to assign male friends to females was that of Smuts' (1985) 'Affiliates': males had to rank as first or second favourite regarding both a female's grooming and proximity preferences. There is an inevitable degree of arbitrariness in the procedure, attempting as it does to create a discrete category out of technically continuous data. The results, however, do agree extremely closely with a 'common sense' assignment of friends based on the available data. They are presented in Table 9.1.

Stability was calculated as follows. For each time block, starting with Nov/Dec, the percentage of the previous time block's friends that were still held was calculated (where no friends were held in the preceding time block, analysis of the stability between those blocks was omitted). This provided a measure of stability per female/time block. The data were subjected to Mann-Whitney U tests, using the factors of group and reproductive state.

Results

Non-parametric tests are used here since the data are severely non-normal. The mean stability of all relationships in the dataset was 31%. Stability of

Table 9.1 Male friends of focal females (see text for criteria)

| Females | sep/oct | nov/dec | jan/feb | mar/apr | may/jun |
|------------|-------------|---------|---------|-------------|-------------|
| <i>MLK</i> | | | | | |
| DE | RT | RT | CB, RT | RT, ND | SQ |
| DQ | SQ | HK | HK | none | none |
| MC | PH | RT | none | PH | none |
| RM | none | PH | RT | ND | RT |
| <i>STT</i> | | | | | |
| AL | not sampled | GM | JY | JY | none |
| AM | SI | none | IL | DJ | WE |
| KN | RZ | RZ, WE | MJ | not sampled | not sampled |
| MA | DJ | DJ | GG | none | DE |
| OP | none | GM | none | not sampled | not sampled |
| WT | WE | GG | SI | SI, DJ | SI, DJ |

relationships did not differ significantly between groups (Mann-Whitney U test: $X_{\text{mlk}}=0.27$, $X_{\text{stt}}=0.34$, $Z=0.42$, $N=29$, $p=0.67$) or between reproductive states (Mann-Whitney U test: $X_{\text{cycling}}=0.38$, $X_{\text{anoestrous}}=0.21$, $Z=0.98$, $N=29$, $p=0.33$).

Discussion

As far as the methods used here can show, stability of friendship did not differ between troops: we can conclude then that instability in relationships by no means inevitably grows with group size. This measure is of course opaque as to the question of whether the dynamism (Hinde 1983a) internal to the relationship grows. The absence of any effect of reproductive state on stability was surprising and, perhaps, undermines our faith in this analysis. However, it may be that populations differ.

Summary

Few results emerge from this chapter. General female-male association was reasonably high but seemingly unaffected by the size of a female's group or matriline. There was some evidence that high-ranking females associated with males more than did low-rankers. Study animals were shown to have friends but the stability of friendship was not affected by group size.

The conclusion would seem to be that these baboons were not exercising the flexibility which Byrne et al. posit regarding cross-sex bonding. It has been difficult to formulate clear predictions about group size, complexity and friendship. This may partly result from the complexity of the construct of friendship itself. Pitched at the level of relationships, friendships serve different functions for the two parties concerned and it is fair to say that friendships may modulate a fair chunk of baboon society: grooming; agonistic aid; infanticide; sex. By comparison, the measures used here were fairly crude and pitched at detecting gross differences which proved not to be present.

Chapter 10: Frequency of Interaction

Frequency of All Interactions

Introduction

In Chapter 3, interaction frequency was listed as a dimension of social complexity. We have seen that social complexity results from social behaviour because the target of the behaviour is a decision maker, making contingent responses, possibly on the basis of the prediction of future events. However, the processing demands posed by social interactions are further increased purely by the *rate* of exchange between subjects of a social interaction.

Within an interaction this high rate discriminates in favour of individuals who can assimilate the signals they are receiving and modulate their own behaviour to achieve the desired outcome of the interaction. Stereotypy of behavioural sequences in such situations probably indicates that speed of response is favoured over intelligent assessment. Nevertheless, from a purely computational perspective, there must be greater complexity in a system that can mediate motivational, cognitive and environmental input *fast* since these processes must initially proceed simultaneously (implying extra cognitive requirements).

Across interactions the processing demand is in assimilating the implications of the outcome of one interaction for the next. If we beg the question temporarily of how social complexity is generated in the first place, assuming simply that it is there, then it can be seen that a high rate of interactions in a socially complex group will discriminate in favour of individuals who quickly assimilate the social consequences of what has occurred.

This chapter examines interaction frequency i.e. across-interaction complexity in the study troops. Listed below are a number of factors that might be expected to affect the frequency with which an individual experiences interactions.

(1) Group size. Regardless of the possible requirements of extra social manipulation in a large troop, there are simply more individuals there to be interacted with. Thus we might expect increased interaction frequency in STT. On the other hand, group size is known to correlate with day journey length (Clutton-Brock and Harvey 1977b) and data in Chapter 6 showed that STT spent more time feeding or moving than did MLK. This might indicate an activity budget constraint on at least the total duration of social interaction. A third possibility is that interaction rates could be maintained constant across a number of group sizes but

that the quality of interaction changes. This possibility recognises the conflicting pressures of extra social and foraging demands and the consequent possibility of a change of strategy in attempts to affiliate.

(2) Sex. Female and male baboons are playing quite different 'games' within the group's social structure and interaction frequencies might reflect this. Baboon groups show male transfer and have been described as female bonded (Wrangham 1980). The cohesion that this entails or requires might cause us to expect a greater degree of interaction between the females. However, Byrne et al. (1990) have questioned the female-bondedness of savannah baboons. This was discussed in Chapter 9 where data was presented showing that, indeed, females groomed males as often as they groomed unrelated females and juveniles. However, interaction counts are made up of both within and between sex encounters. Males certainly take an interest in greeting and grooming interactions with females. However, outside of consort activity, male-male interactions tended to be rare in the study troop. In contrast, the females sought contact with both sexes.

(3) Sexual status. Relationships between females and males are likely to change depending on whether the female is cycling or anoestrous. This may reflect the kind of resource that the female represents in these various states, an issue Smuts (1985) has considered. She shows that female olive baboons in her study troops groomed a much wider number of males when they were cycling than when they were not. The effect of a female's sexual status on her interactions with other females is difficult to predict. Barton (1989) has shown that the percentage of months spent cycling by females in STT is negatively correlated with the approach rate they experienced from other females, but uncorrelated with their own approaches. This of course might be a result of cycling females tending to associate more with males.

(4) Food availability. The effect of food availability on social interaction is likely to be via activity budgets, the most plausible hypothesis being that interaction frequencies go down as foraging requirements go up. However, as with group size, this effect may be reflected in the quality rather than quantity of interactions. Interestingly, Marsh (1992) found that juveniles in STT did alter their social behaviour in periods of low food availability. What was surprising however, was that grooming durations were unaffected whilst time spent in affiliative approaches markedly declined. This is a counter-intuitive result since greetings ought to be a much more economical way of maintaining relationships than grooming. It is

possible that the change in behaviour reflected a change in the value of certain kinds of relationships, perhaps resulting in a kind of 'siege mentality'. In this, effort would be put only into quality relationships such as those with kin, for which relationship's servicing there would be no substitute for grooming.

Another possibility is that seasonal stress exerts its influence on energy rather than activity budgets. In so far as it can be done whilst stationary, grooming might be energetically more economical than greeting.

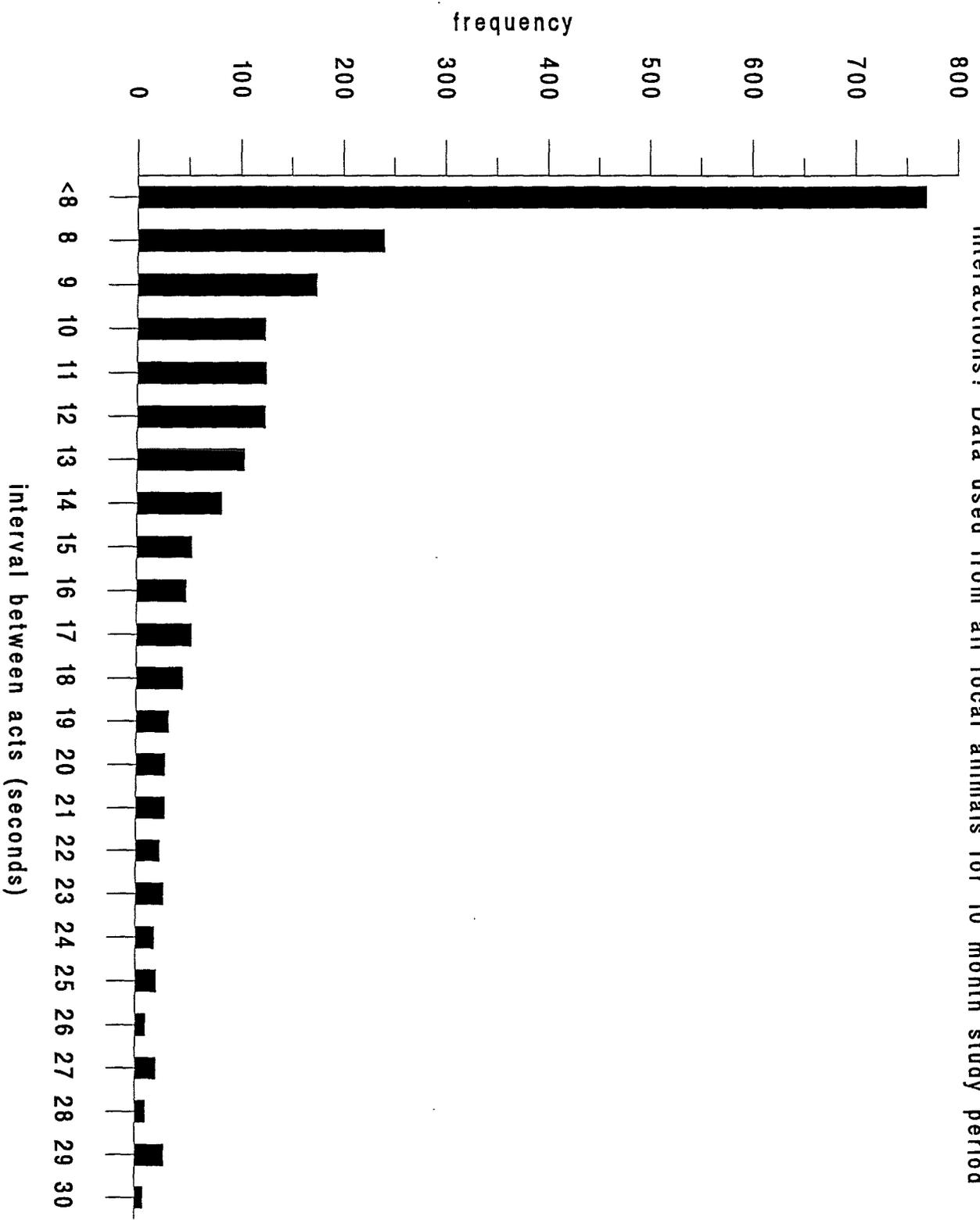
(5) Rank. Rank makes predictions about and is defined by the direction of various types of interaction but does not predict their frequency. Some prevailing aspects of models of baboon social structure might, however, might lead us to expect greater interaction rates for high rankers. Priority of access models of affiliation could generate this expectation in that all other animals are assumed to be trying to affiliate with high rankers. Also, if high rankers occupy a more central position in the troop as has been suggested (e.g. Chance and Jolly 1970) they might be expected to experience interactions more often purely on the basis of chance. However, Barton (1993) found that whilst dominant females in STT did occupy a more central position in their group, he also found (Barton 1989) that they did not experience more interactions.

Defining an interaction

I define an interaction as one or more other-directed acts exchanged between two or more individuals in rapid succession. Interactions are thus distinguished from their composite acts: this recognises the importance of the context of previous and following acts in understanding any single one act. A problem arises in deciding the number of previous acts that constitute this context. From the point of view of the analyst this is a question of deciding when one interaction has ended and another has begun.

It is possible that there are discontinuities in the interval between acts exchanged by individuals that would indicate the existence of some natural compartmentalising of acts into interactions, perhaps that the baboons recognised themselves. In order to investigate this I created a histogram of the time interval between acts exchanged between the same two (or more) individuals using all the focal data. This is presented in Figure 10.1. (Note that for time intervals of less than eight seconds, my speed of typing (and hence the recorded time interval) was slower than the speed with which acts were exchanged. Of necessity then, intervals of less than eight seconds have been lumped together. Note also that the histogram does not represent values greater than 30 seconds: these are of no interest as, being

Figure 10.1 Intervals between acts in interactions: are there natural breaks that indicate new interactions? Data used from all focal animals for 10 month study period



in the order of minutes, they clearly indicate new interactions in the sense defined above)

Figure 10.1 reveals no clear discontinuity of the kind hoped for, though there are small discontinuities at 10 and 15 seconds. An interval of 15 seconds was chosen as the criterion for a new interaction having started between the same individuals. This was because it was felt that to err on the side of the interval being too long was preferable since this lessened the chance of acts appearing in interactions without important context. Fifteen seconds seemed a generous allowance.

Not all acts in the ethogram were considered as constituting interactions. I have taken as my guiding principle that the animal to which an act is directed should be forced to make a new *decision* for it to be considered to have entered an interaction. The following acts were considered not to reach this requirement;

approach or leave passively
 look at
 avert gaze
 scan
 be vigilant
 wahoo

However, it should be noted that apart from the passive approaches and leaves, all these acts were retained as part of an interaction *once it had begun* (assuming they met the other requirements discussed previously). Grunting to an animal that has just presented to you is different from exchanging a series of affiliative grunts whilst feeding. In the former case the interaction, the need for a decision, has been *forced* and the grunt constitutes a definite response.

Notes on analysis

The basic datum in the following analyses is the number of interactions of any particular kind that a focal individual experienced in a bimonthly block divided by their sampling time in that period. The resultant figure is expressed as a rate: interactions/hour. As the following analyses demonstrate, the rate of interaction is much higher for animals in consorts or engaged in consort follows. For this reason, the two types of data have been separated at the outset; consort/consort follow interaction rates have been calculated using the amount of time the individual was sampled in consort/consort follow and non-consort/consort follow rates likewise, using total non-consort/consort follow sampling times.

These analyses are fairly basic. They take no account of whom animals are interacting with or the context of the interaction. High interaction rates do intuitively seem to index complexity. In this case however, as in others, we are left unsure whether high frequencies of interaction comprise or result from complexity.

Results

Before dealing with interaction rates themselves it is worth setting some context by establishing whether the *density* of individuals differs between the troops. This will have implications for the kind of explanations that would be sought for differences in interaction rates. Density was estimated using data on animals within the five metre proximity grade in 2 minute focal samples. In so far as this is a sufficiently great distance for individuals to tolerate those other than close affiliates, it was assumed that density in this grade would change according to troop density as a whole. The measure used to compare density between the troops was;

total number of animals captured within 5m grade during point samples / total number of point samples

This quotient was computed for each individual. As might be expected, STT proved to have a higher density as can be seen in Figure 10.2. Given the great discrepancy in variances a Mann-Witney test was used and proved to be significant ($Z=2.06$, $N=19$, $p=0.039$).

The interaction frequency was greatly higher for individuals in consorts than for those who were not ($X_{\text{consort}}=15.0$, $X_{\text{no-consort}}=7.3$, $t=4.6$, $N=136$, $df=48.36$, $p<0.001$). Consortships clearly represented a special social scenario for the individuals involved. The data set on consorts is small and lacking in the detail that is required for a separate but worthwhile analysis of such socially 'charged' situations. Neither the variable of troop nor sex significantly affects interaction rates in consorts. In consequence, the following analyses pertain solely to data on unconsorted animals.

Individuals in STT have a significantly higher interaction rate than do those in MLK as shown in Figure 10.3 ($F=11.0$, $N=90$, $df=1$, $p=0.001$). Females have significantly higher rates of interaction than males as shown in Figure 10.4 ($F=20.9$, $N=90$, $df=1$, $p<0.001$). The interaction of these effects is non-significant ($F=2.6$, $N=90$, $df=1$, $p=0.114$) but an examination of Figure 10.5 shows that in the sample, it is the females in STT that accentuate the difference between troops.

