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The Social Behaviour of Neutered Domestic Cats (*Felis catus*).

by

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ABSTRACT

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THE SOCIAL BEHAVIOUR OF NEUTERED DOMESTIC CATS (*Felis catus*)

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This study assessed the existence and nature of sociality in three colonies of neutered domestic cats. All three colonies exhibited a social structure whereby cats recognised individuals, or at least individual status, and reacted accordingly. In two colonies the overall flow of interactions was most clearly represented by the flow of head rubbing, and in the third group by the flow of aggression. Interaction within each group was higher between dyads that were present together less often. Head rubbing may reinforce social structure, flowing from subordinate towards more dominant individuals, particularly when cats return to their communal core area.

Cluster analysis, of the probabilities that two behaviour patterns were performed by one individual within a single interaction, was used to produce an objective method for categorising behaviour. Many patterns clustered similarly in all three colonies, particularly with respect to two clusters - these were termed Affiliative and Approach/Sit categories.

Analysis of the sequencing of behaviour patterns between cats during interactions revealed the importance of the tail-raised posture in cat communication. Its close association with head rubbing suggests it may be an appeasement display indicating a subordinate cat's intention to rub on a more dominant individual.

The use of the tail raised posture and head rubbing by cats towards a familiar human was investigated experimentally. Contact from the human increased the tail-raised response and head rubbing on the person and on an inanimate object. The presence of more than one cat created competition between the cats for attention.

The results are discussed in relation to the possible effects of neutering on heritable aspects of cat behaviour and the welfare aspects of neutering.

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DEFINITIONS OF SOME COMMON TERMS AS USED IN THIS THESIS

Behaviour pattern - a single element of behaviour fitting one of the descriptions given in Appendix 1. Only behaviour patterns that are directed by cat towards another are considered in this thesis - these are therefore termed "interactive behaviour patterns". The term is often abbreviated as "pattern" in the text. Many patterns may be performed in rapid succession during an interaction.

Behaviour sequence - the order of behaviour patterns occurring between two cats during an interaction.

Behavioural style - the combination of behaviour patterns used by and therefore characteristic of particular individuals or pairs of individuals.

Core area - usually the site where supplementary food, if provided, is supplied. Many cats spend a large amount of their time in this area, sleeping or resting, and congregate here when food is expected.

Dyad - a pair of cats

Home range - the area over which an animal travels regularly. In the case of cats this usually encompasses the core area and includes areas in which the cat may hunt.

Interaction - defined in detail in Chapter 2 but refers to the whole sequence of behaviour patterns performed between two cats until one of them moves away or until no patterns have occurred for two minutes.

Social structure/organisation - the form that sociality takes in a particular cat group, i.e., the roles of particular individuals, behaviour patterns and relationships in the maintenance of sociality.

Sociality - defined by Alexander (1974) as "group-living", this term is used in this thesis in reference to groups where the cats recognise other individuals, or at least individual status, and react accordingly.

CHAPTER 1

Introduction to the Study

FA from the University colony.

CHAPTER 1 - INTRODUCTION TO THE STUDY

1.1. Introduction

The domestic cat (*Felis catus*) was, for many years, thought to be a largely solitary animal. In fact, group sizes vary from one to over 50 animals, and population densities vary from less then one to over 2000 per square kilometre (reviewed in Macdonald, Apps, Carr & Kerby, 1987; Liberg & Sandell, 1988). They are found in habitats ranging from temperate farmland and urban areas (Rees, 1980) to sub-antarctic islands (Van Aarde, 1978). They also exhibit great variation in their dependence on man, ranging from none in remote island populations (Corbett, 1979) to almost complete in city populations (Natoli, 1985b). Correspondingly, different populations vary considerably in their feeding ecology (Fitzgerald & Karl, 1979).

This intra-specific variation in social organisation is a feature common to many species in the Order Carnivora, of which the domestic cat and all other felids are members. In comparison with most wild carnivores which are shy, rare and often live in remote or inaccessible areas, domestic cats have the advantage of being relatively easy to observe and, due to the large intraspecific variation in coat colour, easy to recognise individually. They therefore provide an excellent "model" for studying how different ecological factors shape social organisation within a carnivore species to produce group living in some environments and a solitary lifestyle in others.

The literature contains a wealth of information documenting the benefits and disadvantages of group living for a species. The two main environmental influences suggested for carnivores are food and predators (Alexander, 1974; Wilson, 1975; Bertram,1978). Group living often increases an individual's chances of locating, catching and defending food, especially if prey is large (Mech, 1970; Kruuk, 1972; Schaller, 1972; Caraco & Wolf, 1975). Living in a group may also offer protection from predators through increased vigilance and cooperative deterrence, e.g., Rasa (1977). These potential advantages must be weighed up against disadvantages which include increased conspicuousness, increased competition for food, greater risk of disease and increased possibility of aggression or injury (Gittleman, 1989). For many species only certain of these potential advantages and disadvantages will apply and the balance of the two will influence the degree of sociality (Bertram, 1978).

Wrangham (1983) stresses the importance of ecological factors on grouping. He suggests that the ecological conditions in which the species is living, whilst not

necessarily having positive effects on grouping, may be permissive, thus allowing, but not favouring, the evolution of groups. Macdonald (1983) agrees, suggesting that resource (particularly food) dispersion is fundamental to carnivore society in that it may set the limits to the group and territory sizes within which other combinations of selective pressures operate.

Kerby & Macdonald (1988) suggest that the domestic cat illustrates a continuum of social organisations with solitary and group-living lifestyles as the two extremes. This occurs because of differences in patchiness and predictability of available resources, as proposed by Carr & Macdonald (1986) for carnivore systems in general. Groups will generally be favoured where there is heterogeneity in the pattern of food available. Clumped patches of food, characteristic of provisioning, voluntary or otherwise, by man, will mean that the minimum territory size required to support one cat also contains sufficient resources for several others.

Liberg (1980) suggests that the domestic cat has experienced parallel evolution to the lion, moving from solitary to group living in response to a new source of food. In the case of lions this is represented by the large prey available on the open plains, whilst for the domestic cat the concentration of food around human settlements allows many individuals to share a single food source. Where food is sparse, individual domestic cats forage and generally live alone (Corbett, 1979).

Where permanent groups of carnivores do form, involving long lasting associations of the same individuals, social behaviour is often in evidence. Alexander (1974) gives three reasons for this. Firstly it may enhance the original advantage of group living e.g., thwarting of predators is often aided by alarm calls and bunching of the group. Secondly, Alexander claims that social behaviour might actually *reduce* the likelihood of disease and parasite transmission (an increased likelihood of this being listed as one of the disadvantages of group-living above). This could be achieved via mutual grooming thus removing external parasites in some species and through the spread of genetic resistance to disease in lines of closely related individuals. Thirdly, social behaviour may evolve as a way of controlling reproductive competition and aggression within the group and may also arise as a mechanism for maintaining the group as a social unit.

The result is often a complex system of social relations based on individual or status recognition. Such social systems have been described for many carnivores, including hyaenas (Kruuk, 1972), wolves (Mech, 1970), wild dogs (Frame, Malcolm,

Frame & van Lawick, 1976), mongooses (Rood, 1975), lions (Schaller, 1972; Bertram, 1975; Rudnai, 1975; van Orsdol, 1981) and the domestic cat (reviewed in section 1.2).

The domestic cat has a unique status as a domestic animal. There has been little artificial selection by man in cats and many pet cats are allowed complete freedom of movement by their owners. Many have reverted back to a more independent, free-living state, and are subject to more of the ecological constraints experienced by wild carnivores, outlined above. Both pet and free-living domestic cats depend on man to various extents as a source of food and often the strongest constraint for them is the influence of man himself. Probably the most significant form of man's influence on the social development of the cat is the modern habit of neutering pet cats - a practice even more recently extended to larger colonies of feral cats. In evolutionary terms this is a very recent phenomenon, the effects of which may not yet be fully apparent.

This introduces an element to domestic cat social organisation unlikely to be seen in wild carnivores and, with the removal of certain aspects of social behaviour (i.e., sexual behaviour and rearing of kittens) provides an opportunity to investigate the importance of these in maintaining social cohesion within a group. The emphasis of this thesis has been to discover how social behaviour is organised within group-living domestic cats that have been neutered, and how this might relate to social relationships between neutered cats and their owners.

1.2. Literature review

General reference to the domestic cat (which henceforth will be referred to simply as "cat") encompasses all ecological categories of the species *Felis catus*. This includes feral cats, farm cats and house cats of the commonly seen domestic short hair variety (i.e., excluding oriental and other pure breeds). Feral cats are generally regarded as having escaped from domestication and reverted to a wild state. They are not attached to any particular household although this does not prevent them from living close to humans on a more anonymous basis. A feral cat may subsist entirely on its own, hunting and scavenging like any wild carnivore, or by being fed unwittingly by humans via their rubbish, or by direct hand-outs from "cat-lovers". The latter situation seems to be especially common in larger cities (Tabor, 1983). Farm cats are generally feral in temperament but, living on an agricultural establishment along with

variable numbers of conspecifics, receive supplementary food provided by the farm owners or workers. Feral and farm cats are often referred to collectively as free-living, free-ranging or free-roaming cats.

The house-cat, or house-based cat, lives in close connection with a household which assumes some responsibility for feeding its cats. These animals are much tamer in temperament than their feral relatives and tend to develop social relationships with their owners. As mentioned earlier, many of them are also allowed to roam freely by their owners, putting them under the title of free-roaming or free-ranging cats.

The terms free-living and free-roaming or ranging are rarely defined in the literature despite their frequent use. They are often used as alternative terms and it sometimes becomes unclear as to whether they include house-cats or not.

The following review will attempt to cover the behaviour and ecology of all categories of the cat, many of which are not mutually exclusive, with different degrees of ferality in evidence in different populations. The categories will therefore all be considered together as free-ranging/roaming cats since they are only arbitrary labels given to different sectors of the population. House cats will be included in this to a certain degree but a special section detailing studies carried out on housecats and the cat-human relationship in particular will also be included. Finally, a section detailing the specific case of neutered cats will highlight in more detail the areas studied in this thesis.

Most of the early studies of cat social behaviour were laboratory based - these will be covered first.

1.2.1. Laboratory studies

Most of these early studies focussed on the question of whether or not cats in groups form dominance hierarchies. Although experimental designs varied, they nearly all involved ranking cats through their success at gaining access to food. The results vary. Winslow (1938) found that one male invariably dominated all other cats in a group and there was no apparent continuation of the social hierarchy below the leader. Masserman & Siever (1944) reported that a linear and temporally consistent dominance hierarchy emerges when a group of cats are tested in pairs, but these investigators failed to provide any quantitative data regarding the establishment of the dominance order.

Both these authors agree that, among cats, aggression most frequently occurs as

a frustration behaviour caused by failure to obtain food rather than as an instrumental technique for food getting. Fonberg et al. (1985), investigating predatory success of cats in relation to dominance, support this view. They conclude that predatory dominance is not based exclusively on aggressive mechanisms, since it may be formed and sustained without overt aggression.

Still in the laboratory, Baron et al. (1957) found evidence of a linear dominance hierarchy in a group of cats, but reported that this hierarchy was subject to change over time. Leyhausen (1965) reported that penned laboratory cats exhibited a loose, social order, with some individuals ranking higher than others. Cole & Shafer (1966) found that reliable dominance hierarchies involving up to eight cats were stable, and unperturbed by differential levels of hunger.

A study by De Boer (1977) attempted to assess dominance using different criteria to success at acquiring food. He used criteria based upon approach/withdrawal or threatening postures similar to those described by Leyhausen (1979).