The bimonthly sampling period has a significant effect on interaction

Figure 10.2 Density of animals in the study troops. Data is from 2 minute point samples on focals; it is assumed to generalise to whole troop. Standard errors shown

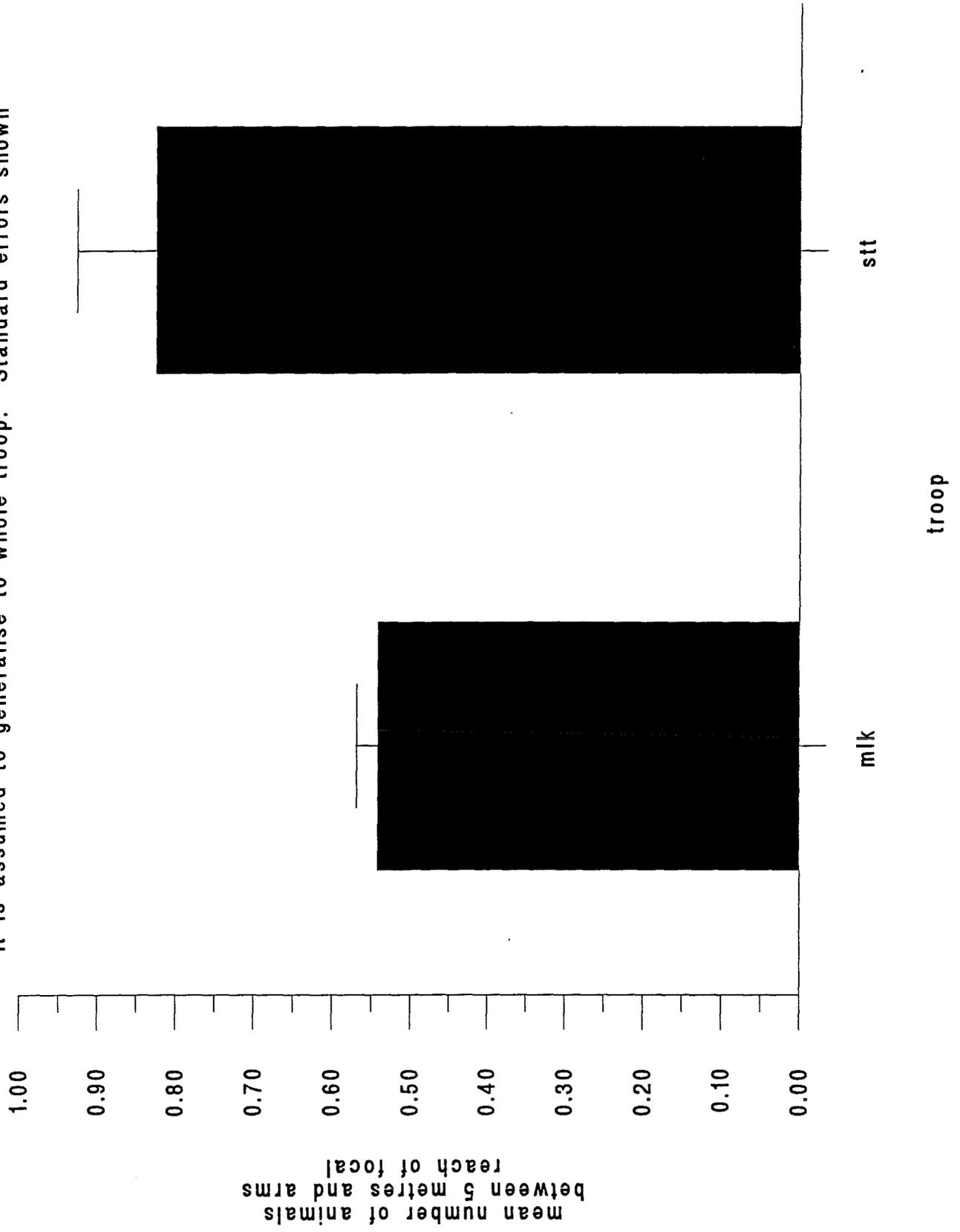


Figure 10.3 Interaction rate in the study troops. Focal data from 10 month study period. Standard errors shown.

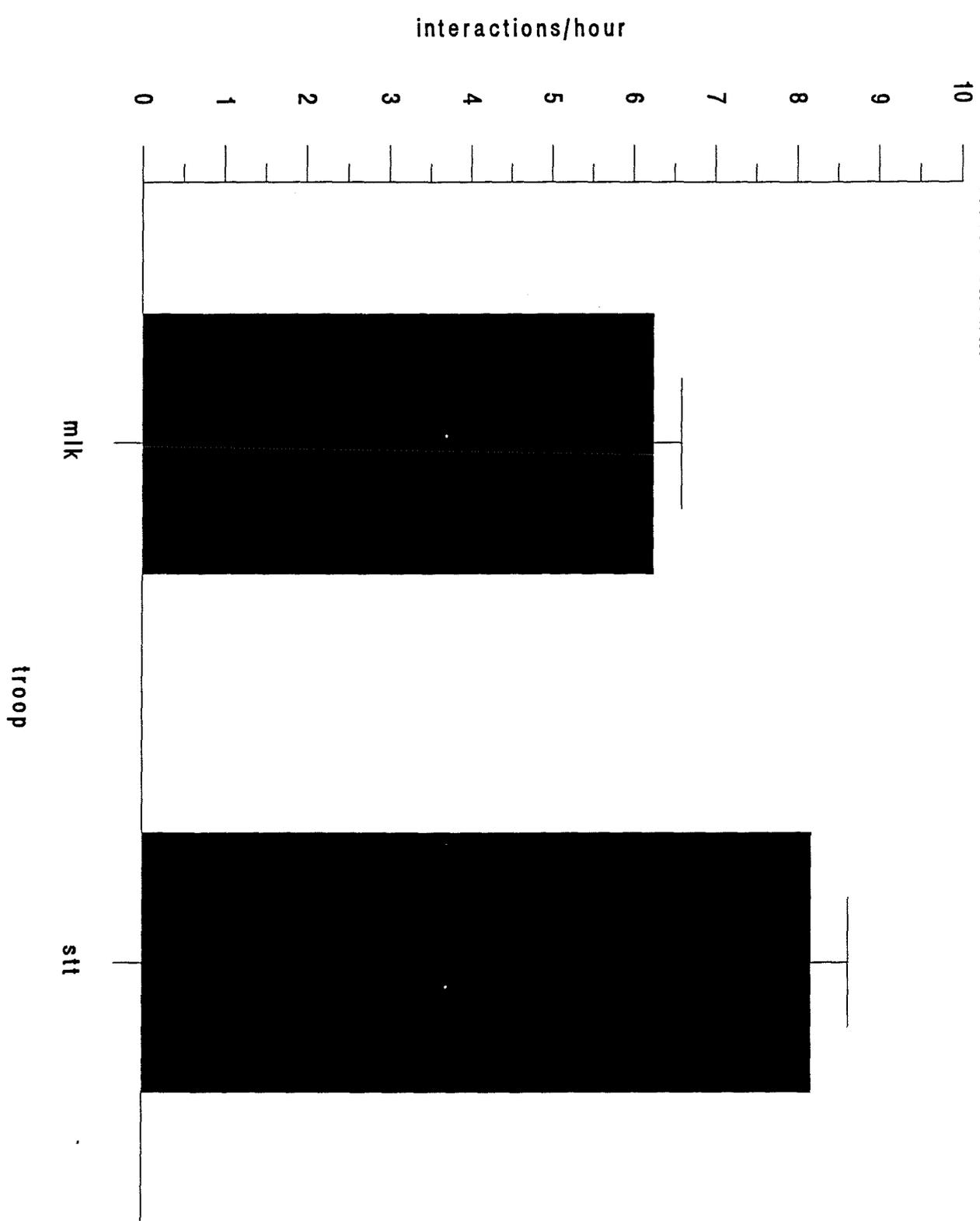


Figure 10.4 Interaction rate compared across sexes. Focal data from 10 month study period. Standard errors shown.

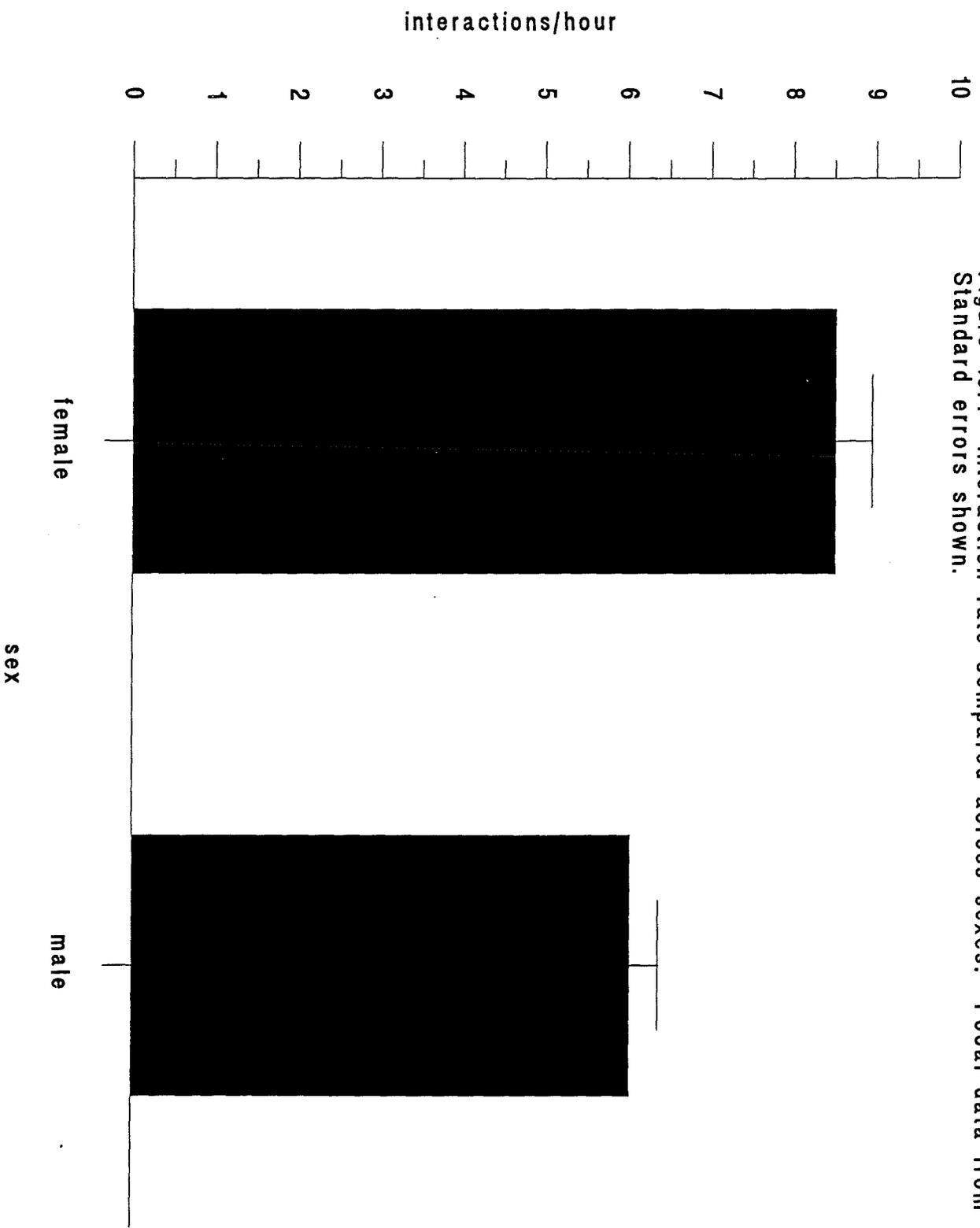
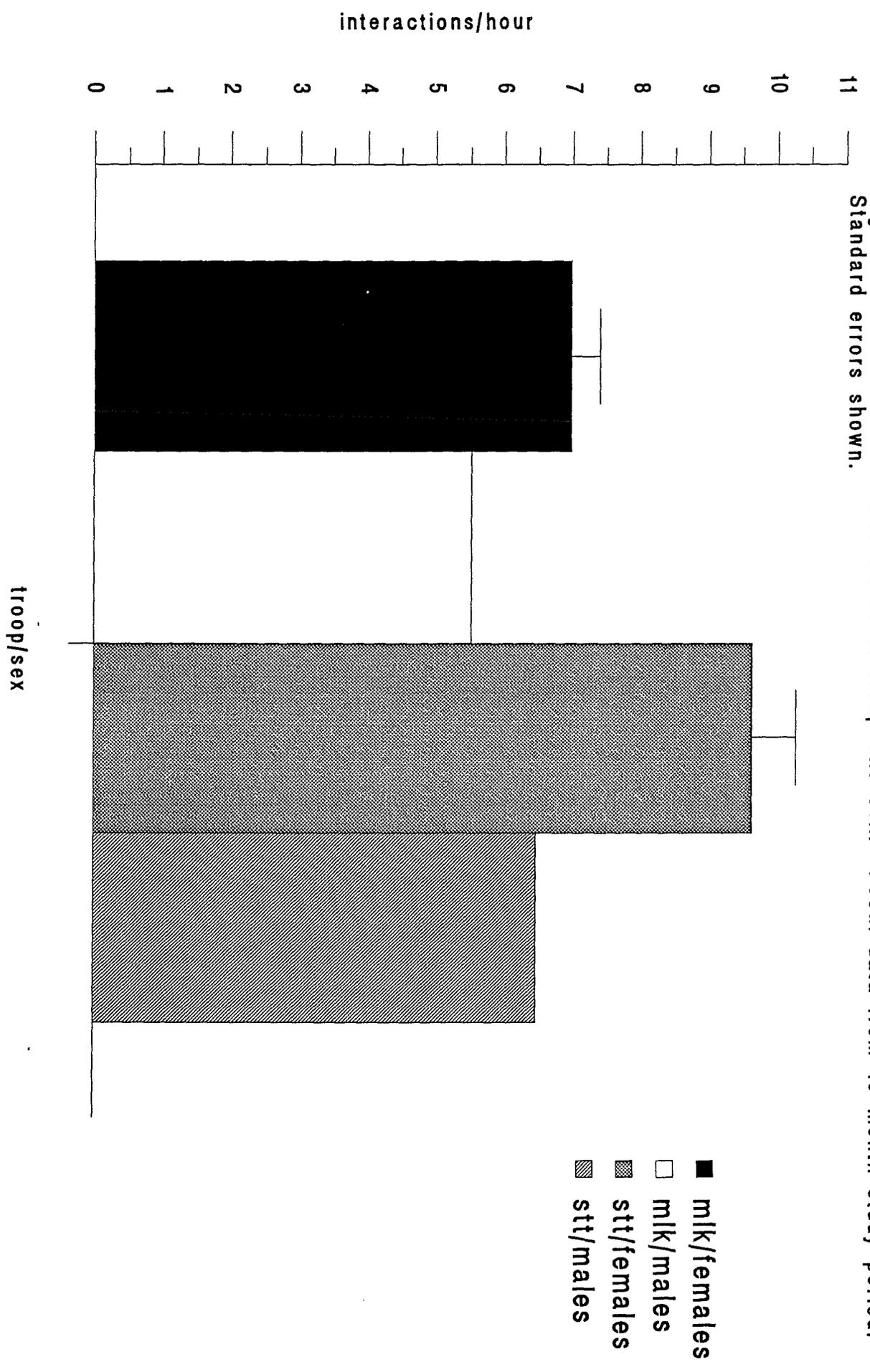


Figure 10.5 Interaction rate: effect of troop and sex. Focal data from 10 month study period. Standard errors shown.



frequency ($F=2.6$, $N=90$, $df=4$, $p=0.46$). To investigate the possibility that this was an effect of food availability, interaction frequencies were correlated with food availability estimates (see Chapter 4 for a discussion of these). The correlation was found to be non-significant ($r_s=0.03$, $N=90$, $p=0.71$), a result unaffected by the treatment of each troop separately. There was no evidence of non-linear (e.g. parabolic) correlation. The sparsity of data on food availability make these analysis rather coarse and it is possible that an effect on interaction frequency would emerge with more data.

The effect of a female's rank on her interaction frequency was investigated. Two strategies were employed for characterising rank across the troops. The first was to treat rank as a quotient (female's rank/no. of ranks) which enabled animals from both the troops to be placed in a single rank order of ranks. Since seasonal factors were shown to be important (see above), use of data from focal animals who were absent for part of the study could constitute a confound. The following solution was applied: Karen, properly sampled for only the first three months of the study period was excluded from the analysis. Data from Opuntia and Alison, studied respectively for the first six and last seven months were amalgamated on the basis that their ranks differed by only two places. Means were taken of the interaction frequencies during the three months in which they were both studied.