All of the studies described so far were made on cat populations living under extremely artificial and crowded conditions, focussing on instances of overt aggression and threat rather than the more subtle behavioural cues that one might expect under natural conditions.

1.2.2. Studies of free-ranging cats

The spatial organisation of the domestic cat has been extensively reviewed in the literature, recently and comprehensively by Liberg & Sandell (1988).

a) Density

Population densities reported in the various cat studies show tremendous variation, from about one cat per square kilometre (Fitzgerald & Karl, 1986; Jones & Coman, 1982) to around 2000 cats per square kilometre (Izawa et al., 1982). Densities above 50 cats per square kilometre have been reported only in urban areas where cats feed on rich supplies of rubbish or are fed by large numbers of "cat lovers" e.g., in the centre of Rome, (Natoli, 1985b), and Portsmouth dockyard (Dards, 1979). Intermediate densities of 5-50 cats per square kilometre have been found in farm cat populations where the cats were supplied with all, or at least part, of their food requirements by owners, e.g, Panaman (1981), Turner & Mertens (1986). Similar

intermediate densities occurred in rural feral populations feeding on very rich, often clumped natural prey such as colonies of burrow-nesting seabirds, e.g., on Marion Island (Van Aarde, 1979; Bloomer & Bester, 1992). Densities below five cats per square kilometre were only found in rural feral populations subsisting on widely dispersed prey, mainly rabbits and rodents e.g., Corbett (1979), Jones & Coman (1982).

Liberg & Sandell (1988) hypothesise on the basis of the documented distribution of cat densities that density of both free-ranging house and feral cats is determined by absolute food abundance. They note that a second factor that might seriously affect densities is human control.

In a study of free-ranging, unowned cats in Brooklyn, New York, Calhoon & Haspel (1989) found that the distribution of individuals within the area varied with the availability of shelter and was not dependent upon food. Thus shelter may produce an additional limit to the density of cats that an urban environment can support.

b) Home range sizes

Along with the variation in cat densities, there is a huge variation in mean home range size recorded in the different studies. Female ranges vary from 0.1-1.8 hectares in a Japanese fishing village (Izawa et al, 1982) to 170 hectares in the Australian bush (Jones & Coman, 1982). Liberg & Sandell (1988) found a significant negative correlation between female home range size and density and suggest that they are both correlated to food abundance. The smallest female home ranges were found in urban feral populations that subsisted on rich clumped food e.g., Dards, (1979); intermediate ranges were found in farm cats such as those observed by Panaman (1981); and the largest ranges were shown by feral cats living on dispersed natural prey, e.g., Jones & Coman 1982.

In addition to absolute food abundance, Liberg & Sandell (1988) suggest that female home range size is determined by food distribution. Konecny (cited in Liberg & Sandell, 1988) reported that when food occurred in patches, the feral cats in his study moved over larger areas than when it was evenly distributed, despite there being higher overall food abundance in the former case.

Other requirements may also affect the distance that females will range. In Izawa et al's (1982) study in Japan, for example, the female cats, despite having small

home ranges, still wandered much further than they needed to for food, apparently in search of resting places.

Variation in range size between different areas is just as large for males as for females. On average, male ranges are 3.5 times larger than those of females. As this is much larger than their energetic requirements relative to females dictate, Liberg & Sandell (1988) suggest that food is not the factor most important in determining male range size. They propose instead that the primary factor determining male range size is female density and distribution. This would only be the case for breeding males and only during the mating season. At other times of year breeding male ranges might be determined by the same factors as those of females and subordinate males. Few studies have made the distinction between breeding and non-breeding male ranges but the changes according to season do seem to be in evidence, e.g, Corbett (1979) and Izawa et al (1982) both showed that male ranges were larger during the breeding season than during the rest of the year.

The home ranges of well-provisioned solitary housecats, and in particular neutered individuals, have not been well documented in the scientific literature. A recent study by Chipman (1990) mapped the home ranges of 126 urban pet cats which ranged freely during the daytime. He found, as in other studies, that home range size was different between the sexes with the average range of an entire male being larger than that of a neutered male which in turn was larger than a typical female range. Up to nine years old, the range sizes of entire males correlated positively and significantly with age; females ranges correlated significantly with weight; whilst neutered males' ranges showed no significant correlation with any variables measured. Radio-tracking of a neutered female and a neutered male housecat in another suburban study (Bradshaw, 1992) showed the female to have the slightly larger range (0.45 ha compared to 0.27ha).

c) Spacing

Studies of rural and urban group-living cats have shown that the home ranges of the females overlap extensively, especially at the primary feeding place, i.e.,the farm, rubbish dump or provisioning site used by cat lovers. Examples are provided by Dards (1978; 1979) and Natoli (1985b). Between groups, however, there is little female range overlap e.g., Izawa et al (1982). Turner & Mertens (1986) measured degree of range overlap quantitatively within and between groups in their study of

farm cats and found it to be, on average, 55.1 and 3.5 % respectively. Rural free-ranging housecats showed a similar pattern of spacing (Liberg, 1980; Warner, 1985).

For rural solitary-based females living on natural prey, food is usually more dispersed and less predictable than for group-living cats. In general, it appears that the more patchy the food the greater the degree of overlap between female ranges. Fitzgerald & Karl (1986) and Apps (1986), both studying cats living on patchily distributed resources, found overlap between solitary female ranges. The cats in Konecny's (cited in Liberg & Sandell, 1988) Galapagos population were divided between two systems: where food was more uniformly dispersed overlap between ranges was less than in an area where food was concentrated in richer patches.

In the urban owned pet-cat situation, Tabor (1983) proposed, without presenting any experimental evidence, that female cats had home ranges consisting of the house plus the garden plus any further space the cat density would allow. As a result, a series of parallel female home ranges were seen, reflecting the pattern of housing. Tabor suggests that these females regard their house and human companions as their core area and group members resulting in minimal range overlap between neighbouring female cats as between different feral female groups. Chipman (1990) showed that within the multi-cat households in his study, 92 % of which were known to contain mother/offspring dyads/groups, home ranges of members of the groups overlapped extensively, as documented for free-living groups.

Most studies with information on male spatial organisation have reported overlapping male ranges, encompassing the ranges of several females or groups of females. This seems to be the case around urban groups (e.g., Natoli 1985b) and farm-living groups of females e.g., Turner & Mertens (1985). It also occurs in rural (Liberg, 1980; Warner, 1985) and urban free-ranging housecats (Tabor, 1983). In rural areas where solitary females show range overlap, this again, is reflected by the males, e.g., Apps, 1986, Corbett, 1979. Turner & Mertens (1985) showed that whereas overlap between females from different groups was only 3.5 %, for males from different groups range overlap was 14.4 %. They suggest that, if overlap between ranges is indicative of tolerance, then males from different farms are far more tolerant of each other than are females from different farms.

d) Communication

The most important avenue of communication in felids in general appears to be

olfactory, and this is obviously of even greater significance to the solitary individual because of the long-lasting nature of scent marks. Possible sources of odours in the domestic cat include their urine (Natoli, 1985a), faeces and anal glands (Corbett, 1979; Panaman, 1981), and various skin glands on the head (perioral and temporal glands), pads of the paws (pedal or eccrine glands) and tail (caudal glands)(Verberne & De Boer, 1976). As in other species (Macdonald, 1985) the way in which scent marks are used in domestic cats vary between both individuals and populations.

Most of the descriptions of the use of scent marks have been made on group-living cats and the majority of these record the rate and location of spray urinating by males, e.g., Macdonald et al (1987), Liberg (1981), and females e.g., Panaman (1981). Corbett (1979) provides the only detailed description of the pattern of scent marking in solitary cats.

Other forms of communication, requiring direct contact between individuals, have been poorly documented in the literature. Leyhausen (1979) described visually in detail the various facial and overall body postures of cats showing fear/aggression conflict, but did not describe other behaviour in such detail. References by authors to "aggressive" and "friendly" encounters between individuals are common, but explanations of the specific behaviour patterns involved are rare. Dards (1979) recorded a selected range of behaviour patterns in her dockyard colony. More recently Kerby (1987) produced a much more extensive list of definitions of behaviour patterns which she categorised on a subjective basis.

e) Structure and characteristics of groups

All cases of group-living cats reported have been associated with a concentrated and stable food source large enough to support more than one individual - Liberg & Sandell (1988) suggest that this is the essential factor favouring the formation of groups.

Two categories of group-living cats have been described: farm cats in rural settings e.g., Leyhausen (1965), Panaman (1981) Laundre (1977), Kerby (1987), Macdonald et al., (1987); and feral cats subsisting on food concentrations such as rubbish dumps in urban areas, e.g., Natoli (1985b), Dards (1979). Group-living has never been clearly documented in cat populations living on natural prey, e.g., Corbett (1979), Jones & Coman (1982) all reported solitary cats. Van Aarde (1978) claimed that at least some adult cats lived in small groups on Marion Island but this was based

on only a few sightings.

Since cats living on natural prey do not form groups, Liberg & Sandell (1988) suggest that the behavioural advantages such as communal care and cooperative defence of kittens are not responsible for the appearance of group-living in the domestic cat, but arise as secondary benefits once groups have arisen as an effect of food distribution.

Although once thought to be merely structureless aggregations of animals around a food source, group-living cats have been shown in many studies to have a complex social organisation. Groups tend to be composed largely of adult females and their young of both sexes. Many of the females are related and litters from different queens have been seen to become mixed. Macdonald et al. (1987) reported communal nursing and rearing of kittens by sisters. In Wolski's studies in Ithaca, New York (1982), one female gradually deposited a litter of three over a period of two weeks with the litter of another resident, unrelated female.

From her study of two colonies of farm cats, Kerby (1987) discovered that females within the group who gained nest sites close to the food resource and pooled their litters with relatives, had more success at rearing kittens than females that raised their kittens alone, away from the food source. She concluded that the matrilineal unit (the long-term affiliation between a female and successive generations of her direct descendants) is of fundamental importance in cat society.

Males usually have a much looser attachment to groups. In several studies the majority of males dispersed from their natal groups after reaching sexual maturity e.g., Liberg (1980), Warner (1985). In a detailed study of adult male farm cats Liberg (1980) identified four categories: Breeders (of which a single "Central" male monopolised copulations at a given farm), Challengers (2-3 years old and involved increasingly in aggressive challenges of Breeders), Outcasts (young male emigrants, avoiding contacts with other cats), and Novices (yearling males remaining with their natal group and subject to increasing attack from older males). The ranges of Breeders overlapped widely, but their dominance relations varied with location - each central male being dominant on the farm with which he was particularly affiliated.

Kerby & Macdonald (1988) reduced the classification to two categories following their studies, Breeders and Non-Breeders. Breeder males were characterised by infrequent attendance in the core area of the group, avoiding close proximity to other cats, and by interacting at a higher rate than Non-Breeders when

present. They were also more "alert", more overtly aggressive, and mate-called and scent-marked more than Non-Breeders.

These classification systems did not appear to be rigorous, with some males changing status within groups either as they became older and stronger, or in response to other males losing status.

f) Social interactions within groups

From the groups of cats studied it appears that the social relationships of the two sexes differ greatly. Kerby & Macdonald (1988) have summarised the literature on this. Within female groups, Izawa et al (1982) found that feeding activity was synchronised and interactions between group members were generally amicable. Dard's (1978) data supports this: within family groups, individuals rested together, greeted (defined as any combination of the "tail-up", "sniff noses" and "head-rub" behaviour patterns) and sometimes groomed one another, whilst females often nursed kittens communally. Fighting was rarely observed within groups, however the behaviour of adult females towards both female and young male outsiders tended to be aggressive. All the serious aggression observed by Macdonald & Apps (1978) was directed to outsiders.

Dards (1979) found that adult males were never amicable but either avoided, tolerated or attacked one another, and actively persecuted younger males. The breeding males were not apparently affiliated with particular groups and maintained a hierarchy amongst themselves.

The pattern of social interactions within the core area of a farm was studied in detail by Macdonald et al.(1987). The cats' social relationships were structured by differences in the numbers, rates and types of interactions with one another. Some individuals were classed as net initiators of interactions, whereas others were net recipients. The tendency to rub the perioral and cheek regions of the face on another cat was the clearest single indicator of initiator status. Kittens were initiators to adults, females to the adult male, and some adult females were initiators to others. Macdonald et al. (1987) conclude that in their study colony the net flow of initiations in general, and of rubbing in particular, indicated social position. This suggestion is addressed further within this thesis.

1.2.3. Cat personality and the cat-human relationship

The independence and individuality of the cat has made it one of the most popular domestic pets of today. In a survey of reasons for liking and choosing a cat as a pet, Podberscek & Blackshaw (1988) found that the personality of a cat was at least one reason for choosing it in 23 % of 16-38 year-old people and 20 % in people interviewed over 55 years old. This was only in respondents who were actively able to choose their cat - when adjusted to account for people who adopted stray cats, the values were 30 % and 32 % respectively.

It has been shown that human observers can reliably rate cat personalities, and that these ratings correspond to actual frequencies of various behaviour patterns performed by individuals (Feaver et al, 1986),e.g. approaching, sniffing and rubbing on a person correlated well with observer ratings of cats as "sociable with people". Mertens & Turner (1988) divided cats into three categories based upon their approach to unfamiliar persons: initiative/friendly, reserved/friendly and an unfriendly type. The most significant factor affecting each cat's behaviour towards the humans was its personality, which was more important than the sex of the cat, or the behaviour, age or sex of the human. Turner (1991) found two types of friendly personality among Swiss house cats, one preferring play contact, and the other petting.

With such a wide variety of both cat and human personalities available, it is not surprising that the cat-human relationship can occur in many different forms. Amongst the idiosyncracies of individual relationships, workers in the field have found a number of common characteristics of the cat-human relationship.

Turner (1991) found that interactions initiated by the cat tend to be longer than those initiated by the owner, particularly when the owner is very active in starting the interactions. In families with children, Mertens (1991) found that, while children tend to approach the family cat more than their parents do, the cat itself prefers to interact with the adults. She found the cat-human relationship to be most intense (in terms of quantity of interactions that occur) when the human partner is female. This is probably because it is often a female member of the household who feeds the cat. The size of the family is also of importance to their relationship with their cat. Mertens (1991) found that in small families social play towards individual family members lasted longer and the frequency of head or flank rubbing was higher. This suggests that additional family members represent some competition for the love of

the cat.

This competition factor may also work in reverse, where more than one cat is kept in a household. In this situation the question arises whether cats use cat partners as substitutes for humans or humans as substitutes for conspecific partners. Hediger (cited in Mertens (1991)) suggests that a cat's socialisation with conspecifics and with humans follow independent paths. Feaver et al's (1986) separate dimensions for "equable with cats" and "sociable with people" tend to confirm this. Thus, the cat-human relationship may have a dimension of its own, not interfering with cat-cat relationships. Nevertheless, data from the study by Mertens (1991) show a connection between a second cat within the household and the interaction frequency with humans.

Single cats spent longer at home, spent more time in close proximity to their owners, played more with their owners, and generally had higher interaction frequencies with their owners than did cats in multiple-cat households. Similarly, in a study by Bradshaw & Smart (1993) on kittens homed singly or in pairs, the paired kittens played with each other, and correspondingly less with their owners than the singles.

Assuming two independent socialisation processes in the cat, it seems possible that cats well socialised to both cats and humans can overcome a lack of cat partners by more frequent contact with their owner(s) and vice versa. Thus, additional cats who are social intraspecifically may represent some competition for the human in human-cat relationships (Mertens, 1991).

Studies on the more specific behavioural aspects of the cat-human relationship are discussed in Chapter 7 of this thesis.

1.2.4. The special case of neutered cats

In a survey of the distribution and abundance of feral cat colonies in Great Britain, Rees (1981) located 704 colonies living mainly around hospitals, industrial sites and private residential properties. Cats were considered to cause problems in 84.8% of the colonies investigated by questionnaire and to be a definite or possible benefit to 46.0% of the premises occupied by a colony.

Nowadays, in order to reduce the ever-increasing number of feral cats in urban areas, attempts are usually made to control populations. Traditionally, feral cats causing a nuisance (through fighting tom cats, sprayed urine, calling females etc.)

were either shot, or trapped and gassed. More recently the concept of neutering feral cats as well as housecats has gained acceptance, its credibility having been increased by the Universities Federation for Animal Welfare (UFAW) adopting neutering as their recommended method of control of feral cat colonies. In Rees' survey, 9.5% of the colonies investigated had been controlled in this manner. Amongst pet cats, too, more owners now have their cats neutered at an early age.

Neutering can be seen to have a number of advantages in addition to the direct effect on fertility. Some of these are outlined by Tabor (1989). Life expectancy increases, particularly so in the male - but females also benefit. Cats are vulnerable to tumours of the mammary glands. Dorn et al (1968) showed that neutered queens have seven times less chance of developing such tumours than those left intact.

Physical changes apart, neutering is reported to reduce many of the behaviours regarded by humans as a nuisance. Urine spraying, for example, has been shown by one survey to stop or be greatly reduced in 87% of cases following neutering (Borchelt & Voith, 1981). Intermale fighting is also usually considerably reduced following castration (Blackshaw, 1985). Where castration occurs prepubertually about 90 % of males and 95 % of females never exhibit any spraying later in life (Hart & Cooper, 1984).

However, most feral cats are neutered after reaching sexual maturity. Even so, Hart & Barrett (1973) found a pronounced and rapid postoperative decline in fighting, roaming and urine spraying in 53, 56 and 78 % of cats castrated in adulthood. A gradual decline in these patterns of behaviour occurred in an additional 35, 38, and 9% of the cases respectively. In the remaining cases, no decline in any of the behaviours was evident. In the same cat, a rapid decline in one pattern often occurred with only a gradual or unnoticeable reduction in one or both of the other patterns. Age at the time of castration was not related to the rate of decline.

Following his study of urban pet cats, Chipman (1990) suggested that for neutered males age at castration may exert some influence on subsequent range size and a mature male with an established home range may not alter his ranging behaviour much, if at all, after gonadectomy. The neutered male with the largest home range in his study had not been neutered until the age of four.

It would seem from these studies that neutering a colony of adult feral cats should produce a vast change in the social dynamics of the group with some individuals changing behaviourally more than others. In addition, prevention of the

production of kittens has theoretically reduced the functional benefits of sociality it itself, in terms of the communal rearing of kittens by related individuals described by Kerby (1987). Little is known, however, of the post-neutering effect on a colony's social structure.

Two experimental studies have been carried out on feral cats, one in Regent's Park, London (Neville & Remfry, 1984), and the other in Louisiana, U.S.A. (Smith & Shane, 1986). In both cases small groups of unowned, intact cats were neutered and released. The Regent's Park study showed that control by trapping, neutering, marking and returning feral cats to their own site is a humane and effective method, provided the colonies continue to be fed and subsequent immigrants can also be trapped and humanely destroyed or neutered and returned to the site to conserve a desired level of population.

The Louisiana colony failed following neutering due to lack of food provisioning, implying that adequate food must be supplied to maintain the integrity of the group. Some observation of social interactions was attempted for the Regent's Park cats, for a month prior to and then for a period after neutering. The cats were in two groups, both of which were observed. After being returned to the site, all cats appeared to become more affectionate towards each other, affectionate interactions being initiated by both sexes more often after neutering. Aggressive interactions remained rare or fell after the cats were neutered. The authors conclude that neutering appeared to have strengthened the social bonds between members of the study groups (Neville & Remfry, 1984).

With the increase in number of cats being neutered both in the domestic household situation and as larger groups of ferals, it seems that much of the literature which is largely devoted to the social organisation and behaviour of intact, breeding individuals, may not be directly relevant to the majority of cats. Only through in-depth studies of colonies of neutered cats can the long-term effects of neutering on cat social behaviour be understood.

Since, in addition it would appear that much of the interactive behaviour between housecats and their owners includes many components derived from behaviours shown between cats in social contexts (Bradshaw & Lowe, unpublished), our understanding of cat-owner relationships will also be facilitated by increased knowledge of the social behaviour of neutered cats.

1.3. Aims of the study

1. To examine the structure of interactions between cats in three colonies that had been neutered, by investigating temporal links between behaviour patterns used both within and between individuals. As a result of this to produce an objective method of classifying neutered cat behaviour.

2. To discover what, if any, social structure existed within the three neutered colonies. In a socially structured group of cats, individuals recognise one another and the amount and type of interaction between them depends on which particular pair of cats is involved. In other words, cats interact at different rates and in a different manner according to the identity of the interaction partner. In a non-social situation, Macdonald et al. (1979) suggest that interactions occur randomly and the number of interactions between each pair of cats would be directly proportional to the time they were available to interact with one another. This, however, does not allow for variation between individual personalities within the group, in particular, for more interactive cats - an aspect which must be considered when looking at overall sociality.
   Hence:

3. To examine the interactions within each colony at an individual and dyadic level to identify whether particular individuals and dyads were behaving in a socially structured manner, and to identify those individuals and relationships of most significance to each colony.

4. To examine the characteristics of sex and, where possible, age classes within each colony. Such characteristics provide a means of comparison both between neutered groups and between neutered and breeding groups, that is reasonably independent of differences between individual cats.

5. To compare quantitative and qualitative aspects of the social behaviour of these neutered groups with those of breeding groups, particularly with current collaborative studies on entire farm cats in Oxford.

6. Leading from the colony studies, to select key behaviour patterns, thought to be of particular importance to cat society and investigate their use during cat-human encounters.

CHAPTER 2

Study Sites, Methods and Statistical Techniques

TW1 (left) and T1 (right) on bonnet of observation vehicle at Exbury courtyard, Knowle.

CHAPTER 2
STUDY SITES, METHODS AND STATISTICAL TECHNIQUES

2.1. Study sites and animals

At the outset of this study the aim was to find three colonies of free-living cats, all semi-dependent on humans, and all neutered as part of a control scheme. Apart from this the only criteria laid down were that there should be five or more resident adult cats in each group, and that the majority of the cats should be reasonably easy to observe. In practice, observable groups of this kind proved very difficult to find in the Southampton area. Help from local cat welfare groups revealed many locations with semi-wild neutered cats but these were mostly in groups of two or three or living in completely inaccessible locations.

One suitable site housing many neutered cats was found, in the grounds of Knowle Hospital, Fareham, Hampshire. A second group was established specifically for this study on Kennels Farm, Chilworth, using a group of cats removed from a local school as part of a control scheme. The third study colony was maintained by the University but had more restricted ranging ability then the other two groups, in addition to receiving much more human contact.