These data were subjected to a Spearman test and no correlation of rank and interaction frequency was found ($r_s=-.05$, $N=40$, $p=0.754$).

A second method of examining the effects of rank was to order individuals by their rank within each troop and do a two-way analysis of variance using the factors of rank and troop. This also showed rank to be non-significant ($F=3.8$, $N=40$, $df=3$, $p=0.584$) The data are shown as a scattergram in Figure 10.6.

Frequency of Agonistic Interaction

Introduction

There are at least two good reasons for counting the frequency of agonistic interaction. The first is that agonism may lead to injury, and perhaps even death and, as such, it comprises an aspect of the social environment that we would expect individuals to be attempting to deal with optimally. This is more likely the case in males where the severity of wounding in a number of species seems to be higher (see Smuts (1987) for review). Gregar, one of the focal animals in this study fell from high rocks during a consort fracas and appeared to have damaged his back so severely that he had trouble moving at the speed that STT were accustomed to

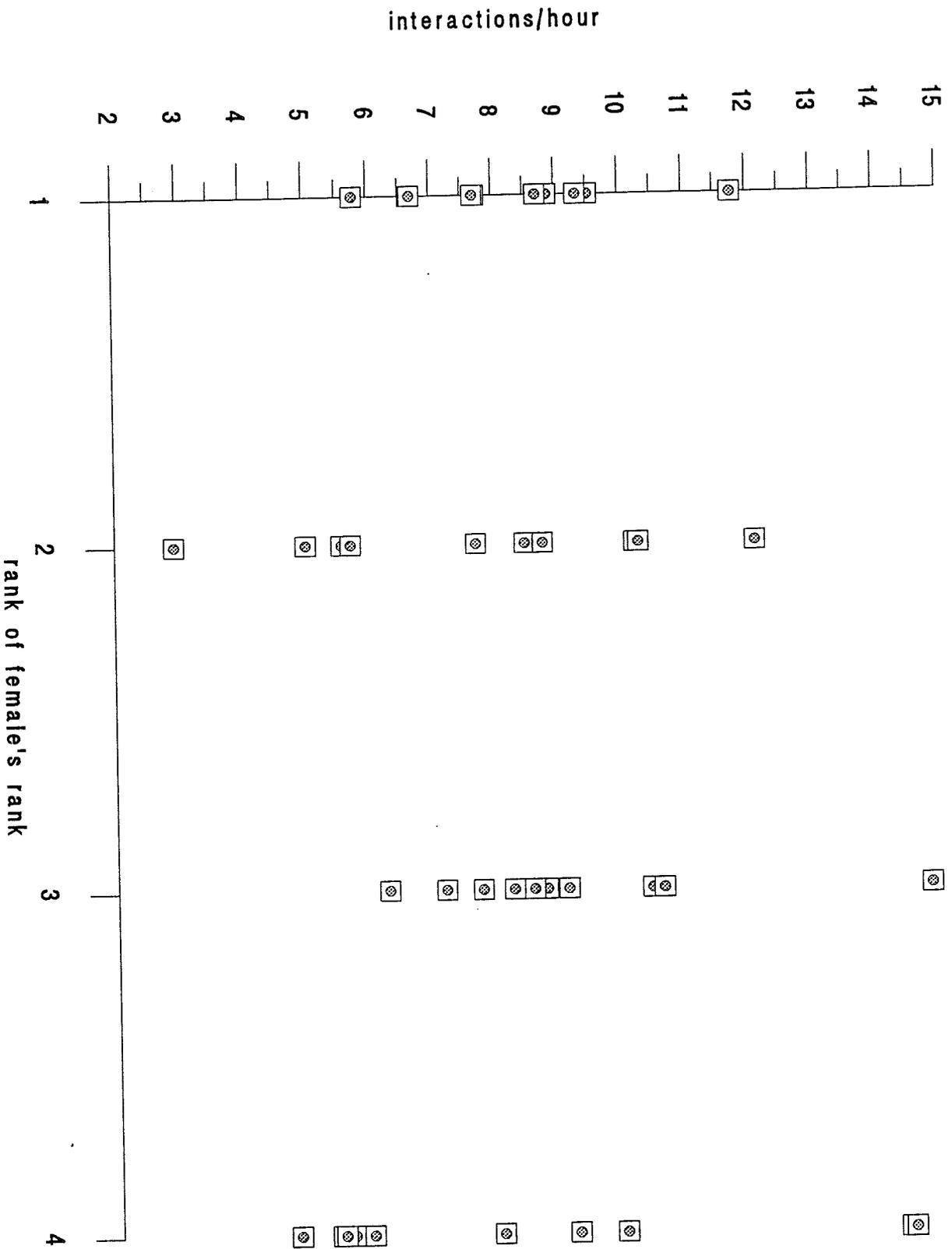


Figure 10.6 Effect of female rank on interaction rate. Females in each troop are ranked by their place in the hierarchy (ie rank distances ignored). Focal data used from 10 month study period

range. He left the troop a few weeks later having shown no sign of improvement.

A second reason is that aggression and, by association, agonism, might be advanced as a general index of instability. Situations in which aggression may be expected to occur include; consort takeovers, attempts to increase dominance, attempts to maintain dominance, resource competition, support by third party for any of the above and males preventing females from interacting with other troops.

Aggression directed towards changing dominance will *cause* instability. Conversely, aggression directed towards maintaining dominance may be a *response* to perceived instability. Fights that break out over resources indicate that dominance is not sufficiently strong to prevent this occurring. In troops with only two large males, for example, consorts may be simply 'handed over' since the dominance relationship is so strong and no opportunity for coalitions exists (Henzi pers comm). Nothing could be further from the truth in STT and MLK however, where coalitions are an important, perhaps the most important determinant of consort takeover success. The opportunity that coalitions afford is the flip side of the instability they comprise.

More generally, violence can be expected to break out when the usual methods for mediating conflict fail. Calculated aggression constitutes a different case of course. I witnessed one episode where the high ranking female Withania simply walked up to the lower ranked Duiker and bit her hard whilst she was grooming their mutual male friend, Stilton. Whilst Withania's motives can only be speculated upon, of the fact that the attack *was* motivated there can be little doubt. But much aggression may result from uncertainty in the relationship between two animals; certainly in terms of which is dominant but also as regards the resources available to each (such as allies). It is my guess that if each animal had complete information on the recent social history of potential combatants, fights would be more infrequent.

The instability of relationships and the uncertainty this generates in those that hold them ought to be factors feeding each other. As troop size grows, members will have access to an increasingly small fraction of the total social information available and even if they have access to this information, will be under increasing processing and memory constraints. For these reasons we might expect greater agonism in STT.

A further means by which uncertainty might result in unintended escalation to aggression lies within the scope of interactions rather than relationships. This is the misinterpretation of signals. Just as an individual with perfect information on another's relationship with both itself and others could restrict aggression to calculated sorties, so could an individual with perfect knowledge of its opponent's

internal state. This moves the discussion back to 'mindreading' of the Krebs and Dawkins (1984) variety.

Instances of polyadic agonism are also addressed in this section. The complexity that these interactions embody has been discussed by a number of authors (e.g. Harcourt 1988; Kummer 1988) and also earlier in this thesis.

Notes on analysis

This analysis proceeds in much the way as that done above for the case of frequency of all interactions. An agonistic interaction is defined as one containing a behaviour from the category of AGONISM (see ethogram in Chapter 4). Polyadic agonistic aggression is defined likewise with the additional requirement that at least three individuals be involved.

As before, consort/consort follow samples have been separated from others at the outset. The problems of dealing with consort data have already been discussed. They are exacerbated in the case of agonistic interactions in that the dataset is yet smaller and the agonistic interaction rate highly variable, depending on the current state of the consort or consort follow. In consequence, no analysis has been attempted of the consort data.

The number of polyadic agonistic interactions was sufficiently low that for many individuals there were bimonthly periods where none were observed. Since the sampling times were variable across animal/bi-month blocks, these 'zeros' could not really be considered equal. For the polyadic agonism analyses, therefore, data has been collapsed across all bimonthly periods for each animal.

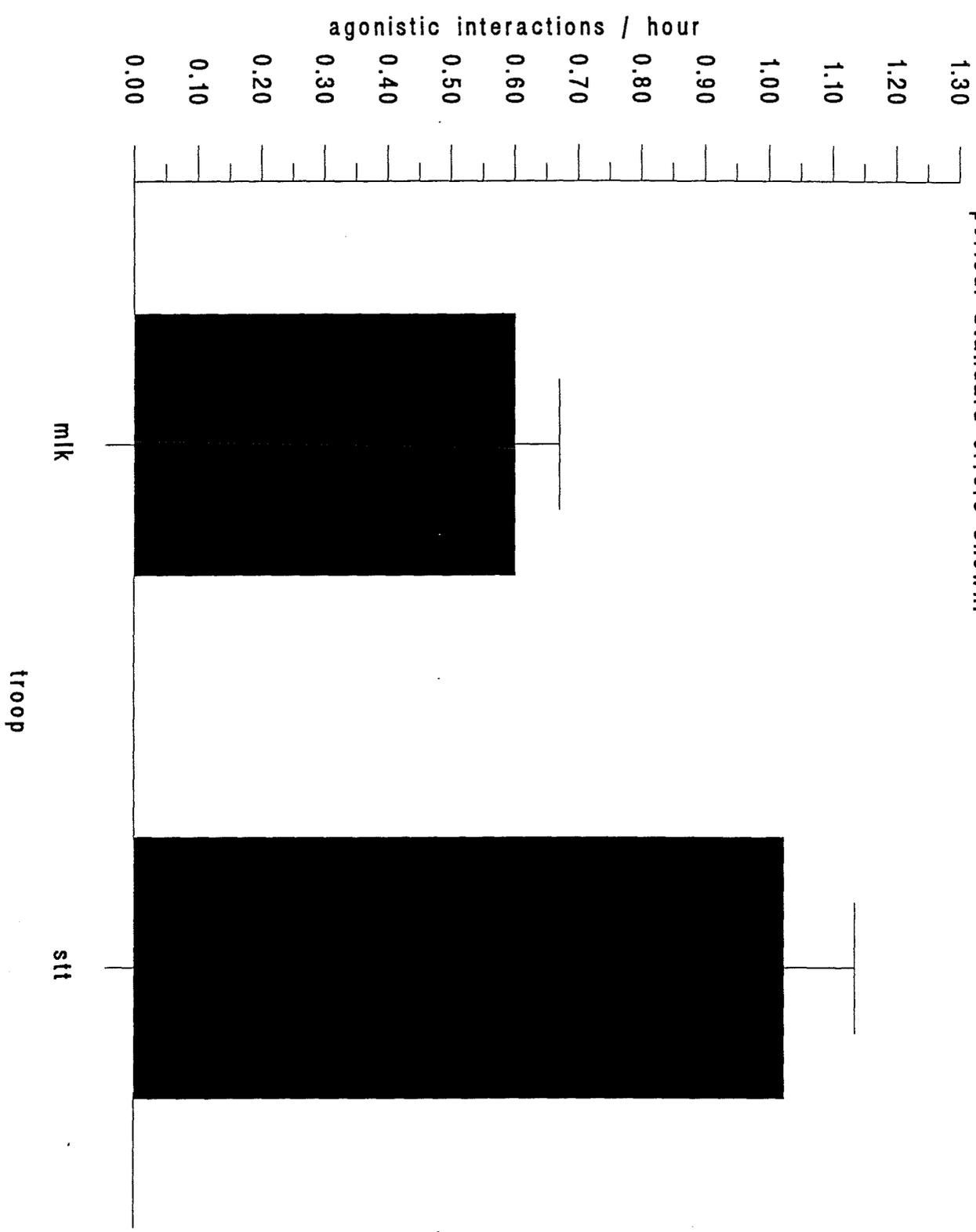
Results

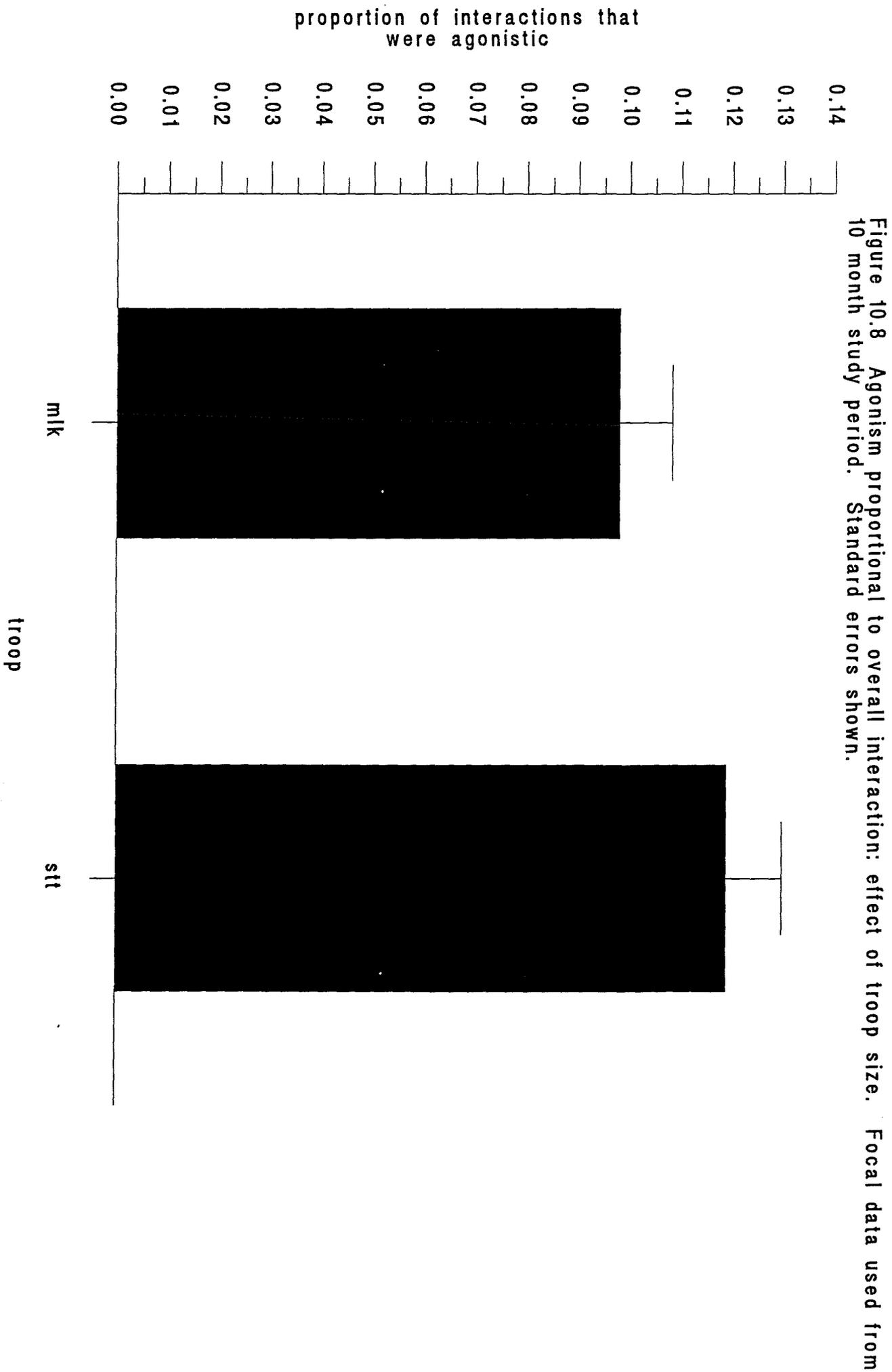
There were significantly more agonistic interactions per focal animal in STT than in MLK ($F=10.16$, $N=90$, $df=1$, $p=0.002$). However, this partly reflected the general trend towards more interactions in STT. The proportion of interactions that were agonistic still favoured STT but the difference was less striking ($F=2.99$, $N=90$, $df=1$, $p=0.088$). These results are shown in Figures 10.7 and 10.8

There was no significant difference between absolute rates of agonistic interaction compared across the sexes ($F=0.20$, $N=90$, $df=1$, $p=0.653$). It should be borne in mind however, that the overall interaction rate was higher for females (see above). Thus, comparing the *proportion* of interactions that were agonistic, males showed much the greater amount ($F=11.01$, $N=90$, $df=1$, $p=0.001$). This is shown in Figure 10.9.