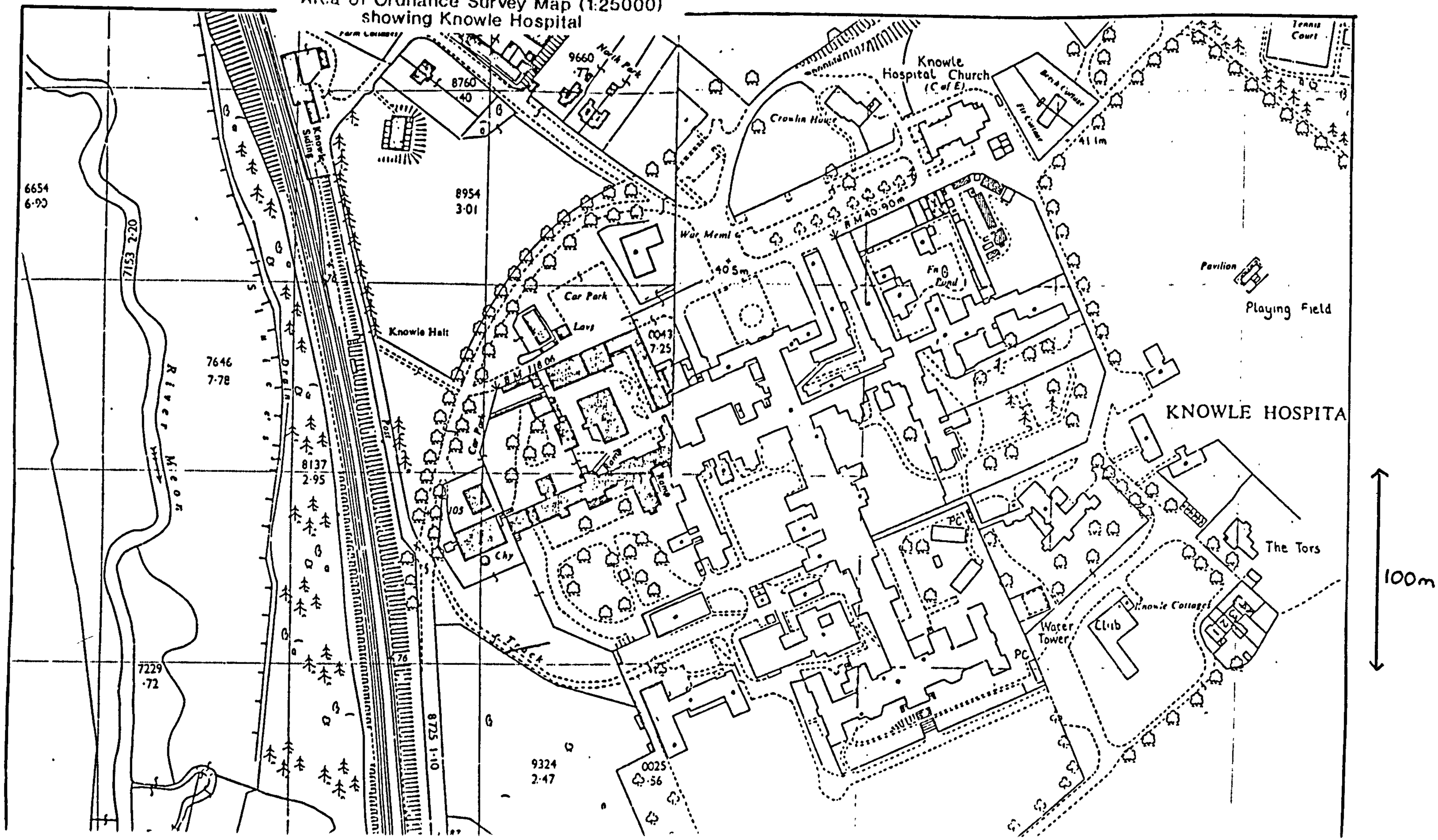
2.1.1. Knowle Hospital, Wickham.

The initial site chosen for study was the grounds of Knowle Hospital near Fareham, Hampshire. The hospital is a long-stay mental institution, set in a fairly remote location, surrounded mainly by farmland and small settlements. (see Figure 2.1.1). The buildings are of traditional red-brick Victorian style and beneath them runs an extensive system of basements with ventilation shafts running from the basements to openings in the outside walls. The heating pipes of each building run through these basements.

Cats were known to live around the hospital in large numbers, many left there as unwanted pets and having subsequently reproduced. The hospital had for approximately five years prior to the study been attempting to neuter and return all the established cats. Some of the cats were very wild and unapproachable - these, combined with the constant influx of new kittens and unwanted pregnant females, left a small section of the population unneutered. On neutering, cats were fitted with a collar in an attempt to enable subsequent identification of neutered individuals.

Figure 2.1.1.

Area of Ordnance Survey Map (1:25000) showing Knowle Hospital



Unfortunately many of them had subsequently lost these collars, so possession of a collar was not an accurate means of determining whether or not a cat had been neutered. Most of the regularly sighted cats were known by the porters at the hospital who, as instigators of the neutering campaign, could confirm whether or not they had been neutered. Unneutered cats were either rarely seen (in the case of the very feral individuals), or were readily identifiable as pregnant females or kittens.

In order to assess the numbers and distribution of cats present at the hospital, the site was surveyed thoroughly for cats by means of regular patrols around the hospital once or twice a week for a month prior to the start of the study. A fixed route, encompassing all areas of the hospital, was traversed in different directions and at different times of day. Detailed descriptions of each cat seen, its activity, location and proximity to other cats were noted. Over 60 individuals were identified, living as a number of separate subgroups in different areas of the hospital. Some of these groups lived permanently under established buildings or, being extremely wary of humans, bolted into basement openings when approached. These were unsuitable for extended observation. One subgroup, consisting of 5 core individuals and several occasional visitors were based around a small courtyard where they gathered to receive their daily provisioning of food. This was termed Exbury courtyard, after the name of a ward that overlooked it..

The courtyard comprised a weed-covered tarmac area, surrounded on three sides by outside walls of the building. Staff entered and left the building via a door on one of these walls which opened on to a ramp designed for wheelchair access (see Figure 2.1.2). Food was provided every day at the top of this ramp (see next section) so this became a focal point of attention for the cats in the yard, both from the point of view of waiting for food to appear and to avoid human contact. The yard was used by some of the staff to park their cars - the cats were therefore habituated to the presence of vehicles.

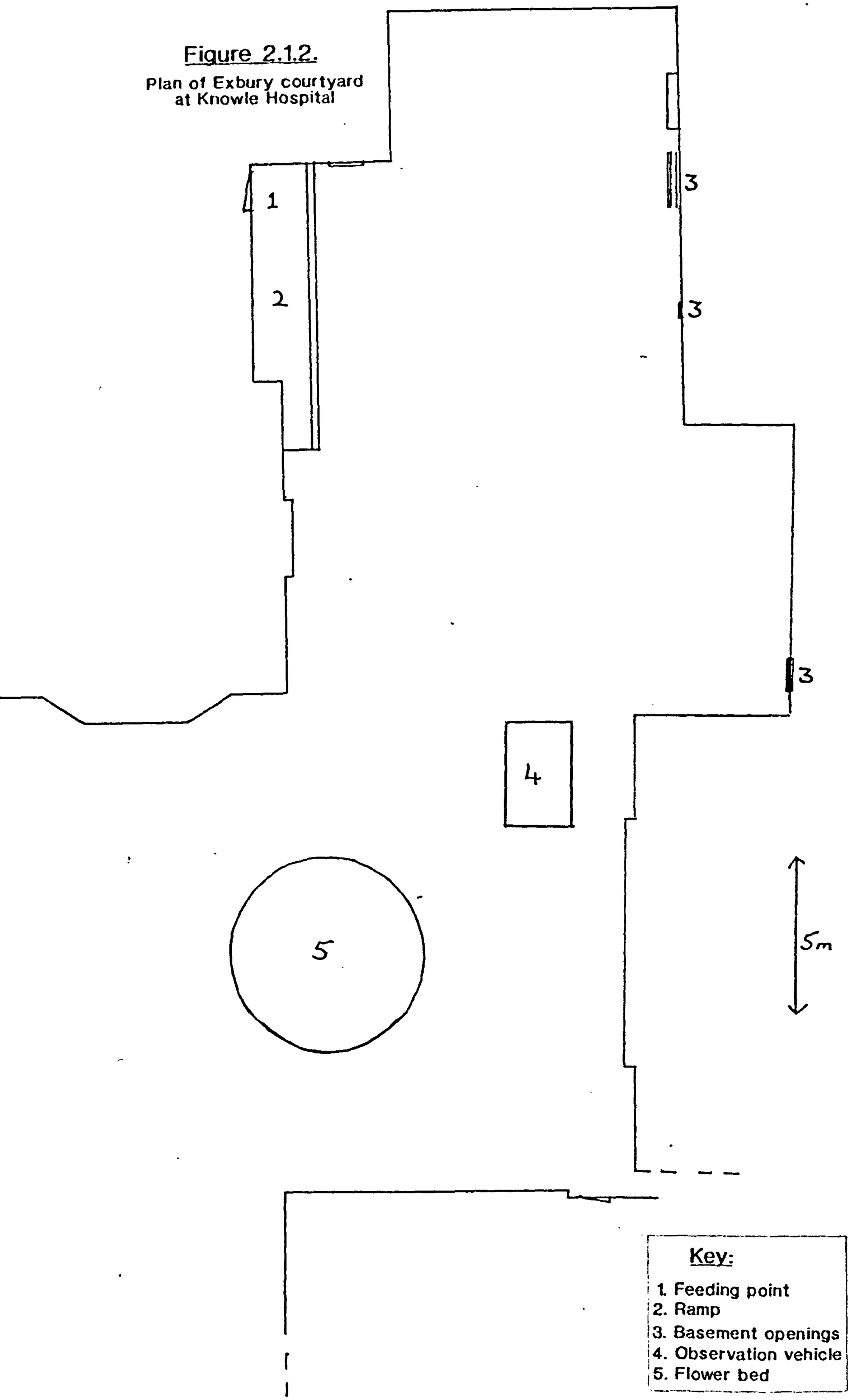
Food

A variety of canned and dry cat foods, and occasionally milk, were provided for the hospital cats (financed from a central fund) every day at fixed feeding stations around the hospital. One of these feeding points was in Exbury courtyard (See Figure 2.1.2). Food was provided here between 12.00 midday and 2.00 p.m. every day.

In addition to this, waste food from within the hospital was provided around the

Figure 2.1.2.

Plan of Exbury courtyard at Knowle Hospital



hospital grounds in large quantities at various times of day as it became available - this took many forms, from scrambled eggs to meat scraps. Such was the surfeit of food available for the cats that it was rare not to observe uneaten food when patrolling the hospital grounds.

Shelter and resting sites

Only selected cats were allowed inside the hospital buildings -these "ward cats" appeared to form a separate population to the more feral cats outside, rarely venturing outside themselves. As for the rest of the cat population, some subgroups of cats sheltered under sheds and other raised buildings, but the majority took advantage of the extensive heated network of basements. In Exbury courtyard, there were three ventilation shaft openings leading down into the basements - whether these led to the same or different areas of the basements could not be ascertained since the hospital authorities could not permit any access. The study group quite evidently regarded these openings as prime resting sites, providing a warm point from which to wait and watch for the provisioning of food and a quick escape route should danger arise. In addition to these holes, sunny window ledges, warm car bonnets and under parked cars proved to be the most frequently used resting places.

Cat demography

There were five regular attenders in Exbury courtyard, two male and three female. Four of these appeared regularly from the basement entrance holes and one (BW1) male appeared from elsewhere in the hospital. This male was a less frequent attender than the others but nevertheless maintained this throughout the study. All five individuals survived throughout the study. The three occasional visitors to the yard (described in Chapter 4) were also present at the hospital throughout the study.

All of these cats were extremely cautious of humans and rarely allowed anyone to approach closer than three metres without fleeing. Therefore, to investigate the possibility that some of the cats might not have been neutered, all five core individuals, and the most frequent occasional visitor (TW3), were trapped and taken for veterinary examination -this confirmed that they were all neutered. The other two occasional visitors both wore collars, indicating their neutered status. No information concerning the relatedness of individuals was available.

2.1.2. Kennels Farm, Chilworth.

The search for a second site with a resident population of neutered feral cats was unsuccessful so it was decided to establish one. Eleven cats were "rescued" from a local school where they were considered to be causing a potential health hazard to the children, and were housed temporarily at a local animal sanctuary. They were all neutered, vaccinated and treated for various ailments. Four of the females were pregnant -they were allowed to have their kittens and wean them before being neutered, and the kittens were all homed. Once in a healthy condition, the cats were taken to the new field site at Kennels Farm, Chilworth, Hampshire.

Kennels Farm is an old farm owned by Hampshire County Council currently used as a tree nursery. Situated to the south-west of Chilworth village, to the south it is bounded by the M27 motorway and to the north is bordered by woodland (see Figure 2.1.3). West of the farm is mainly pasture land and to the east are the grounds of Chilworth Manor, now forming part of the University science park. Staff at the tree nursery agreed to accept the cats on the farm site to help control an increasing rat problem there.

Although many sheds and buildings were in existence at the farm, these were all in use at the time of the study and so a garden shed 6 foot by 4 foot was erected as a shelter and feeding base for the cats. A cat flap was installed in the side of the shed so that, once established at the site, the cats could gain access to the food whilst hopefully keeping out other potential consumers, e.g., foxes and magpies.

The site chosen for the shed was on a rough area of grass next to the woodland on the north edge of the farm. A wide sloping farm track ran between the shed and the wood (see Figure 2.1.4) used once or twice daily by workers manoeuvring farm vehicles but apart from that the area was relatively undisturbed. It was hoped that the shed and adjacent track would form the core area of the cats' range where they would return for provisioning. The close proximity of the wooded area where they could seek refuge encouraged this.

Establishment of the cats on this new site required a period of confinement to the shed for them to accept this as their new feeding point. During this period of confinement, a 1m x 1m x 0.75m caged area was connected onto the shed (accessed by the catflap) providing the cats with outside access and familiarising them with their new environment before being released. The cats were established here in two groups (The pregnant females and one tom were taken later than the rest so there

Figure 2.1.3.

Area of Ordnance Survey Map (1:25000)
showing Kennels Farm, Chilworth

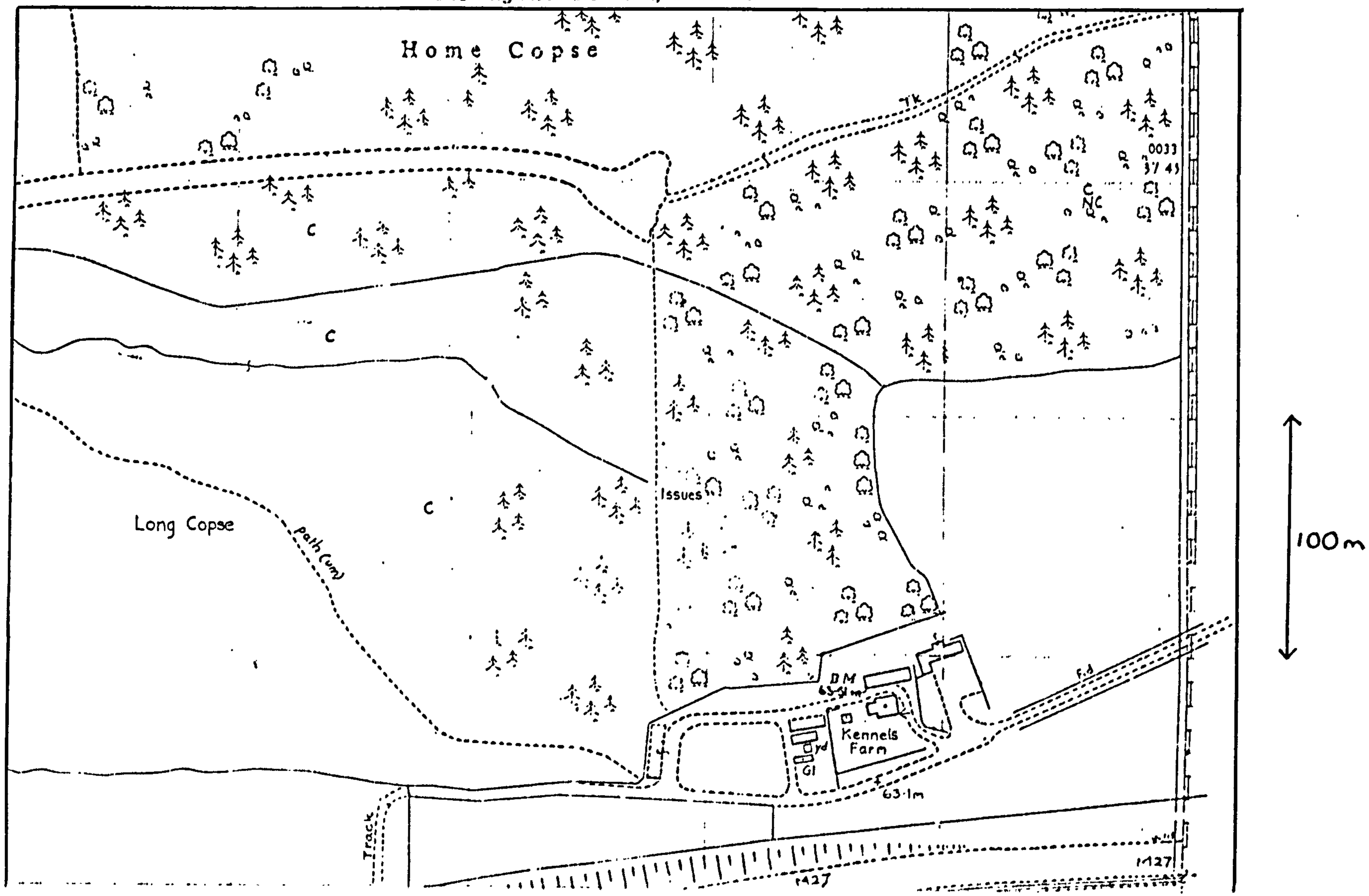
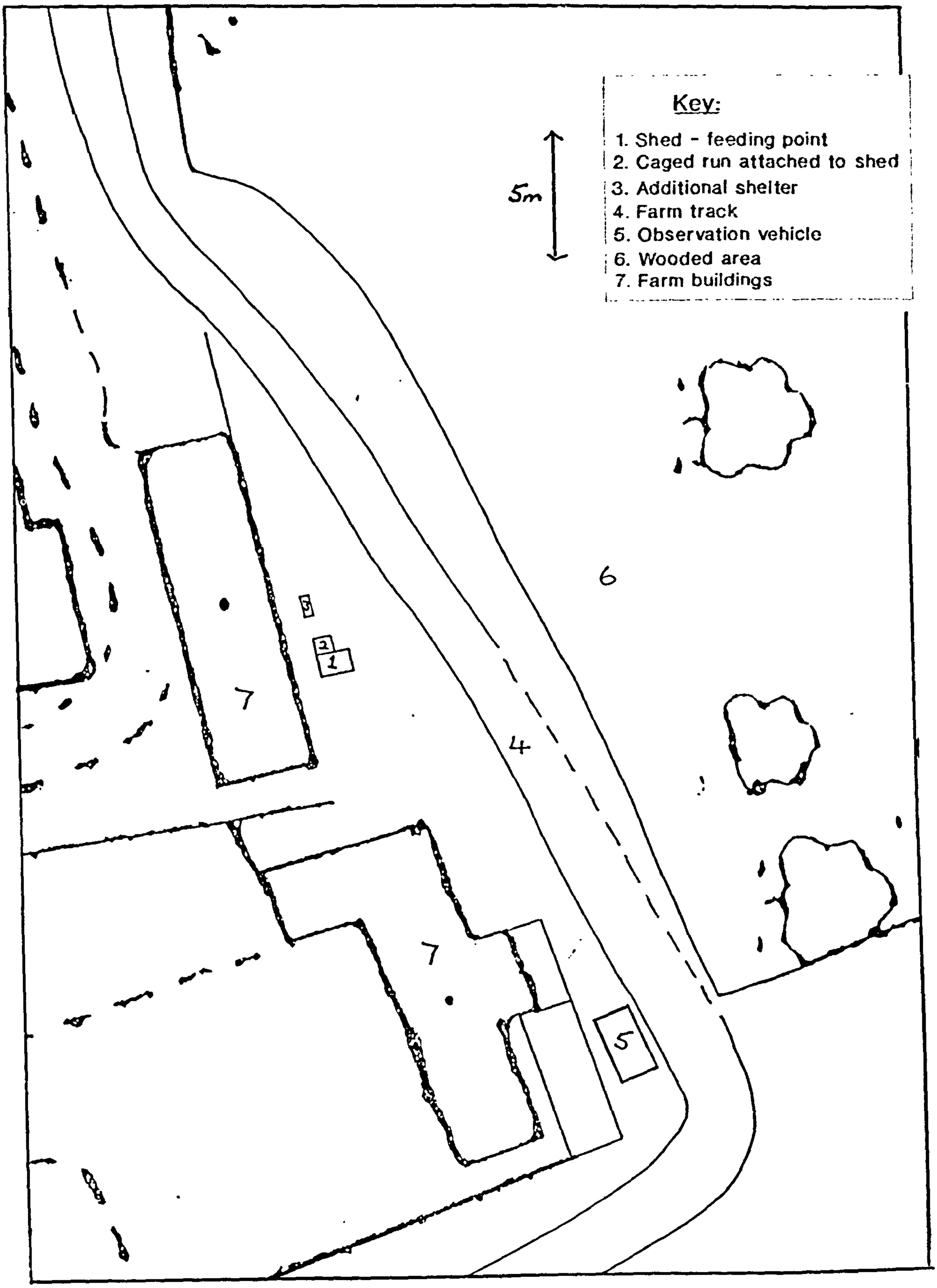


Figure 2.1.4.

Plan of observation area at Kennels Farm, Chilworth



were never more than six cats confined to the shed at any time).

The first group were confined initially to the shed and run where they were fed for three weeks and then released on June 5th 1989. After their release, none of this first group was seen for several weeks. The food continued to disappear regularly, however, so presumably they were emerging after dark. Gradually they began to habituate to the feeder and could be seen in the undergrowth and nearby woodland as the food was put out.

On July 11th the second group (four females and one male) were brought to the site, confined to the shed and caged area, and then released two weeks later. This second group habituated to the feeder much faster than the first. The two groups were then allowed to settle and hopefully reintegrate with each other until mid-August when observations began.

Observations continued until May 1990 when, due to complaints from the staff at the farm about fouling by the cats, it became necessary to relocate the cats once more. A local farmer in need of some rat control agreed to take the cats on his farm so the cats were trapped and transported to the new farm. Observation at the new site proved much more difficult than previously and so behavioural studies of this group were terminated at this point.

Food

Canned and dry cat foods were provided at the shed every day, normally although not invariably in the late afternoon. The food, unless particularly unpalatable, was usually all gone by the following day. Any remaining was removed and fresh food provided.