The bi-monthly period exerted an effect on the proportion of interactions that were agonistic ($F=2.8$, $N=90$, $df=4$, $p=0.031$) and this factor interacted with the

Figure 10.7 Rate of agonistic interaction: effect of troop size. Focal data used from 10 month study period. Standard errors shown.





proportion of interactions that
were agonistic

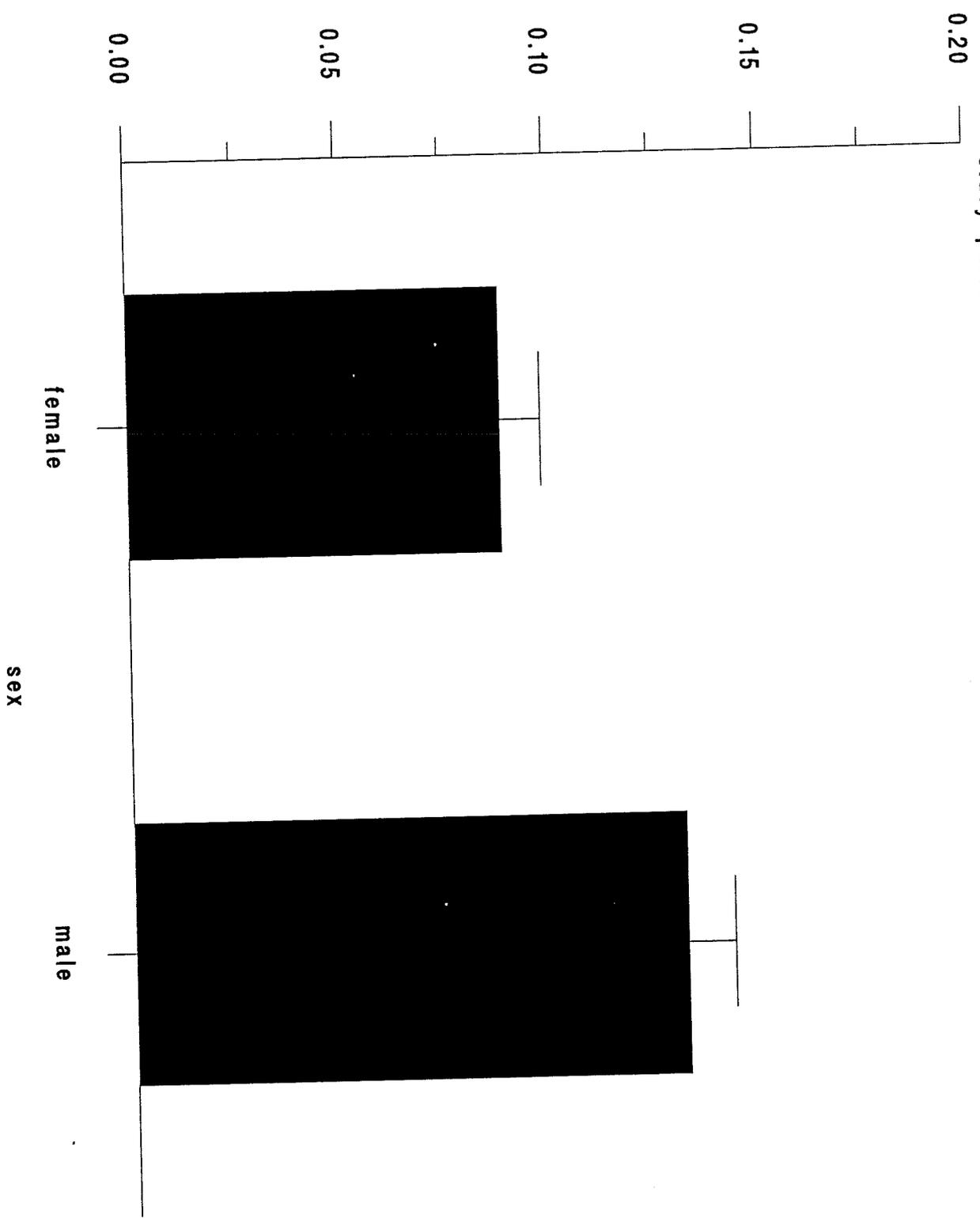


Figure 10.9 Agonism proportional to overall interaction: effect of sex. Focal data from 10 month study period used. Standard errors shown

factor of troop to a close to significant level ($F=2.43$, $N=90$, $df=4$, $p=0.056$). Consequently, a test of correlation between food availability and proportion of agonistic interaction frequency was performed on each troop separately. The results show that in STT the proportion of interactions that were agonistic rises significantly with food availability ($r_s=0.39$, $N=50$, $p=0.005$) but that no relationship is found in MLK ($r_s=-0.06$, $N=40$, $p=0.69$). The scatterplots for these data are shown in Figures 10.10 and 10.11.

The frequency of polyadic agonistic interactions was only marginally higher in STT than MLK ($F=0.11$, $N=19$, $df=1$, $p=0.744$) and only marginally higher in males over females ($F=0.70$, $N=19$, $p=0.800$). Transforming this figure into the proportion of agonistic interactions that were polyadic, we find that the rate was higher for MLK but that this difference was not significant ($F=2.12$, $N=19$, $df=1$, $p=0.166$). The proportion was almost identical when compared across sexes.

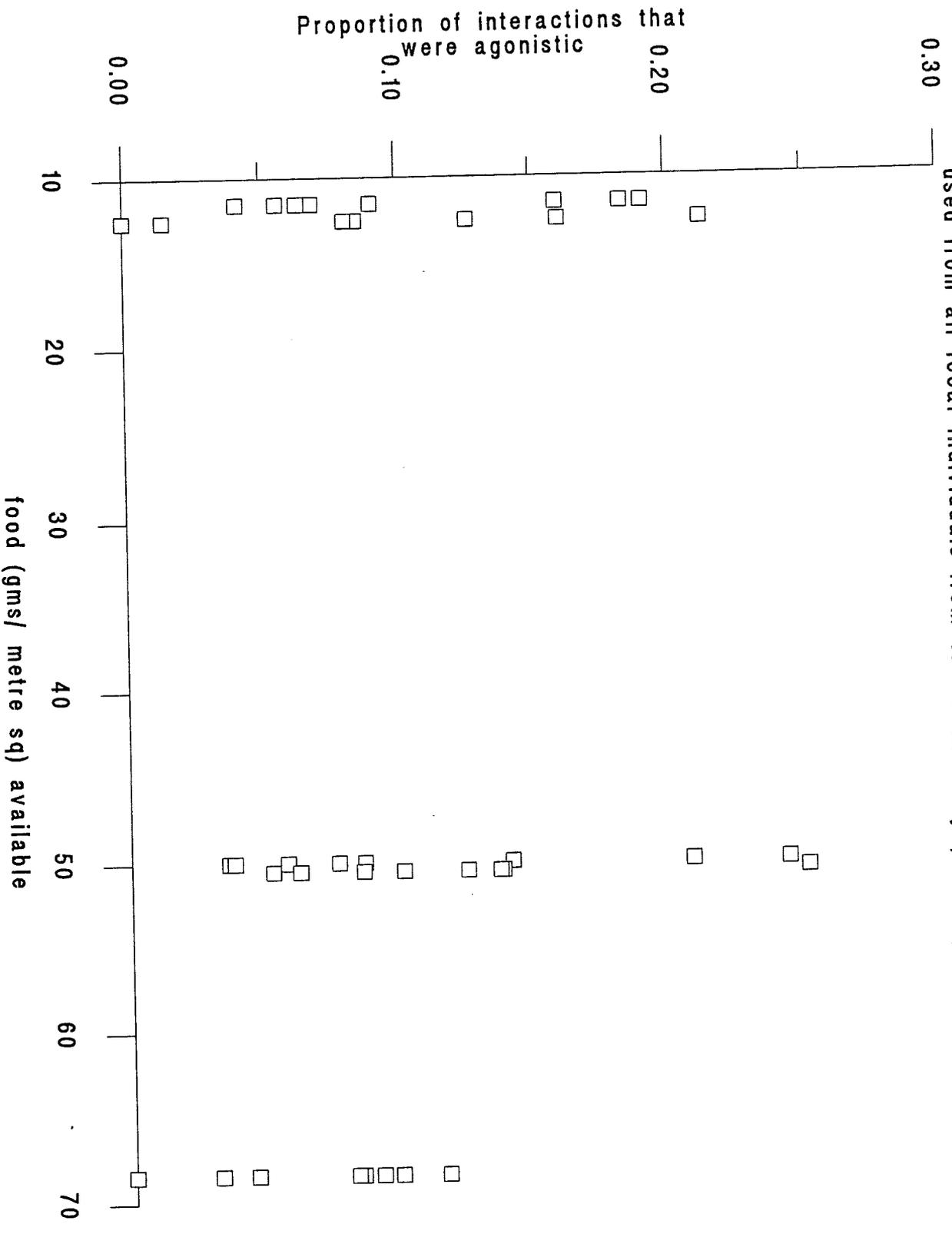
The effect of rank on rate of agonistic interactions was assessed using the two methods described previously for the case of all interactions.

Rate of agonistic interactions was not related to female rank when females from both troops were ordered together by the quotient of female's rank/number of ranks (the first method given in the previous section) ($r_s=0.25$, $N=40$, $p=0.127$). Nor was a difference in agonistic interactions found across ranks when animals were ordered within their own troop only (the second method given in the previous discussion) ($F=1.88$, $N=40$, $df=3$, $p=0.153$). When data from this second method were subjected to a correlational test there was a close to significant effect of low-rankers experiencing more agonistic interactions ($r_s=0.31$, $N=40$, $p=0.054$).

The same three tests were then applied to the proportion of a focal individual's interactions that were agonistic. Correlation of this variable with rank as collapsed across troops was non significant ($r_s=0.25$, $N=40$, $p=0.126$). Differences in the variable as a result of a rank ordering purely within troop failed to emerge from an analysis of variance ($F=2.00$, $N=40$, $df=3$, $p=0.136$). The correlation of within group rank and agonistic proportion of all interactions did yield a significant result however ($r_s=0.32$, $N=40$, $p=0.046$). Separating the data into two troops allows us to see that the basis for most of this effect is in STT ($r_s=0.47$, $N=20$, $p=0.035$) rather than MLK ($r_s=0.20$, $N=20$, $p=0.403$). These last three correlations are shown as plots in Figures 10.12, 10.13 and 10.14.

The discrepancy between the two correlational measures both with regard to rate of agonistic interactions and agonistic proportion of all interactions suggests either a troop/rank interaction or some artificiality in the rank/number of ranks quotient as a means of ordering individuals from different groups by a common

Figure 10.10 Agonism proportional to overall interaction: effect of food availability in MLK. Data used from all focal individuals from 10 month study period (split into 5 bi-months)



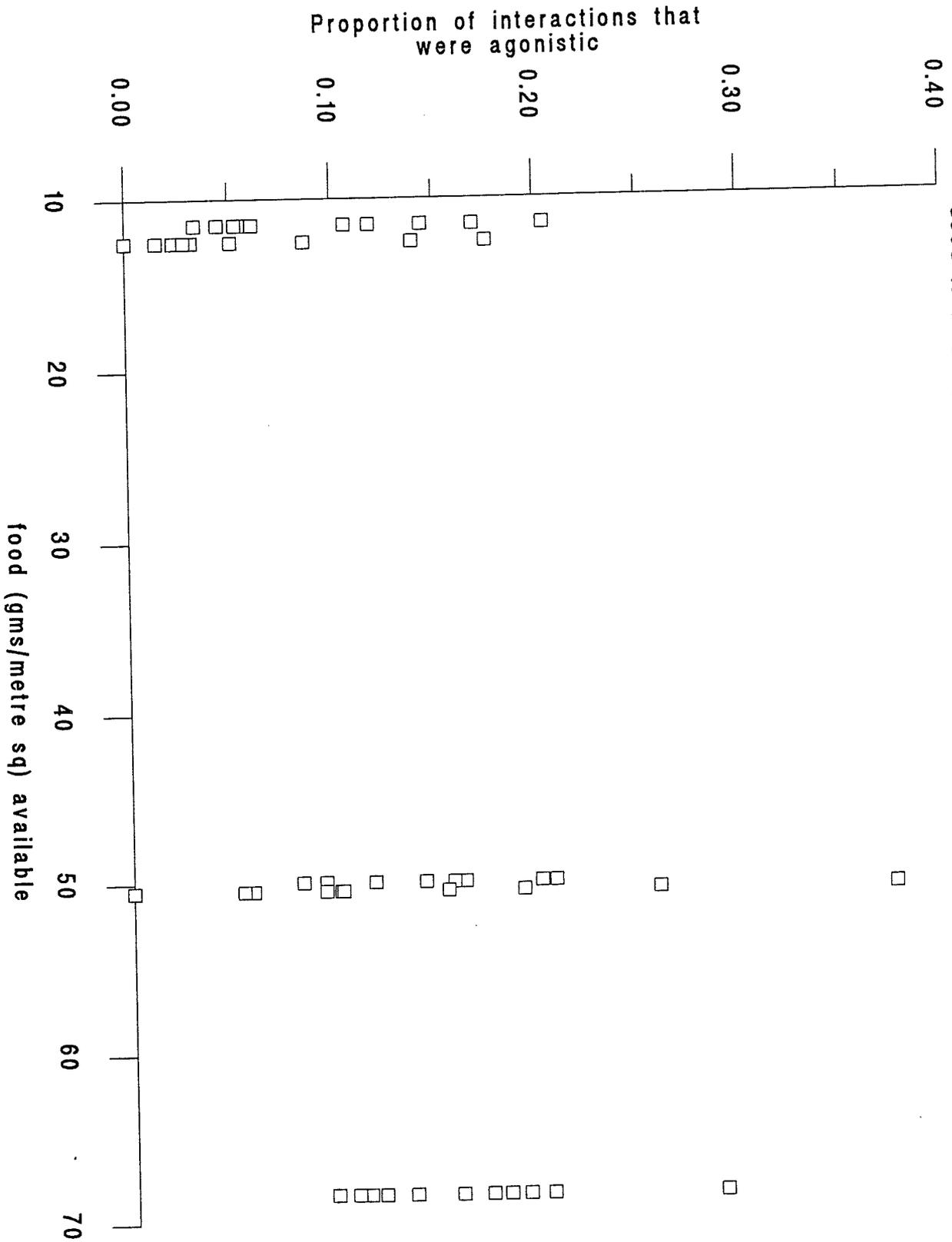


Figure 10.11 Agonism proportional to overall interaction: effect of food availability in STT. Data used from all focal individuals from 10 month study period (split into 5 bi-months)