The staff at the farm reported finding a number of dead rats around the farm, presumably killed by the cats. The shed also bore evidence that they were catching and eating prey in the form of the inedible parts of birds and small mammals. Occasionally whole prey, particularly shrews were abandoned in the shed. Regular provisioning did not therefore seem to have reduced the cats' inclination to catch wild prey.

Shelter and resting sites

As hoped at the establishment of the colony, the shed became the focal point of activity for the cats. As well as feeding there, many of them slept in boxes provided

for them on shelves inside the shed. During the winter of 1989 a second smaller shed-like structure was erected next to the original shed to provide further shelter for the cats. This roofed wooden structure comprised four compartments separated by partitions, but all interlinked and accessible to the outside through small catflap-sized entrance holes. Several of the cats adopted this as a sleeping shelter.

Away from the shed, the cats frequently rested under the large pieces of farm machinery parked at the bottom of the sloping track (see Figure 2.1.4) and perched on top of the sheds or in trees at the edge of the wood.

Cat demography

Eleven cats were present at the start of the study, seven female and four male. One female (SM) disappeared during October 1989, leaving 10 cats, four males and six females. A second female (BE) disappeared in February 1990, reducing the numbers to 9 cats. The cats varied in their attendance during the study, one male in particular (GH) showing a very reduced attendance towards the end of the study.

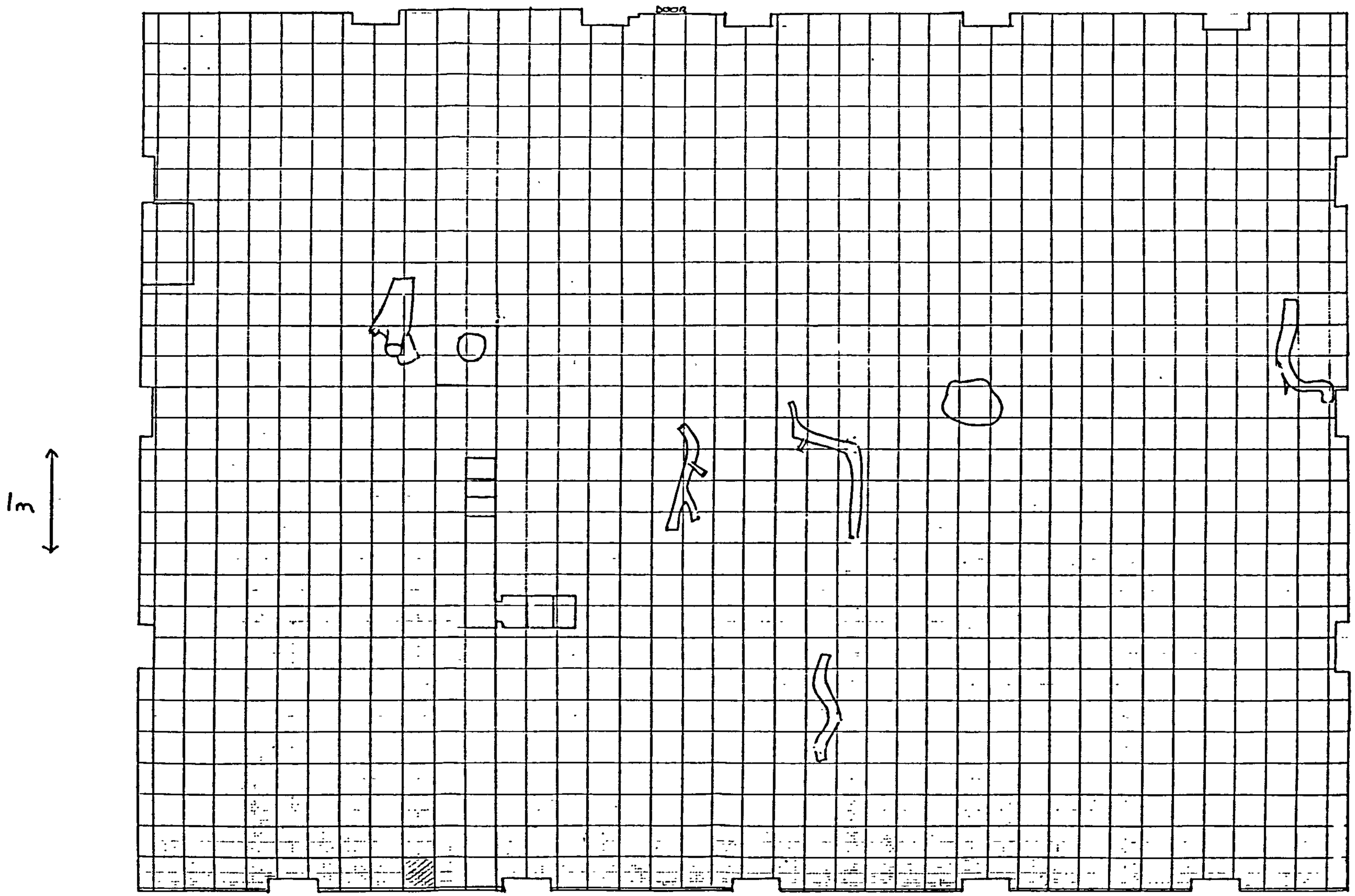
No precise information concerning the relatedness of individuals was available. Coat colours did, however, allow for some speculation on possible relatedness. Many of the cats, were basically black (a recessive gene and therefore suggesting some relatedness between individuals). Most of these also exhibited a large amount of white spotting (SS) on the body. One male, GI, exhibited the O (orange) gene. The existence of three tortoiseshell-and-white females in the group suggested that he may have been their father. Most of the kittens born to the females in 1989, prior to the colony being neutered, carried the O gene. GI was presumably also the father of these and therefore possibly the dominant male with regard to mating success at that time.

2.1.3. University cat colony

The University has a colony consisting of 26 neutered domestic cats, 14 male and 12 female. The cats are enclosed and have the run of two indoor rooms each having several layers of shelves around the walls with boxes on for sleeping in. These rooms are connected by an indoor corridor which also leads to an outdoor paved yard, area 96 square metres (see Figure 2.1.5). Covered with chicken wire to prevent escape, this yard contains environmentally-enriching objects including logs for the cats to scratch on, children's playground climbing frames, and cat toys. The cats have

Figure 2.1.5.

Plan of observation yard
at University colony



access to all these areas during the day, but are restricted to the indoor rooms at night (they are allowed to choose which room to sleep in, half the group goes into each room and the corridor is shut off for the night). The study was carried out in the outside yard area, this being the most observable and most popular area used by the cats.

Most of the cats had lived as a colony for over three years at the time of the study (6 of them joined the group a year later) and were very familiar with humans. The majority of the group were very friendly towards humans with a smaller number being less approachable and in some cases completely unapproachable. The colony thus provided an example of a neutered group of domestic cats, not feral as before, exhibiting complete dependence on humans for food, and, as a result showing a higher level of tolerance of humans. It was felt that this group would provide a study slightly closer to the domestic situation than the feral groups, whilst still examining the social interactions within a neutered group. Also, after a period of watching the group as a whole, should any behaviours emerge as warranting more detailed investigation, this group would lend itself very well to more experimental studies and to studying cat-human behaviour to see how that relates to cat-cat sociality. Table 6.2.B (Chapter 6) gives details of the animals.

Food

Canned and dry cat food was provided daily, available in the two indoor rooms of the colony's range. This was left for the cats to feed ad-lib during the day and overnight and the food trays removed the next morning. The time of provision of food was variable and, during the period of the study, was always after observations had finished for the day. This was to prevent all the cats going indoors to feed on the fresh food whilst observations were continuing outside.

With no access to foraging areas, the cats' opportunity to catch wild prey was limited. However, when outside they spent much of their time chasing, catching and consuming insects whenever these flew down through the mesh roof.

Shelter and resting sites

The indoor areas of the colony's range were amply equipped with boxes and shelves for sleeping in. Outside, the cats tended to rest in sunny areas of the yard or on favourite objects.

Cat demography

The original population of twenty cats had been increased by six two years prior to the study, but for the duration of the study numbers remained constant. A full veterinary history was available for each cat plus the identities of its mother, father and littermates. From this the lineages of the colony members could be determined. These are illustrated in Figure 2.1.6.

2.2. Observation methods

Observation techniques were broadly similar for all three study colonies, with minor modifications for each due to different observational constraints. The basic techniques will therefore be described first and any methodological differences described for each colony in turn.

Cats in all three colonies were readily distinguishable by coat colour and markings. A period of familiarisation with the cats in each group enabled distinguishing colours and features to be learnt, making identification during the studies rapid and easy.

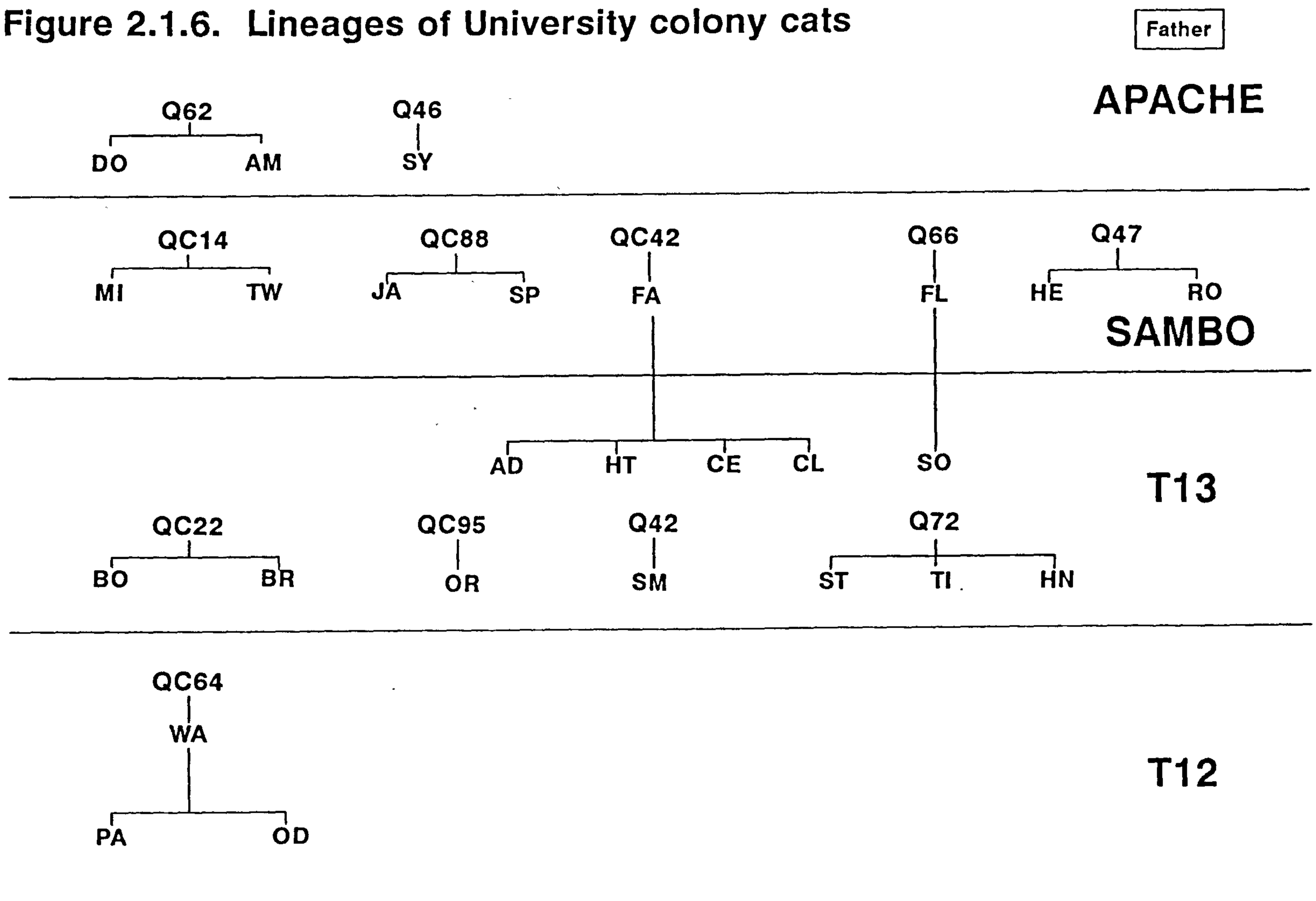
Observations were made from whichever point within the study site afforded the best view of the maximum number of interactions between animals, whilst causing the minimum of disturbance to the animals themselves. Observations were made according to two protocols: "interactive" and "proximity", described below.