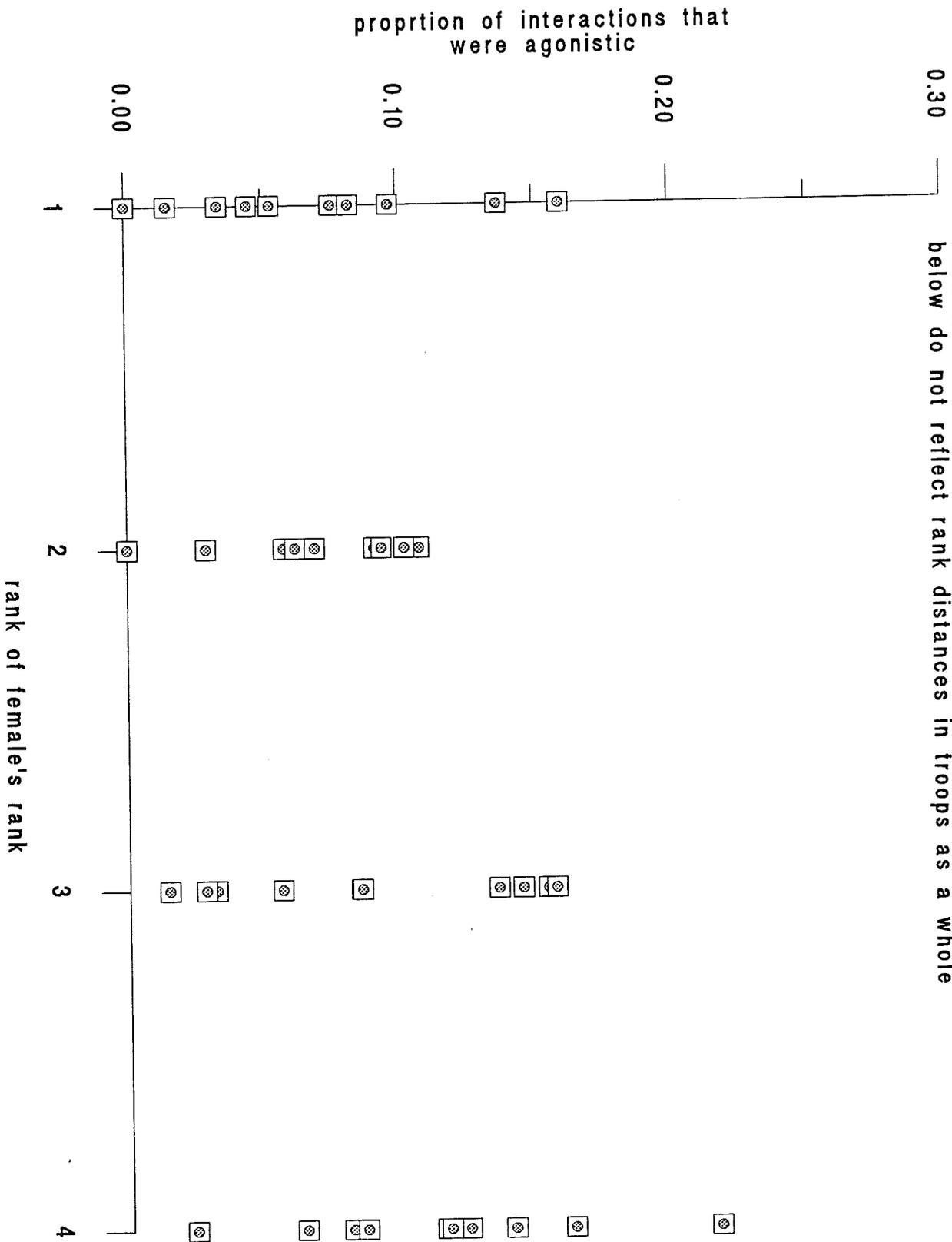
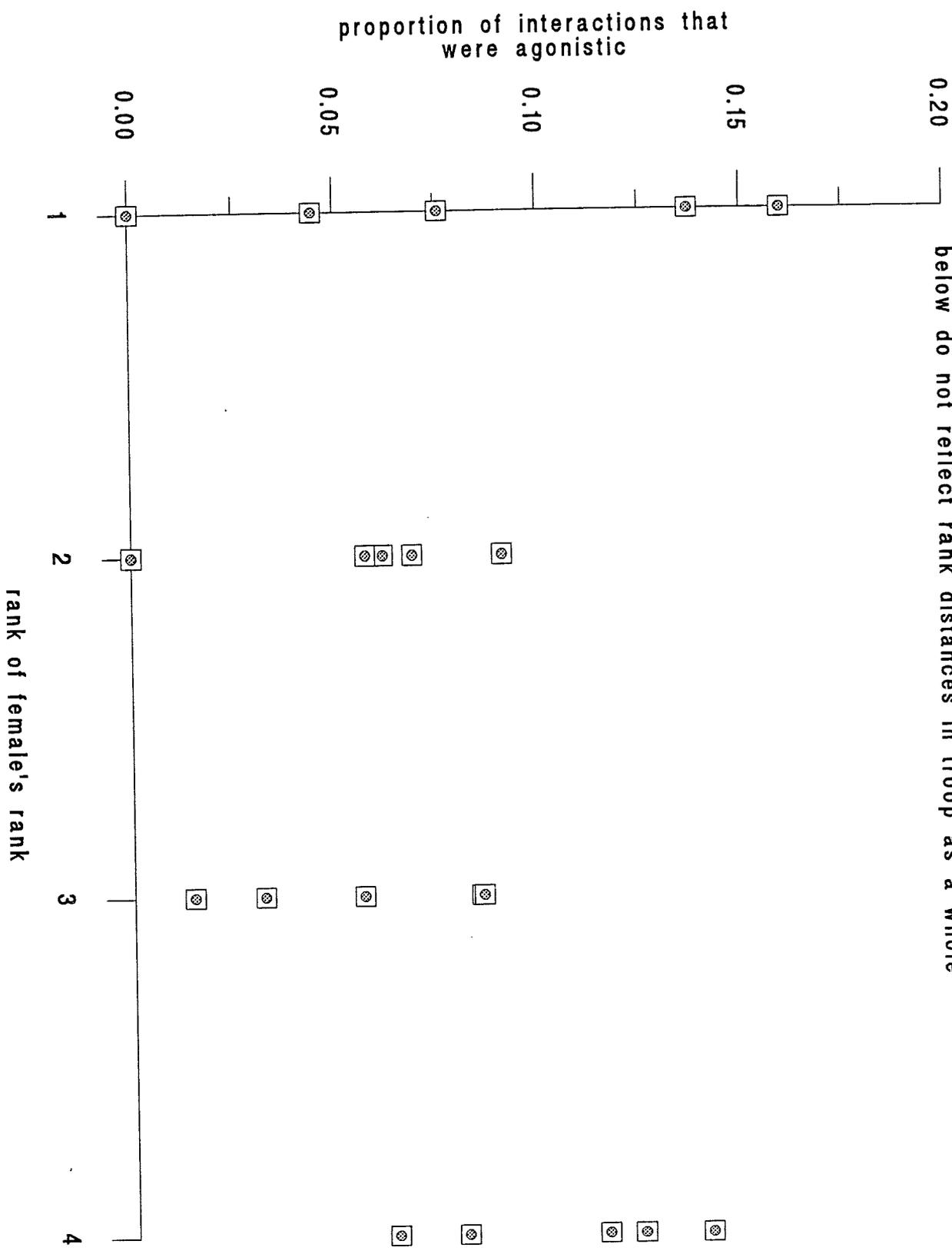


Figure 10.12 Agonism proportional to overall interaction: effect of female rank (both study troops). Data from all focal animals in 10 month period. Females ranked within focal pool (i.e ranks shown below do not reflect rank distances in troops as a whole

Figure 10.13 Agonism as a proportion of overall interaction: effect of female rank in MLK. Data used from all focal individuals in 10 month period. Females ranked within focal pool (i.e. ranks shown below do not reflect rank distances in troop as a whole)



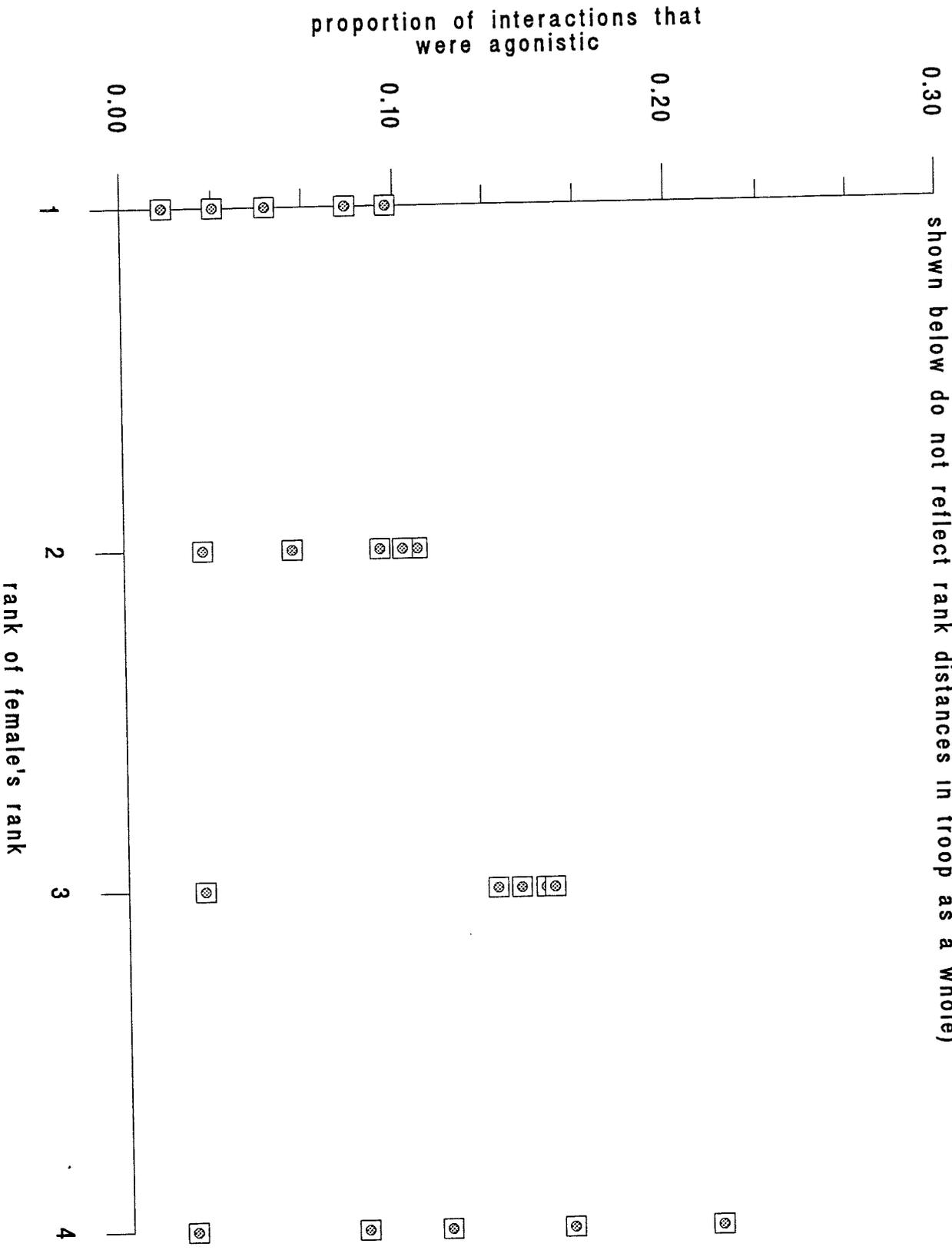


Figure 10.14 Agonism as a proportion of overall interaction: effect of female rank in STT. Data used from all focal individuals in 10 month period. Females ranked within focal pool (i.e. ranks shown below do not reflect rank distances in troop as a whole)

rank. Since the analysis of variance did not show any interaction approaching significance, the latter conclusion seem the more plausible.

Discussion

In so far as focal individuals from STT interact more frequently, we may assume that their social life is more complex in that aspect. It is difficult to go much beyond this statement however. One of the most immediate questions begged is what exactly caused this heightened interaction rate. One possibility is that it was simply a result of the higher density that was shown to exist in STT. The factor by which STT interacted more often than MLK, 131%, was comparable to the factor by which they were more dense, 152%. Mildly repellent gas molecules constitute an appropriate metaphor for this 'random model' explanation of results.

At the other extreme one could imagine all interactions as being planned or at least foreseen events resulting from entirely rational choices. Under this assumption, the heightened interaction frequency in STT would imply a greater amount of interactional work needing to be done. This recalls the discussion in earlier chapters on grooming concerning the problems of living in a troop where bonds have not been established with all others. Heightened interaction rates could simply indicate the extra number of animals needing to be greeted, say, or it could indicate an extra need for politicking.

In fact, the most plausible interpretation of interaction rates is to assume that all interactions exist on a continuum from planned to accidental with much scope for hasty 'ad-libbing' in between. Thus a portion of the extra interactions in STT probably result from the greater chance of two animals finding themselves accidentally converging on the same point (the 'random' model). Another portion may result from the greater number of animals that want and plan to interact with an individual even if it doesn't want or plan to interact with them (e.g. in the case of a feeding supplant or a not-terribly-welcome affiliative overture. And a third portion arises from the costs of failing to interact with other individuals being in keeping with the number of individuals so neglected (if indeed that is the case). For larger groups, the deleterious effects of this neglect requires extra social interaction. In terms of balancing the social budget, it is this last origin of increased interaction rate that probably has most to say about social complexity.

Ultimately, all plausible intuitions would lead us to expect interaction rates to increase with group size with only the demands of an increased activity budget constraint exerting a contrary influence.

Similarly the finding that females interacted more frequently than males was not very surprising. Much of this discrepancy may be due to the high rates of affiliation between kin but this can be seen as the most tangible form of a more general female-bondedness of baboon troops. Both sexes 'cross-bond' to a degree, with females and males set to enjoy different but perhaps equally important privileges from special relationships with each other. In contrast to females however, male-male interactions outside the temporary liaisons formed for consort turnovers were rare, appeared tense and had a high rate of negative outcomes. Grooming, for example, never occurred between males except as an apparent displacement activity during agonism against a third party.

Does this greater interaction rate indicate greater social complexity for female baboons? It is difficult to say. The first problem is that a crude interaction rate statistic is opaque to the *diversity* of interactions that constitute it. Perhaps female interactions are less diverse, perhaps the acts within them are more stereotyped. A second point is that the interaction rate has only been established as being higher outside of consorts or consort follows. A male baboon's reproductive success ultimately depends on his access to oestrous females. Gaining this access is not a simple task, as evinced by the swiftness with which acts are exchanged and relationships transfigured during an afternoon's consort activity. Thus, complexity, either cognitive or social, is perhaps better assessed by *maximal* performance regarding it, rather than normative.

The third qualifying point is that the proportion of each sex's interactions that were agonistic was much greater for males, indeed, the total number was somewhat higher. Previous discussion in this chapter suggested that agonism ought to be an index of instability and therefore complexity. Similarly, it has also been noted that because of the possibly serious consequences of agonism, optimal performance in these situation has high payoff. Also, these interactions may contain the greatest within-interaction complexity as regards the unpredictability of responses. Smuts' (1987) review of gender and aggression found no significant effect of gender on rate of agonism across a number of primate species. In the specific case of olive baboons, Bercovitch (1983) found females showing more aggression. In fact, it is difficult to come up with any reason why males should show a greater degree of agonism. Indeed, these data show that the agonistic interaction rate is only marginally higher for males; it is the ratio of agonistic to non-agonistic rates where the difference is found. Thus we might equivalently ask why the non-agonistic interaction rate of females is so high. The answer to this presumably lies in the extent to which baboons *are* female bonded. The most obvious case of this is within-family interaction where contact is frequent but

agonism relatively low (though certainly not absent).

Differences in the tendency of interactions to become polyadic might have had interesting implications for interactional complexity, politicking and general Machiavellianism. No differences in polyadic behaviour were forthcoming however.

The effects of food availability on interaction rates were unclear. The sole significant effect was that of food availability correlating with the proportion of interactions that were agonistic; this effect in STT only. Wrangham (1980) has suggested that primate diets take two aspects. One of these is the subsistence diet, faced in periods of scarcity, in which troops feed on low quality, dispersed resources and face little intra-troop competition. The other is the 'growth diet'; exploitation of high quality food patches in which intra-troop competition increases. If agonistic interaction is associated with competition then this data at least agrees with Wrangham's model. However, studying STT, Barton and Whiten (1993) found that supplant rate (presumably a more reliable index of competition) was *inversely* related to available biomass. A case could be made for agonism to rise in periods of plenty in that recuperation from injury would be easier. A case could also be made for the agonistic proportion to rise as general interaction rates rise if this general rise represents interacting beyond ones close friends and kin. However, why these trends should only affect STT remains mysterious. It is perhaps safest to concede that the paucity of the available ecological data precludes legitimate theorising.

The data suggest that low rank in STT females is associated with high rates of agonistic interactions. Neither Seyfarth (1976) nor Bernstein (1970, reported in Seyfarth 1976) found such an effect in their baboon studies. However, Seyfarth's data at least were taken from a troop with eight adult females, and being thus comparable to MLK where no rank effect was observed, his data are in accordance with those presented here. However, Barton (1989) found no rank effect on overall rates of agonism in females in STT.

If the focal data is representative of the troop as a whole then there is clearly more agonistic interaction in the lower parts of the dominance hierarchy. Why this should be is not clear. Cheney and Seyfarth (1990) review a wide range of studies suggesting that cohesion within matrilineal lines decreases with rank. They attribute this to the fact that low rankers are attracted to non-related high rankers as well as to their own kin whilst for high rankers other high rankers *are* their kin. The situation would seem to thus be more complex for low rankers. Some such effect may be occurring here.

Regardless of its cause, heightened rates of agonism must be unpleasant for

the animals involved. In a number of documented cases of troop fission including that of STT in 1987 it proves to be the bottom third of the hierarchy that 'leaves' (Henzi pers comm). The stress of heightened agonism for low rankers, if this is a genuine phenomenon in large groups, might be a proximate cause of fission.