2.2.1. Interactive data

This method involved continuous recording of social interactions between cats during observation sessions of between 30 minutes and three hours at the different sites. For the purposes of this study a social interaction was defined as "any sequence of behaviour patterns directed by one cat towards another including any behaviour patterns the other cat may perform in response". The cat starting the interaction was termed the "Initiator" and the cat which received the first behaviour pattern, the "Recipient". Regardless of which cat performed the next behaviour pattern, initiator and recipient status remained the same throughout the course of that interaction.

Behaviour patterns were allocated two-letter codes (see Appendix 1) and interactions were recorded as strings or sequences of behaviour codes suffixed with an I or R to differentiate between the initiator and recipient of the interaction. The

Figure 2.1.6. Lineages of University colony cats



following example illustrates the recording of an interaction where one cat initiates an interaction by approaching the other with its tail lowered and sitting with the Recipient. the Recipient sniffs the Initiator, grooms him and then moves away with his tail lowered:

API, SWI, SNR, GCR, MAR

The end of an interaction was denoted by one or both of the cats moving away from the other in some way and/or no further behaviours occurring between the pair for two minutes.

Interactions were recorded by hand on paper and later put into the computer for analysis.

2.2.2. Proximity Data

Every 15 minutes during observation sessions a census was taken by noting the location of all individuals present and in sight. The location of each animal was marked, using a different mark for each scan, on a map of the observation area. This scan information was later examined in detail and transcribed to give information on which cats were present on each scan and which pairs of cats were less than one metre apart on each scan.

2.2.3. The behaviour

Behaviour patterns were based on those of Kerby (1987) with a few additions. As stated by Kerby, during the recording sessions the aim was to record the behaviour of the individuals without interpretive prejudice. Therefore, the names given to each behaviour code are intended to be no more than descriptive labels and have no motivational implications *per se*. The list of behaviour patterns is presented in Appendix 1.

2.2.4. Field notes

In addition to the quantitative data, detailed supplementary field notes were taken, recording any events which might have influenced the behaviour of the cats.

2.2.5. Observations on each colony

1. Knowle colony

This group was observed for a total of 181 hours from November 1988 until October 1989, once or twice weekly for most of the study, but less frequently during the last two months.

Initially the courtyard was attended for 2-4 hours at a time at different times of day to ascertain the cats' activity patterns. It was found that the cats only began to emerge from the basement openings about one hour prior to the provision of food and they dispersed shortly after feeding. Watches were therefore concentrated around midday as the cats gathered to wait for their food. Observations were made from a parked car near the entrance to the yard (see Figure 2.1.2) with which the cats were familiar. They showed no indication of fear towards the presence of the car and seemed unaware that anyone was even inside it.

Due to the small number of cats present at any one time in the yard, it was possible to monitor the presence of each individual constantly, recording when each entered or left the yard area. This gave a very accurate assessment of the time that each cat was present and available for interaction with each other cat for the whole study period. Proximity data, as described in section 2.2.2, was only collected from February to October 1989.

In addition to the concentration of observation on this sub-group of cats, the presence and distribution of the other cats in the grounds of the hospital were regularly monitored by once- or twice-weekly patrols, as in the initial pre-study surveys (section 2.1.1). Patrols were carried out at different times during daylight hours to avoid missing any changes in activity which might occur over the course of a day. Five dawn and five dusk patrols were carried out during the summer of 1989 to ensure that all daylight hours were covered by these patrols.

The purpose of these patrols was to keep track of other subgroups of cats which might prove suitable for more extensive observation alongside the Exbury courtyard group. Although a suitable group was never found, these patrols did enable easy identification of the occasional visitors to the Exbury yard as well as providing an indication of where they were normally seen.

2. Chilworth colony

Observations began on this colony in mid-August 1989 and continued until May 1990 when they were relocated. During this time the cats were observed several times a week (weather permitting) for 1-2 hours as they assembled prior to feeding each day. Total observation time was 54 hours. Observations were made from a car parked at the top of the sloping track (Figure 2.1.4) -the cats were habituated to this vehicle and showed little interest in it once the engine was turned off.

3. University colony

As described above both the Knowle and Chilworth studies had used a car as a hide from which to observe the cats. Due to the enclosed nature of the University colony yard, this was not possible for this study, so some other form of concealment was sought. Methods of observation tested included a standard fieldwork hide erected in one corner of the yard and a window of one-way glass installed in the wall of the yard. Neither of these methods concealed the presence of the person satisfactorily and the cats exhibited an unduly high amount of interest in these attempts at concealment.

A simpler approach tested was for the observer to sit quietly, unconcealed, on a stool in one corner of the yard, wait for the cats' initial interest in them to fade and then start observations as they returned to their normal interactions. Because the presence of an observer might affect the actual type of behaviours performed by the cats, a six week pilot study was undertaken consisting of periods of observation as described above, interspersed with periods of video recording of the yard with no observer present. The results of the pilot study (discussed in Chapter 6) showed that the presence of an observer was indeed having an effect on the cats behaviour.

The only method apparently suitable for observation of these cats seemed therefore to be video recording. This method was employed and the yard was filmed for between 1 and 6 hours a day (according to weather conditions and status of other work being carried out on the colony), most days from March 13th 1991 until June 4th 1991. The videos were then watched and interactions and scans recorded as for the other colonies. Only interactions that started and finished on screen were recorded, any starting or finishing off camera were discarded as incomplete.

2.3. Statistical techniques

With the intention of looking at the data from the three colonies in several different ways, a variety of statistical tests were employed. These were kept as simple as possible to avoid producing artificial conclusions as a result of type 1 and type 2 errors. The following section outlines the main statistical methods used, giving references to their sources for further information. Other methods were used on occasion where appropriate - these are described in the relevant chapters.

Data was manipulated into formats required for each analysis using Lotus 1-2-3 spreadsheets and Reflex database facilities. Analyses were performed either using spreadsheet facilities or, for the more complicated tests, using Statgraphics or SAS packages.

2.3.1. Average-linkage cluster analysis

This technique was used to analyse several different data sets from the colonies. The method, carried out on SAS, required data to be arranged in the form of a triangular distance matrix -clusters of points were produced based on this. A dendrogram could then be drawn incorporating each of these clusters.

Using this technique, all three colonies are examined in Chapter 3 to investigate links between behaviour patterns occurring within individuals' contributions to interactions. The same technique was used to illustrate the degree of proximity shown by individuals towards each other in the Chilworth and University colonies.

2.3.2. Chi-squared analysis

Chapter 3 includes a detailed analysis of the sequencing of behaviour patterns within interactions. Matrices were compiled of the numbers of transitions between patterns at each colony. These were analysed, following the recommendations of Slater (1973) using chi-squared tests. Chi-squared analysis, the classical method for analysing frequencies is also used elsewhere when appropriate, for example to test the significance of asymmetries in the flow of interactions and behaviour patterns between individuals in Chapter 4. Fowler & Cohen (1990) and Sokal & Rohlf (1981) describe the different methods of application of the chi-squared test in detail.

2.3.3. The Kolmogorov-Smirnov one sample test

This goodness-of-fit test compares the cumulative frequency distribution which would occur under a specified theoretical distribution with an observed cumulative frequency distribution. The point at which these two distributions, theoretical and observed, show the greatest divergence is determined. Reference to the sampling distribution then indicates whether such a divergence is likely on the basis of chance (Siegel & Castellan, 1988). The Kolmogorov-Smirnov test (or K-S test as it is referred to in the text) was used to test both the Knowle and the Chilworth colony data sets for uniformity over the study period. The University study, carried out over a much shorter time span, did not require this analysis.

2.3.4. The G-test for detecting heterogeneity

The data sets for all three colonies were complicated by the variable attendance of different individuals and different pairs at the study sites. This meant that the only way to compare individuals and dyads was to compare either rates of behaviour patterns performed and received, or to compare the overall distribution of patterns used and received by each individual, i.e. compare behavioural profiles. Investigation revealed no suitable statistical procedure that could cope with rates (very low ones in many cases) where no replication was available - as was the case when looking at individuals or pairs of individuals.

Analysis of individuals and dyads in the Knowle and Chilworth colonies therefore took the form of comparisons of behavioural profiles performed and received. The details are described in chapters 4 and 5 respectively but both used the G-test as a measure of statistical significance.

The G-test can be used for detecting heterogeneity between replicates in a one-way classification matrix. This version of the G-test is known as Gh (heterogeneity G) and is described by Sokal & Rohlf (1981). It was used in the analysis of the data from individuals and dyads in the study colonies to test for heterogeneity within matrices of behaviours performed and received by individuals and pairs of cats. Where heterogeneity was detected it meant that one or more of the cats or, in the case of dyad matrices, pairs of cats, differed from the others with regard to behaviours performed or received.

Unplanned tests of the homogeneity of the data

In situations where there was significant heterogeneity among the contributory rows to a matrix, i.e., between individual cats or dyads, unplanned tests of homogeneity were used to test whether all individuals differ from one another or whether there were homogeneous sets of cats differing from other such sets or single individuals. The method is described by Sokal & Rohlf (1981) and may take different forms according to how thoroughly the matrix is to be tested. Thus it is possible to test all pairwise (or fewer) unplanned comparisons of rows (referred to as selective unplanned tests of homogeneity). It is also possible to test all possible sets of rows which requires a still more conservative procedure. For each test an experimentwise error rate (also known as the familywise type 1 error rate) is employed which adjusts the probability according to the number of comparisons made - the critical values of chi-squared for that test can then be found in a special table of such values based on Sidak's multiplicative inequality (see Sokal & Rohlf, 1981).

2.3.5. Principal Components analysis

In principal components analysis the variance in a matrix is accounted for by a succession of components. The first component is defined by the axis along which maximum variance exists. The variance accounted for by the first component is removed, and the second component is found. This accounts for as much as possible of the variance remaining and lies along an axis perpendicular to that of the first component, so that the two components are uncorrelated. This process is repeated, each successive component accounting for a smaller proportion of the total variance and being uncorrelated with previous components.

This process was performed on the data sets analysed by Gh-tests in Chapters 4 and 5. The Gh-tests, whilst revealing that differences between individuals or dyads existed, did not reveal how these differences were manifested, i.e., with respect to which behaviour patterns did the cats differ most. Principal Components Analysis (PCA), performed on the Statgraphics package, therefore provided a visual component to the analysis showing associations between particular individuals or dyads and specific behaviour patterns.