Summary

The data on interaction rates has not yielded many surprises. Interaction rates are higher in STT and in consequence individuals probably spend more cognitive effort processing social information. Interaction rates are higher for females but this is offset by the comparable rates of agonistic interactions in the sexes and the finesse of male consort activity. Rank does not affect interaction rate but there is some evidence that low rankers in STT experience heightened agonism.

Chapter 11: Variability of Response

Introduction

For all the dimensions of social complexity discussed in earlier chapters, such as interaction rate and grooming network size, a case has been made for their constituting complexity in the particular context of primate behaviour. The complexity posed by variability needs no such justification since this is the quality of the environment that ultimately fosters all forms of intelligence. Whilst mindful of the caveat that this variability should be potentially explicable (see Chapter 2), this is a dimension that appears to meet the criteria for complexity on biological, formal and intuitive grounds.

In the context of primate cognition this variability is perhaps best described in terms of *information* and *uncertainty*. Information theory (see Shannon and Weaver 1949) provides an appropriate tool for describing these concepts in quantitative terms. Two information theoretic measures in particular concern us here. The first is **H**, which can be variously described as a measure of uncertainty, information or entropy. It is calculated according to

$$H(X) = - \sum p_i \cdot \log p_i$$

where X is a variable with i values and p_i is the probability of each one's occurring. Logarithms are often taken in base two in order to provide a quantity of information given in bits.

The characterising property of H is that when each of the values of X is equally likely, uncertainty in the system is greatest. Thus, in the context of baboon behaviour, an individual that greets another and in return is greeted, avoided or attacked equally often is faced with more uncertainty than one who is attacked nine times out of ten.

Transmission is a measure of the mutual information of two or more variables. It is calculated according to

$$T(X, Y) = H(X) + H(Y) - H(X, Y)$$

that is to say, the difference between the sum of information in each variable considered separately and the information in the two variables considered together. In probabilistic terms it is a measure of the dependence of two variables and is most

easily conceived of as the reduction of uncertainty of X given knowledge of Y. For the purposes of this analysis Y and X are act and response.

In so far as it is concerned with the frequency of events within categories, it can readily be seen that H is related to the X^2 statistic. High values of X^2 occur when frequencies are unevenly spread through a number of cells, i.e. when entropy is low and there is lessened uncertainty in the outcome. Thus, X^2 bears an inverse relationship to H. Miller and Madow (1954) provide a method for converting both H and T into X^2 in order that they be amenable to hypothesis testing. In this chapter, as in others, we shall be concerned mostly with differences in the value of H and T between troops, sexes, etc. In order to accomplish this comparison, confidence limits will be generated for all values of H and T using the method of David et al. (1956, reported in Losey 1978).

Losey (1978) has discussed the limitations and interpretations of information theoretic statistics in ethology. He urges caution in the use of these measures and draws attention to various assumptions implicit within them. Particularly with regard to transmission, he notes that veracity in the measure can only be expected when; signal and response are properly defined, sample size is statistically adequate, the diversity of signals is representative of the individual or population, signals of different meaning are not confused and relevant signals, responses and contextual signals are not ignored. This is a tall order! The final two assumptions are the most problematic for this study. The problem of meaning in behaviour is considered below. The problem of contextual information is a serious one in baboons, both in the form of social and non-social variables. The ideal approach would be to include all aspects of context but this quickly reduces the sample size of any particular combination of variables. In the light of these considerations, caution is exercised in interpreting results.

Creation of behavioural categories

The categories chosen for the variability of response measure are OBSERVE, AVOID, ASSOCIATE, ANTAGONISE, AFFILIATE, EXPRESS FEAR AND NO RESPONSE. The acts that make up these categories are given under the appropriate heading in Table 4.6 (note that categories of grooming and sniff are subsumed under affiliation and that presents by, or mounts of, swollen females are removed from the affiliation category). Creating behavioural categories is a difficult task and one that taps fundamental questions of how behaviour is described, particularly with respect to the 'meaning' of the behaviour. The categories above are defined in terms of

function rather than form; they essentially represent the interactional stance assumed by one individual towards another. As such, they are assumed to be meaningful but broad enough to maintain viable sample sizes. They are not, literally, independent of each other; affiliation, for example, requires association. However, each ethogram entry subsumed under a category is unique to that set. Acts in the category of ASSOCIATION, for example, are neutral with regard to affiliation or antagonism.

The category of EXPRESS FEAR stands out somewhat, being an emotional response and functional only in the context of long-term evolutionary adaptation. The problem at hand here, however, is a pragmatic one (making variability of response amenable to statistical analysis) rather than a schematic one. Since screams and other fear vocalisations must be assumed to affect the course of interactions and since they cannot be included under other categories, they demand their own.

General notes on analysis

The analysis is performed only on dyadic interactions. Dyadic interactions that escalated to polyadic (quite the minority) have been excluded. Only focal data has been used, thus all interactions involve at least one focal animal. Data which involve the conjunction of two behavioural categories e.g. affiliate whilst expressing fear have been excluded because they form a very small percentage of the data available.

Transmission

Gross differences in variability of response between the two troops were sought with the measure of transmission. Also computed was transmission efficiency: the proportional reduction of the uncertainty in the response reduced by knowledge of the preceding act: $T(X,Y)/H(X)$. This is important since the amount of information the act can impart will be constrained if the variability across acts generally is very low. The analysis used the matrices of act and response shown in Table 11.1 The results are shown below.

Results

An example of the working is given here for MLK. The data are taken from

Table 11.1. Frequencies of response to various behaviour categories: rows are acts, columns responses.

MLK

| | Observe | Avoid | Associate | Agonise | Affiliate | Exp. fear | No resp. | Total |
|-----------|---------|-------|-----------|---------|-----------|-----------|----------|-------|
| Observe | 0 | 2 | 3 | 0 | 9 | 2 | 5 | 21 |
| Avoid | 0 | 1 | 6 | 4 | 5 | 0 | 87 | 103 |
| Associate | 4 | 49 | 2 | 0 | 118 | 19 | 171 | 363 |
| Agonise | 0 | 10 | 2 | 0 | 0 | 23 | 42 | 77 |
| Affiliate | 9 | 48 | 10 | 2 | 313 | 32 | 865 | 1279 |
| Exp. fear | 1 | 3 | 1 | 5 | 26 | 0 | 74 | 110 |
| Total | 14 | 113 | 24 | 11 | 471 | 76 | 1244 | 1953 |

STT

| | Observe | Avoid | Associate | Agonise | Affiliate | Exp. fear | No resp. | Total |
|-----------|---------|-------|-----------|---------|-----------|-----------|----------|-------|
| Observe | 0 | 3 | 0 | 1 | 2 | 3 | 8 | 17 |
| Avoid | 1 | 0 | 19 | 0 | 12 | 1 | 114 | 147 |
| Associate | 11 | 105 | 2 | 2 | 111 | 32 | 235 | 498 |
| Agonise | 0 | 16 | 2 | 9 | 4 | 57 | 87 | 175 |
| Affiliate | 14 | 66 | 5 | 5 | 355 | 14 | 1071 | 1564 |
| Exp. fear | 0 | 2 | 2 | 7 | 18 | 1 | 115 | 145 |
| Total | 26 | 192 | 31 | 23 | 502 | 142 | 1630 | 2546 |

Table 11.1 and the formulae are give in the introduction.

$$\text{Uncertainty in acts (rows): } H(X) = \{ 21/1953 * \log_2(21/1953) \} + \dots + \{ 110/1953 * \log_2(110/1953) \} = \mathbf{1.56}$$

$$\text{Uncertainty in responses (columns): } H(Y) = \{ 14/1953 * \log_2(14/1953) \} + \dots + \{ 1244/1953 * \log_2(1244/1953) \} = \mathbf{1.50}$$

$$\text{Uncertainty in act-response pairs (cells): } H(X,Y) = \{ 0/1953 * \log_2(0/1953) \} + \dots + \{ 74/1953 * \log_2(74/1953) \} = \mathbf{2.95}$$

$$\text{Transmission between row and column } T(X,Y) = 1.56 + 1.50 - 2.95 = \mathbf{0.11}$$

$$\text{Transmission efficiency } TE(X;Y) = 0.11/1.56 = \mathbf{0.07}$$

The same process was repeated for STT, giving the following results

MLK: Transmission = 0.11 bits, Transmission efficiency = 0.07

STT: Transmission = 0.15 bits, Transmission efficiency = 0.10

It can be seen that both transmission and transmission efficiency are low in both troops.

Discussion

The method of David et. al. for calculating confidence limits breaks down at such low levels of the statistic. In any case, Losey's (1978) Monte Carlo simulations of the transmission statistic suggest great caution should be exerted when sample sizes differ and that one should be suspicious of 'significant' differences of only a few tenths of a bit. We must therefore retain our null hypothesis: the troops do not differ in their variability of response.

Variability of response to affiliation

These results and the problems associated with the transmission statistic suggest the use of the simpler information statistic, $H(X)$. Rather than examining the overall transmission, the variability of response to a single act is considered.

The analysis here concerns response to affiliation. There is a statistical

reason for this: Table 11.1 shows that this act is associated with the largest sample size. Furthermore however, much of this thesis has been built on the assumption that affiliation is the means by which baboons manage their relationships and the complex system of benefits and costs that are associated with these. Variability (and hence complexity) in affiliative interactions thus goes to the heart of social complexity.

Analyses were performed separately for troops and for age-sex classes. Consorting or consort-following individuals were excluded from the analysis.

A dilemma arises concerning the inclusion or otherwise of NO RESPONSE as an act. Since all interactions necessarily end with this 'act' its frequency greatly exceeds that of any other. Since its statistical effect depends on the distribution of frequencies across the other acts and since, ethologically, there are grounds for both its inclusion and exclusion, I have performed dual analyses: with and without it. The results are largely consistent with each other.

A statistical note should be made concerning zero cells in some of the matrices being analysed. In so far as they relate to the X^2 statistic, estimates of information may be biased if some cells contain no data. Losey's (1978) Monte Carlo simulation, however, suggests that the alpha error rate of samples that violate this guideline is acceptable provided alpha is set at 0.01 and the degrees of freedom are not large. Only one of the matrices being analysed contains more than one zero cell.

Results

Table 11.2 shows the cell counts of responses to affiliation on the part of individuals in the sub-sample designated. It also shows H, the resultant variability or uncertainty of response.

The results can be summarised as follows. The two troops do not differ significantly in their variability of response (see Figures 11.1 and 11.2). Maximum uncertainties are given: the value that would be obtained were frequencies divided equally between the categories.

When age-sex classes are examined, males prove to face a significantly greater degree of variability than females (see Figures 11.3 and 11.4) regardless of whether the NO RESPONSE category is included or not (a difference of 0.43 bits and 0.81 bits respectively). An examination of the data (see Table 11.2) points to the likely origin of this result. Whilst the response to female affiliation is (ignoring the possibility of NO RESPONSE) almost uniformly, reciprocal affiliation, males often face an avoidant reaction. This bifurcation of likely responses increases the uncertainty.

Table 11.2. Frequencies of various behaviour categories as a response to affiliation on the part of the designated group of individuals. H is the uncertainty of response.

| sub-sample | OB | AV | AS | AG | AF | FE | NO | H ₁ | H ₂ [*] |
|-----------------------------------|----|----|----|----|-----|----|-----|----------------|-----------------------------|
| MLK (whole group) | 7 | 39 | 5 | 1 | 263 | 28 | 656 | 1.33 | 1.17 |
| STT (whole group) | 10 | 46 | 3 | 5 | 296 | 37 | 776 | 1.35 | 1.26 |
| All immatures | 7 | 5 | 1 | 1 | 93 | 2 | 311 | 1.06 | 0.88 |
| All females | 5 | 3 | 4 | 0 | 217 | 16 | 459 | 1.16 | 0.79 |
| All males | 5 | 71 | 1 | 5 | 168 | 29 | 398 | 1.61 | 1.52 |
| Males interacting with females | 4 | 48 | 0 | 0 | 74 | 19 | 251 | 1.52 | 1.55 |
| Males interacting with males | 1 | 23 | 1 | 5 | 94 | 10 | 147 | 1.65 | 1.36 |
| MLK females | 4 | 2 | 2 | 0 | 96 | 7 | 235 | 1.20 | 0.96 |
| STT females | 1 | 1 | 2 | 0 | 121 | 9 | 224 | 1.11 | 0.62 |
| MLK males | 2 | 32 | 1 | 1 | 76 | 11 | 181 | 1.57 | 1.45 |
| STT males | 3 | 39 | 0 | 4 | 92 | 18 | 217 | 1.63 | 1.56 |

* H₂ is the amount of information when the 'no response' category is excluded

Figure 11.1 Uncertainty of reponse to affiliation: comparison of troops, absence of response included

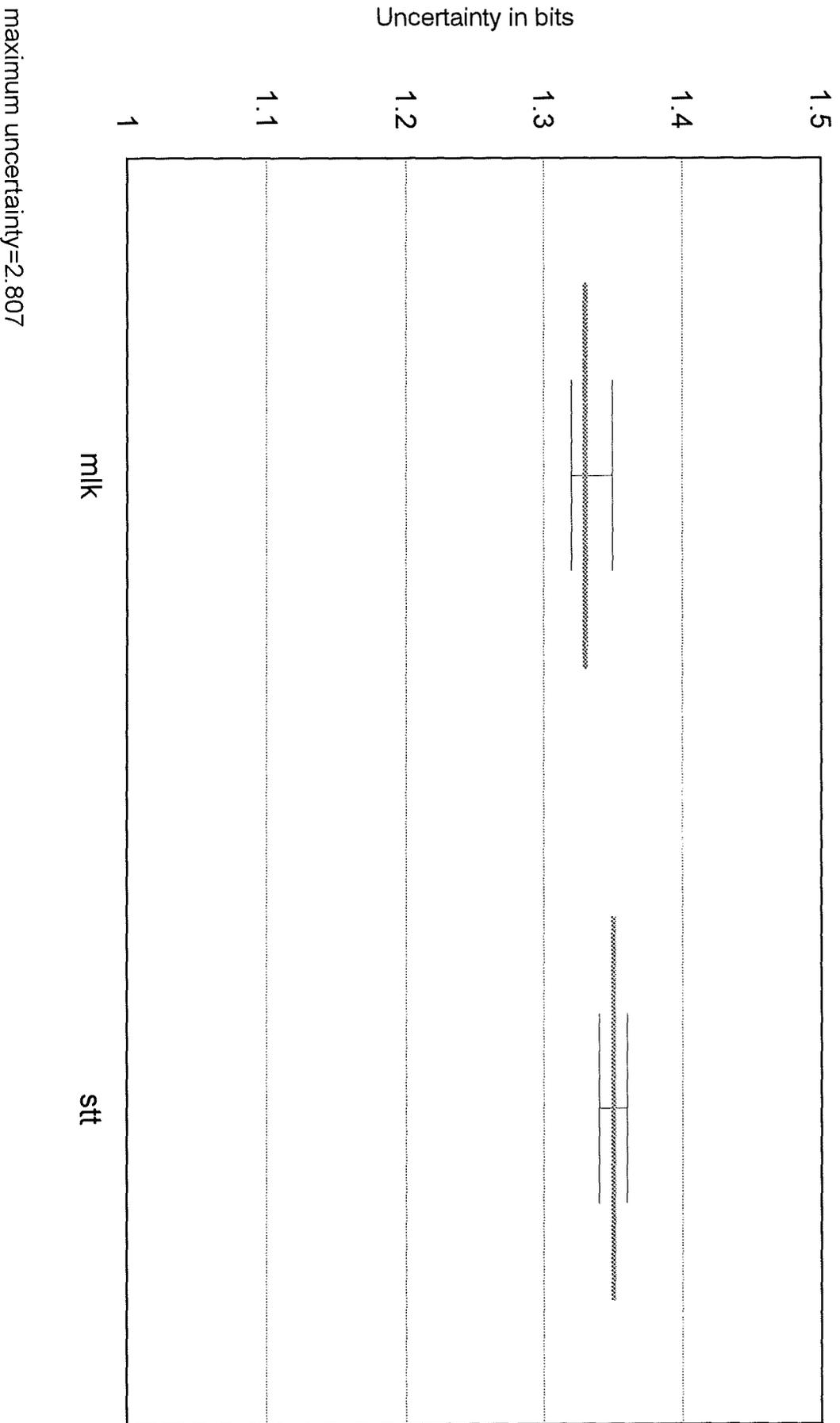
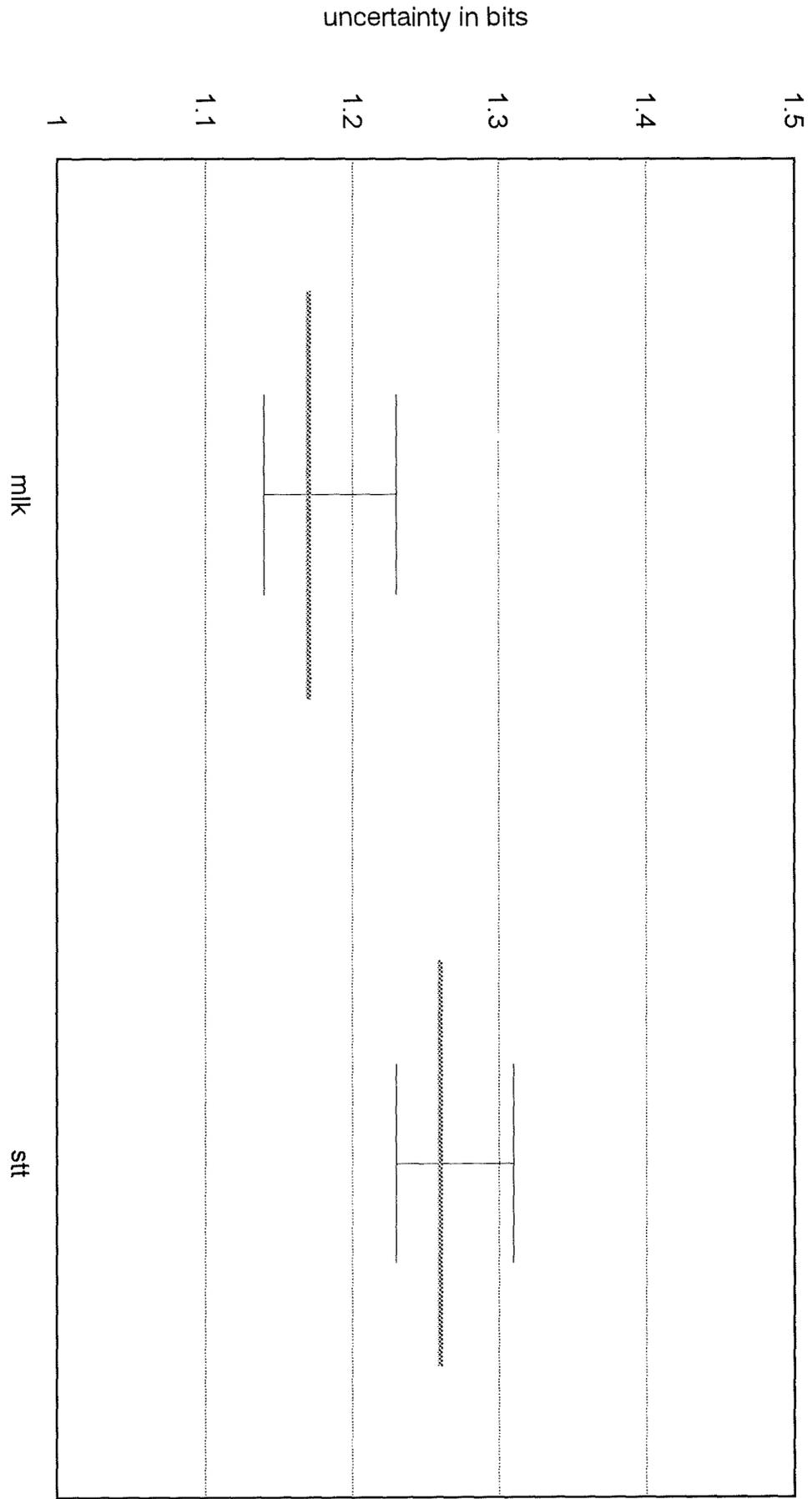
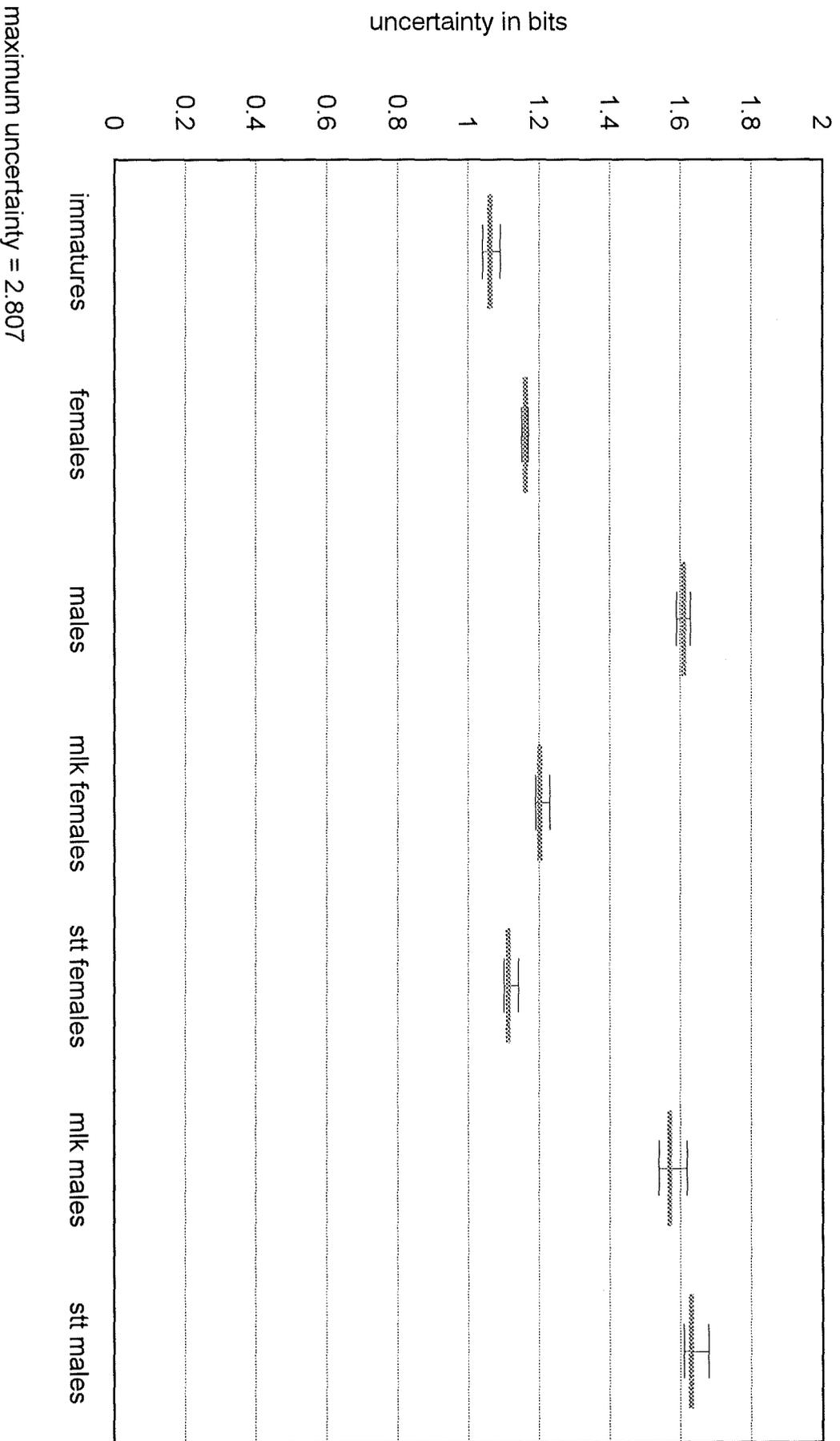


Figure 11.2 Uncertainty of response to affiliation: comparison of troops, absence of response ignored

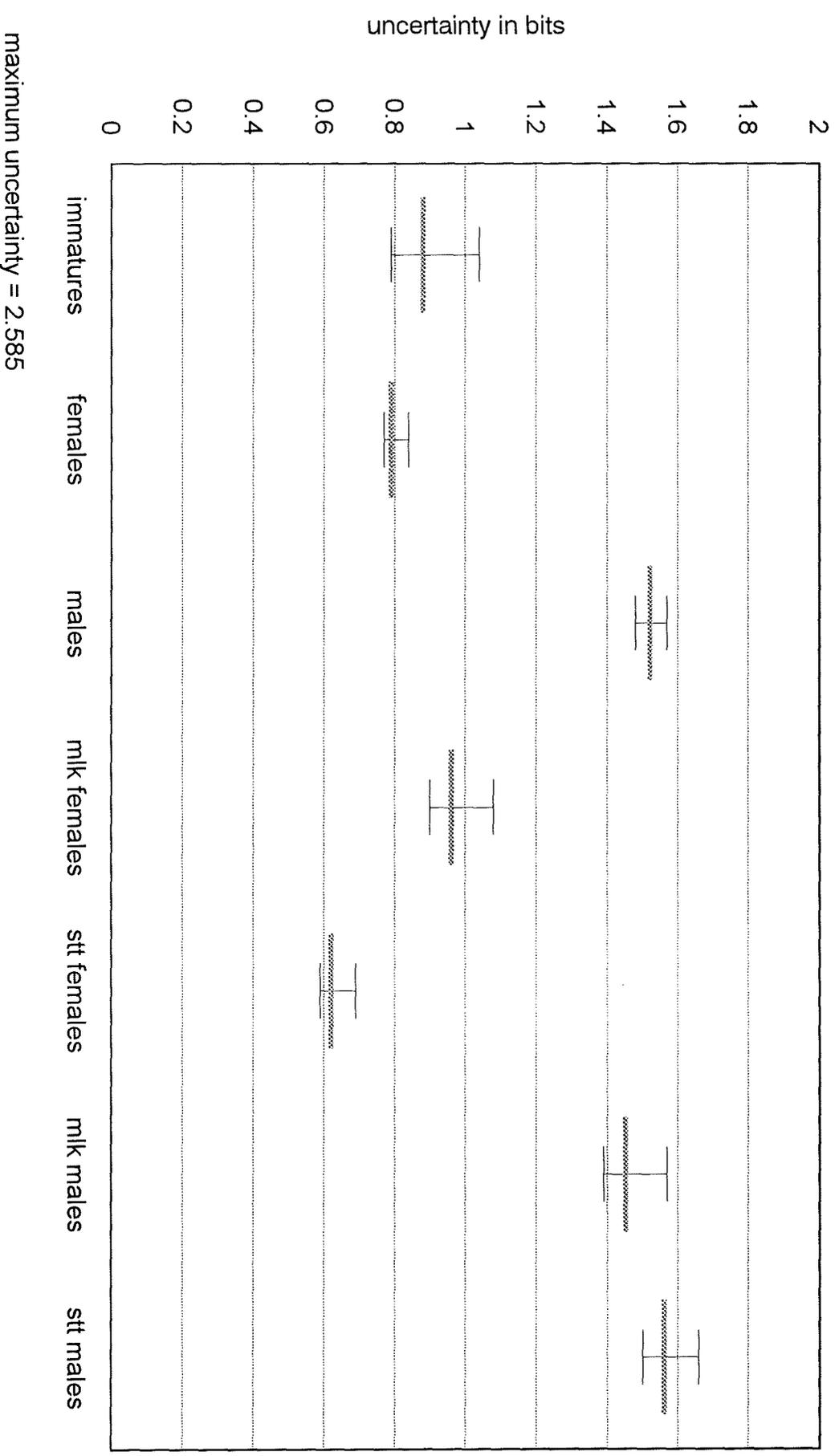


maximum uncertainty = 2.585

Figure 11.3 Uncertainty of response to affiliation: separate age-sex classes, absence of response included



Uncertainty of response to affiliation: separate age-sex classes, absence of response ignored



Immatures experience significantly different variability of response from females under one of the analyses but this result is undermined by the direction of significance being reversed in the other.

Breaking down age-sex classes by troop shows that MLK and STT males do not differ in the variability of response that they face. MLK females, however, seem to face more variability than their STT counterparts: by 0.09 bits when absence of response is included, by 0.34 bits when it is not. This is a small effect and examination of the data suggest that it may result from the rather low cell counts found in the data once the subdivision of the total sample has reached this level. MLK females experience more responses of observation, avoidance and association than STT but since these still only account for 3% of their data it does not seem valid to allow this to characterise the variability they face.

Discussion

Group size and variability of response

Group size does not affect response variability. This is true at least for the troops under study and using rather general categories of behaviour. If this result has general applicability it undermines the plausibility of a link between group size and social complexity. The best way to proceed at this point would be to convert the variability measure into an unpredictability measure by introducing the factors that explain variance and comparing their differential efficacy in the two troops (as outlined in Chapters 2 and 3). The sample size of the current data does not support such a procedure however

Despite failing to distinguish between complexity and confusion (see Chapter 2), variability is still a valid heuristic for gauging complexity. Negative evidence is always difficult to draw conclusions from. However, these results suggest that individuals in a larger troop do not experience greater complexity in their interactions, and, in so far as variability in interactions ought to increase with complexity at other levels (e.g. poorly defined relationships), do not experience greater social complexity in the larger scale of things. This is a conclusion at odds with those drawn in earlier chapters. Chapter 10 uses a straightforward analysis of relatively raw data to demonstrate a result that weakly supports the hypothesis of greater social complexity in large groups: higher interaction rates. In contrast, this chapter uses a less straightforward analysis of relatively processed data to demonstrate equivalence of social complexity in the two groups using a much stronger measure: variability of response. It is not clear whether one of these

results is in error or whether group size affects only some dimensions of social complexity.

Sex and variability of response

Male baboons face more uncertainty in attempting to affiliate to their conspecifics than do females. This is largely due to the high number of avoidant responses, a situation rarely faced by females. It would seem therefore, that males seeking to open an interaction with affiliation (for example as a prelude to a grooming request), ought to require greater social skill than females.

There are two good reasons for mistrusting such a simplistic conclusion however. One is that the very broad categories used for this analysis probably blur important within-category distinctions. All the various forms of greeting have been pooled together into the AFFILIATION category, and yet, one must suppose that such a multiplicity of behaviours must have evolved to serve a multiplicity of functions.

A second point is that if the higher rate of avoidance of males suggests that these individuals require greater skill in initiating interactions, it also demonstrates that they are often lacking sufficient of it. Males, in so far as they can unavoidably be intimidating to both sexes, may simply have to suffer more such 'failed' interactions. However, no inferences can be made concerning the social skills of either sex in social dynamics at the larger scale; how, for example, individuals can *set up* favourable circumstances for affiliating to one another.

Chapter 12: Discussion

Summary of Results

This section simply summarises the main points to come out of the empirical side of this thesis, these largely being concerned with the comparison across troops.

Frequencies of grooming were significantly greater for mature females than for males or immatures, as were sizes of grooming networks. Neither frequencies of grooming nor size of grooming network appeared to be significantly different across troops, for any age-sex class. Thus Dunbar's (1991) demonstration that across catarrhine primates grooming increases with group size fails to hold within this single species, at least with regard to the groups under study here. (Dunbar's study did use a slightly different measure, namely, percentage of grooming, rather than instantaneously sampled frequency of grooming. However, various studies have shown that the latter approximates to the former, (e.g. Dunbar 1976; Leger 1977; Simpson and Simpson 1977)). However, STT spent significantly more time than MLK in feeding and moving so a case could be made for their devoting a larger proportion of their available time to grooming.

A markedly different pattern of grooming emerged between the mature females of each troop, however. Females in MLK tended to groom those of high rank whilst females in STT tended to groom those of similar rank.

The possibility of cliquishness was investigated by applying a number of clustering techniques to data on spatial proximity. There was no evidence in either troop of cliques forming either amongst females only or amongst all natal troop members.

An analysis of interaction rates indicated that mature females experienced many more interactions than mature males. Males, however, experienced a far higher proportion of interactions that were agonistic. There was no difference between the sexes as regards the proportion of agonistic interactions that were polyadic.

A comparison across troops showed that interaction rates were significantly higher in STT and that it was the females who chiefly contributed to this difference. By way of context, it should be noted that the density of individuals in STT was also higher and by a comparable amount to the difference in interaction rates. There was no difference between troops regarding either the proportion of interactions that were agonistic or the proportion of agonistic interactions that were polyadic.

Female rank did not affect general interaction rates. There was some evidence, however, that low-rankers in STT experienced a greater proportion of agonism in their interactions.

Interaction rate did not appear to be affected by food availability, though the data on available biomass were not comprehensive. The proportion of interactions that were agonistic increased with food availability in STT only.

Variability of response, depicted in this thesis as the most penetrating of the complexity measures applied, yielded rather disappointing results. There were no clear differences between troops regarding the uncertainty that individuals faced in their interactions.

A comparison across sexes did show however that males faced much more variability in response to their acts of affiliation: in contrast to the females, the possibility of avoidance as an alternative to a reciprocal act of affiliation was high.

Social Complexity in the Cercopithecinae

The general picture here is that differences in complexity between a large and a small troop of baboons are not obvious. Whilst there appears to be a genuine difference in the configuration of grooming relationships with regard to the dominance hierarchy, differences in interaction rate can be plausibly related to increases in troop density and there is no evidence of greater variability of response in STT. Thus, the suggestion made in chapter 6, that 'cohabiting with more animals...may be expected to increase the unpredictability of interaction outcome', fails to find empirical support.

Furthermore, concerning the 'third level' of the Machiavellian intelligence hypothesis, i.e. that social problems have selected for a particular mode of primate intelligence, this study does not contribute to an understanding of what particular forms of social cognition increased group size might have selected for. In Chapter 3, long term relationships, polyadic interactions and reciprocity were identified as common candidates for social complexity. This study's data did not support an analysis of reciprocity. Relationships seemed unaffected by troop size as were frequencies of polyadic interactions.

Perhaps baboons are in fact not very complex? If sophisticated baboon social tactics are in the heads of ethologists rather than the heads of their subjects we would not necessarily expect different patterns of social interaction as group size and social complexity grow. The possibility that primatologists have been guilty of overestimating the cognitive prowess of their subjects has been aired by a number of

authors recently (e.g. Harcourt 1988, 1992). Coalitions between unrelated individuals are often assumed as being unique to primates, but Zabel et al (1992) report on the existence of these in the spotted hyaena (*Crocuta crocuta*). Third party intervention in their group was usually directed at the lower-ranked of two contestants; however, support against the higher-ranked animal occurred occasionally and supporters could apparently rise in rank as a result of such behaviour. Furthermore, it remains to be demonstrated that coalitions are cognitively demanding. Noe (1989), for example, provides something of a null hypothesis by concluding from his own research that no more than a simple trial and error learning rule is needed to explain the existence of coalitions in unrelated baboons. Similarly, Silk (1993) concluded that coalitions in bonnet macaques did not improve individual's own rank, nor alter the dominance of other males, nor systematically influence dominance stability in the group as a whole.

These claims are in stark contrast to the animal-as-strategist model: Drews (1993) for example explicitly talks of 'relationship management' in which interactions serve the purpose of gaining information as well as exerting influence: clearly a strategic rather than immediate goal. Equally, Strum (1987) could only make sense of male baboons who fight to win females but do not then mate with them by assuming that they were pursuing a strategic aim regarding their opponent rather than just contesting a resource. Such behaviour seems to imply that baboons are either extremely clever or extremely stupid.

This null hypothesis, that Old World Monkeys are no more socially sophisticated than other mammals, serves a useful purpose as a means of evaluating the weight of any data on social complexity, particularly that which purports to support the social intellect hypothesis. It is hard to believe that baboons are not more socially complex than hyaenas however. The high encephalisation of anthropoid primates, and, within that group, *Papio*'s higher than average neocortex ratio (Dunbar 1992), indicate that neural resources certainly exist for sophisticated social problem solving.

Furthermore, primates behave in qualitatively different ways from other social mammals. Regarding alliances, Harcourt (1992) notes that primates show exceptionally high frequencies of polyadic interactions and also claims that only primates show (1) evidence of reciprocity in alliances, and (2) the cultivating of, and competition for, friendships with potential allies. In primates, the link between group size and complexity rests on the assumption that primates are doing particular actions whose processing demands are related to group size; actions which, for example, species of fish in differently sized shoals are not engaged in. Similarly, in the case of alliances, it is the elements within the phenomenon that should be used

to judge its complexity, not the phenomenon itself.

If we look at the relationship between behaviour and goal (the latter being, broadly speaking, reproductive success) a complex picture emerges. Strum (1994) claims that male baboons show the most compelling evidence for alternatives to aggressive competition. In her study troops, a minimum of two to four factors were required to account for consort success and, in many cases, two or three way interactions between factors accounted for more variation than any individual factor. Similarly, Santillon-Doherty et al (1991) demonstrated that in stump-tail macaques, kinship, sex and rank interact synergistically rather than additively in characterising social interactions.

With complex brains and complex social behaviour it seems appropriate to infer complex social cognition mediating the two. Thus, to return to the opening comments of this section, it is unlikely that there is so little complexity to be found in baboons that its variation could not be measured.

Social Complexity and Group Size

Perhaps social complexity does not vary with group size? It is clear that group size does *affect* social behaviour: in this study for example, interaction rate was higher for the larger group. Feeding interference is known to grow with group size: Van Schaik (1983) has shown that within a species, birth rate is negatively correlated with group size. More specific effects have been documented in, for example, pygmy chimpanzees where White (1992) has shown that female-female affiliation predominates in small groups and female-male affiliation in large groups.

However, social complexity of the sort I wish to explore in this thesis results from the *interaction* of individuals' cognition and the particular circumstances in which they find themselves. The key to Humphrey's (1976) 'evolutionary ratchet', in which social sophistication selects for further social sophistication is that social complexity is generated by individuals, (rather than, for example, demography). This is why interaction rate *per se* is not enough to establish a link between group size and selection for encephalisation: it must be established that higher interaction rate reflects a strategic decision on the part of individuals, rather than it just being an inevitable consequence of heightened troop density. Such a perspective highlights the importance of differential grooming patterns as shown in Chapter 7, since, whilst group size could plausibly affect either grooming frequency or diversity in a very simple fashion (e.g. through the availability of partners), these variables are in fact invariant across group size. Thus there is no simple analogue

relationship between group size and grooming, rather, two different rank-based *rules* characterise grooming patterns in the troops. Since the formal status of these rules bears no obvious relationship to the dimension of group size it becomes plausible to suppose that the rules are situated within and enacted by the baboons themselves. This is to be contrasted with the possibility that they emerge from the interplay of demography and very simple behavioural programs and can then be observed with the 'birds-eye view' of the ethologist. In summary, we are interested in social complexity that has *intentionality*. There is little evidence however that this is affected by group size.

One important foundation of this enterprise was Dunbar's (1992) paper on the correlation between neocortex ratio and group size in primates. Dunbar noted that, whilst *ultimately* neocortex ratio would be determined by selection for greater group size, *proximately* it is neocortex ratio (i.e. ability to deal with social complexity) that determines group size. The same reasoning could apply to this study: whilst ultimately social complexity would increase the cognitive sophistication of a species, proximately it is the species' existing ability that determines the complexity generated. Since olive baboons should be assumed to be equally clever regardless of the size of the troop they are in it should not be surprising that great differences in social complexity failed to emerge.

I embarked on the project aware that the social complexity of my subjects would inevitably be constrained by their cognitive complexity. However, I wished to see how tight this coupling was: whether it was possible to identify the properties of large troops that stretched their member's cognitive ability and so, given time, would select greater intelligence. The lack of strong between-group effects perhaps suggests that the study of complexity in evolution will benefit best from cross-species comparisons in which natural selection has had time to act. Perhaps, intra-specific comparisons across group size are more appropriate for overtly ecological effects, such as feeding and predation. Group size clearly affects habitat use: with more bellies to fill, food patches are depleted quicker. The effect of group size on social behaviour may be more eccentric.

Social Complexity and Anthropomorphism

Perhaps the concept of social complexity carries with it a crippling amount of anthropomorphic baggage? Whilst ostensibly applying formal informational methods to the quantification of complexity, I have made use of concepts such as intentions and preferences. Treating baboons as intentional entities is certainly not

foreign to modern ethology, indeed it pervades Dunbar's *Reproductive Decisions* (1984) and Smuts' *Sex and Friendship in Baboons* (1985) even to the extent, it might be argued, of featuring in the titles. Nevertheless, this is the 'new anthropomorphism' by which Kennedy (1992) is so alarmed. Kennedy's concern is that the standard use of 'mock anthropomorphism', in which intentional terms are used as shorthand for behavioural adaptations, can actually slip into genuine anthropomorphism in which intentional states are credited to the animal without direct evidence. Might it be that this thesis has been trying to measure the effect of constructs which have no genuine counterpart in the baboons?

It is possible that assumption of an intentional stance (Dennett 1971) in ethology is a gross error. I believe it is justified however by, a) its apparent explanatory power regarding non-human primates, (for example regarding deception), b) the conspicuous failure of current eliminativism (e.g. Churchland 1981) to devise explanatory constructs for complex behaviour that replace intentional ones, and c) the assumption of biological continuity as espoused by Darwin. The concept of 'intention' can be entirely neutral with regard to consciousness, as formal attempts to characterise the construct in computer programs demonstrate (e.g. Schultz 1988). Kennedy (1992 p.87) criticises Dunbar's intentional stance (Dunbar 1984, p.231) as a confusion of behavioural adaptations and intentions, i.e. of proximate and ultimate causes of behaviour: Kennedy claims that "it is natural selection and not the animal that ensures that what it [the animal] does mostly makes sense". This seems rather naive. Richard Dawkins himself, the doyen of evolutionary reductionism, observes that it is brains, not genes that are in charge of the proximate causation of behaviour (1989 p.59). Indeed, Kennedy's statement is clearly fallacious since natural selection, being selection rather than specification, only operates retrospectively on (brain engendered) behaviours that did or didn't make sense at the time. I see no reason why a set of behaviours which bear a complex relation to each other and the external world and which are co-ordinated with respect to accomplishing some effect shouldn't be described as an intention and perhaps even benefit from the some of the anthropomorphic connotations that accompany that word. In sum, intentionality is an appropriate tool to use in the study of social complexity.

Social Complexity and Ethology

Perhaps the construct of complexity is not a fruitful medium for exploring primate behaviour and the evolution of primate cognition? The opening chapters of

this thesis bemoaned the lack of rigour with which the concept of complexity was used as an explanation. Chapter 2 attempted to demonstrate that complexity could be operationalised and Chapter 3 set about the task of showing that even very complex systems like primate groups could be assessed by heuristics that were related to informational theories of complexity.

Ceiling effects may be undermining the validity of this approach, however. Baboons are not strings of ones and zeros, or if they are then the size of the strings needed to describe STT and MLK is large enough to swamp differences that exist between them. Because of this great complexity, the elements of any analysis in this thesis are really quite high level phenomena. Any act in my ethogram no doubt encompasses a great heterogeneity of features ('approach' for example) and in later analyses these acts are themselves grouped into functional categories. At the least then, I have imposed my own assumptions on what the units of complexity should be. More generally, however, it is now not clear that my approach is more rigorous than those of authors who simply take it *as a premise* that, say, polyadic interactions are more complex than dyadic ones. In any case, assuming such premises may be the more appropriate approach to studying such complex systems. To be reductive is seductive as Noble and Boyd (1993) observe. It is not necessarily practicable however, and these authors note that a reductionist approach runs the risk of simply studying 'noise' rather than the overall logic of a system: under a microscope, an elephant and a hippopotamus look the same (Baerends, cited by de Waal 1991). Yates (1993) goes further in claiming that 'complex' systems are not reducible: that the behaviour we are interested in evaporates when we try to reduce the system.

To some extent the weight of these criticisms rests on how the complexity approach has been applied in this body of work which has spread its net rather wide. More detailed data will be required in order to convincingly demonstrate differences in social complexity. For example, a future study would profit from taking a single social behaviour such as fighting or reconciliation and attempting to exhaustively record the context surrounding it. This would allow an analysis of unpredictability rather than the more ambiguous measure of variability presented here. Such an incisive study might throw up intra-species differences with regard to, say, group size. However, it would be equally applicable across species. For example, there is already evidence to suggest that chimpanzees experience polyadic interactions more often than macaques (de Waal and Harcourt 1992). There is already anecdotal evidence to suggest that baboons employ tactical deception but that lemurs and gibbons do not (Byrne and Whiten 1990). A comparison of how such phenomena are distributed across primates with respect to measures of

encephalisation, for example, would be useful- as Byrne (1995) has done in the case of deception. Even more useful however would be a micro-analysis of how such phenomena actually influence the unpredictability of interactions. This is because the complexity of the phenomena need not then be assumed but can be demonstrated in the behaviour itself; this would provide a much firmer basis for assessing both the viability of the social intelligence hypothesis and its implications. It would be very surprising if the outcome of triadic interactions were not more unpredictable than that of dyadic interactions. For example, dominance transgressions constitute, *par excellence*, a case of the injection of unpredictability into a predictable situation and are greatly facilitated by coalitions. However, that ostensible markers of social complexity like polyadic interactions actually create unpredictability remains to be shown, and so the null hypothesis, which holds that primates are not socially complex, still stands. In covering a large amount of ground, the data on which this thesis is based is inevitably insensitive to the details of context that are required for such a demonstration.

Wider Implications?

A final warning concerning the limitations of the scope of this piece of work should be made. Implicit in much of primatology is the assumption that our biological cousins have useful things to say about our own evolution. The Machiavellian intelligence hypothesis places stress on the manipulation of conspecifics towards social goals; thus Whiten and Byrne's (1988) compendium of tactical deception sorts anecdotes under headings such as 'manipulation of target using social tool'. This overtly instrumentalist scheme is attractive for two reasons. Firstly, it stresses the Machiavellian nature of social interaction: treating others as tools to one's own ends. Secondly, it reduces the complexity inherent to the study of social phenomena by positing a single agent amidst many 'tools'. This done, a formal comparison of the complexity of social tools with, say, material tools appears feasible. Adherents to the social intelligence hypothesis can then point to the exceptional complexities raised by social tools and this has been the main thrust of the thesis presented here.

I think that this is a valid scheme for describing baboon behaviour but, in baboons, the scope for *joint action* is limited. It cannot be doubted that at some point in their evolution, humans began to enact cooperative plans of unprecedented sophistication and that reproductive fitness began to depend on participation in these cooperative units. Hunting and division of labour are obvious examples. It is in

this context that Oatley (1992) has criticised the instrumentalist view of social cognition. Rather than their just constituting a case of extra complexity, he suggests that the problems of interacting with other people involve an entirely different set of principles from those required to deal with the physical world. The need to agree on plans and to communicate about beliefs relevant to those plans requires us to treat other people as people not instruments. Indeed, sophisticated tactical deception and manipulation also require this stance. Reduction of the study of social complexity to agents amongst social objects may fail precisely because it is not a viable scheme for the agents themselves.

Social cognition may be special then, but it is particularly special amongst speaking and empathic humans; we should thus be sceptical of continuity between ourselves and other primates in this respect. Still, baboons are special too: their encephalisation is greater even than most monkeys and they qualify as subjects of a study of social complexity in their own right.

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Appendix 7.1

Calculations in the Interference Model

The computation of the Interference model proceeds as follows.

(i) The process begins with the matrix of idealised attractiveness as in the Engagement model. Start with row A. A's access to all animals is unconstrained and so realistic attractiveness is the same as idealised attractiveness.

(ii) Moving on to row B, B's access to A is unconstrained but its access to C is constrained by A. Multiply BC by AC. This is the fraction of A's and B's attraction to C that overlaps and which will result in interference by A.

$$21\% * 21\% = 4\%$$

(iii) Subtract this value from BC to generate new realistic attractiveness/predicted grooming

$$21\% - 4\% = 17\%$$

This process is continued for BD etc along the line. All values in the row are then scaled up so that the total amount of grooming once again equals 100 units (the value for BC will be scaled to 19%).

(iv) By the time we get to the row that is D's grooming and the cell of D grooming A, the interference has accumulated to

$$(DA*BA) + (DA*CA) = (26\% * 31\%) + (26\% * 26\%) = 15\%$$

Thus the realistic attraction for DA (before scaling) is

$$26\% - 15\% = 11\%$$

This value will later be scaled up to 20% (Note that the value for BA was scaled up during the computation of B's grooming. The figure for CA is a consequence of both interference and scaling)

This process is repeated for each row. Any cell in which interference results in a negative predicted grooming frequency is assigned a value of zero.

The general case is that cells in the matrix are potentially susceptible to interference from all cells in their column above.