2.3.6. Spearman rank correlations.

Many of the variables examined when looking at characteristics of each colony as a whole showed signs of being interdependent. Relationships between colony variables were therefore examined by Spearman Rank Correlation analysis. This non-parametric technique correlates the variables after converting observations to ranks and was performed on the Statgraphics package. Fowler & Cohen (1990) explain the test in more detail.

Rank correlations were used to test the individuals for indicators of sociality by correlating time available for interaction with total number of interactions (irrespective of direction) and rate of interaction per hour available to interact, for all possible dyads. The tests for the Knowle, Chilworth and University colonies are described in Chapters 4,5 and 6 respectively.

2.3.7. Analysis of variance

Described in detail by Fowler & Cohen (1990), this technique was used when examining the characteristics of each colony as a whole and included both one-way and multifactor analyses of variance. Data was transformed in order to approximate more closely to the normal distribution before analysis was performed using Statgraphics. Variables analysed included times, rates and, in the case of proximity data, proportions. Following guidelines laid out in several statistics books e.g., Fowler & Cohen, (1990), Steele & Torrie (1980), different transformations were used according to type of data. Time was transformed by taking the square root of each value. Rates of activities were transformed by taking the logarithm of each rate after adding 0.001 - this was to overcome the problem of being unable to take the logarithm of zero values, whilst not greatly increasing very low rates which were common. Proportions were transformed using the arcsine of the square root of each value. Analysis was performed on the transformed variables but, in order to present the original data more fully, means are displayed in each chapter as arithmetic means, rather than backtransformed values from the transformed data.

CHAPTER 3

The Behaviour

"Sniff Cat" by HE towards FA (University colony).

CHAPTER 3 - THE BEHAVIOUR

With such a large number of interactive behaviour patterns (described in Appendix 1) observed across the three colonies (the largest being 53 in the case of the University colony), some information on the structure of the behaviour sequences is needed in order to understand the social dynamics of the cats. Within a two-way interaction the behaviour of either cat may be affected by the behaviour patterns it has already performed and/or by the behaviour of the other cat. The analysis of behaviour sequence structure therefore took two forms:

i) the structure of behaviour patterns within an individual's contribution to an interaction, i.e., the likelihood that an individual will perform behaviour B in the same interaction as behaviour A;

ii) the sequence of behaviour patterns performed by the two participants of an interaction, i.e., which behaviour performed by either cat would most likely follow behaviour A performed by one or other of the cats.

These structures are almost certainly not mutually exclusive. However, since it is impossible to determine in advance from such complex data how much one cat is influenced by the behaviour of another, the two aspects will be examined separately.

3.1. Intra-individual use of behaviour patterns.

A method, preferably an objective one, of grouping behaviour patterns into "categories" is required to simplify the large number of behaviour patterns recorded. Previous investigators, e.g. Kerby (1987), attempting to establish categories of behaviours objectively, have reported little success and have, as a result, resorted to a subjective behavioural classification system. Data was collected in a different manner from that of Kerby in the current study with sequential information kept intact. This allows an objective assessment of temporal (and therefore probably functional) linkage between behaviour patterns by examining the number of times each pattern was performed in the same sequence as other patterns by the same cat.

For each colony the complete set of recorded interactions was analysed. As outlined in Chapter 2, an interaction is composed of a string of behaviour patterns, some performed by the cat which initiated the interaction (the "Initiator") and some performed by the recipient of the first behaviour (the "Recipient"). Initiator and Recipient status remain the same throughout the interaction, regardless of the order

of performance of patterns. For each Initiator cat it was calculated how often each pattern was performed in the same interaction as every other pattern, thus producing a matrix of associations between behaviours. The same was done for the Recipient cats and the two matrices were then added together. (Initiators and Recipients were not analysed separately, since they were simply labels used to distinguish between the two participants of the interaction, the same behaviour patterns being available to each.)

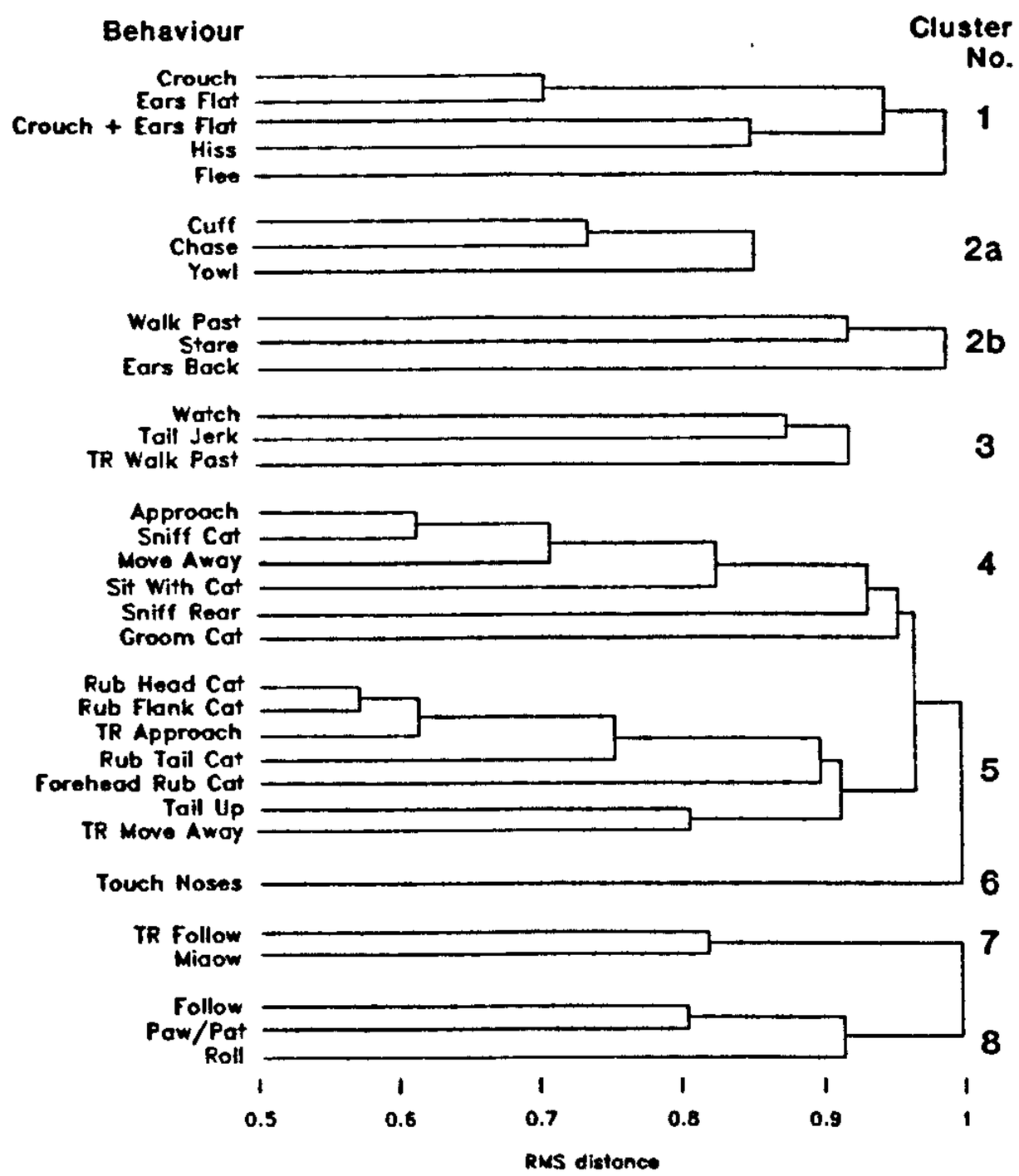
The resulting matrix for each of the three colonies was converted into a triangular matrix by calculating 1 minus the probability of occurrence for each component cell. Behaviours totalling < 10 occurrences were omitted. Average linkage cluster analysis was then performed on each colony's matrix using SAS and a dendrogram drawn of the links between behaviour patterns. Patterns likely to be seen within the same interaction are thus indicated by lines which join close to the left hand side of the dendrogram; patterns or groups of patterns that join further towards the right, or do not join at all, are hardly ever performed together by a cat during a single interaction. RMS distances more than 1 are excluded from the dendrograms.

The resulting set of clusters in each dendrogram can be described functionally. Each dendrogram is described in turn on the following pages and a comparison made of all three in section 3.1.4. Since the Chilworth colony is probably the most "typical" of free-ranging groups, being of medium size and with unrestricted space, the others are described in comparison to this. Cluster numbers are allocated arbitrarily.

3.1.1. The Chilworth colony dendrogram

This is illustrated in Figure 3.1.1. At the top of the dendrogram cluster 1 contains typically defensive behaviour patterns, whilst below it cluster 2a contains aggressive patterns. Cluster 2b may be an alternative aggressive group, possibly a milder form. Cluster 3 probably arises from interactions in which one partner is unwilling to let the other approach. Cluster 4 results from interactions in which one cat approaches another with its tail in the normal position (i.e., not raised above the horizontal), sniffs it ands sits beside it. The locomotory patterns in cluster 5 differ from those in cluster 4 by being performed with the tail raised (TR), and are often followed by rubbing behaviours. Cluster 6 consists of a single pattern (Touch Noses) a form of greeting behaviour which may be highly individualistic. Cluster 7 is

Figure 3.1.1. *Links between behaviour patterns observed at Chilworth from Average Linkage Cluster Analysis. Cluster numbers are allocated on a purely arbitrary basis.*



interaction-seeking and cluster 8 is playful.

3.1.2. The Knowle colony dendrogram

This is illustrated in Figure 3.1.2. The clusters produced by the Knowle colony are on the whole very similar to those produced from the Chilworth cats. Because the Knowle colony consisted of only 5 cats, none of which were young, the number of behavioural elements is reduced (only 18 included). For example, most of the play cluster is absent -a possible function of the age of the animals. Cluster 1 of Figure 3.1.2 contains a single defensive pattern Flee, and below this cluster 2a is still aggressive in nature, consisting of Cuff. Walk Past is the single representative of cluster 2b. Cluster 4a represents the approach with tail down, sniffing and sitting with patterns characteristic of cluster 4 in the Chilworth dendrogram. Move Away and Touch Noses are linked to a certain extent in this group (cluster 4b). Whilst most of the affiliative tail-raised patterns and rubbing are linked as at Chilworth (cluster 5b), three of them, Tail Up, TR Move Away and Rub Foreheads, obviously possessed a different functional link since they have separated into a separate cluster (5a). This is possibly due to one individual exhibiting a limited selection of the affiliative patterns, an individual effect being much more apparent when fewer cats are being considered.

3.1.3. The University colony dendrogram

This dendrogram, illustrated in Figure 3.1.3 contains a number of behaviour patterns not evident in the other colonies. The resulting clusters may therefore reflect the different age structure (all the cats are approximately the same age unlike in the other colonies - see Chapter 6), early neutering and/or more restricted lifestyle of this colony compared to the other two. There are, for example, far more play behaviours and play/aggression in evidence - this may be a result of their more confined environment or simply due to a failure to develop more adult behaviour patterns under such sheltered conditions.

Cluster 1 contains the submissive pattern Flee combined unusually with Tail Up. This may represent an appeasement display on fleeing from an opponent in a confined environment. Aggressive behaviour patterns seemed to be combined with milder contact play patterns in cluster 2, suggesting that aggression in this colony is generally play aggression rather than the escalated aggression observed in entire colonies. This may be a reflection of their neutered status or of their need to restrain

Figure 3.1.2. *Links between behaviour patterns observed at Knowle from Average Linkage Cluster Analysis. Numbers in parentheses refer to cluster numbers at Chilworth (Figure 3.1.1).*

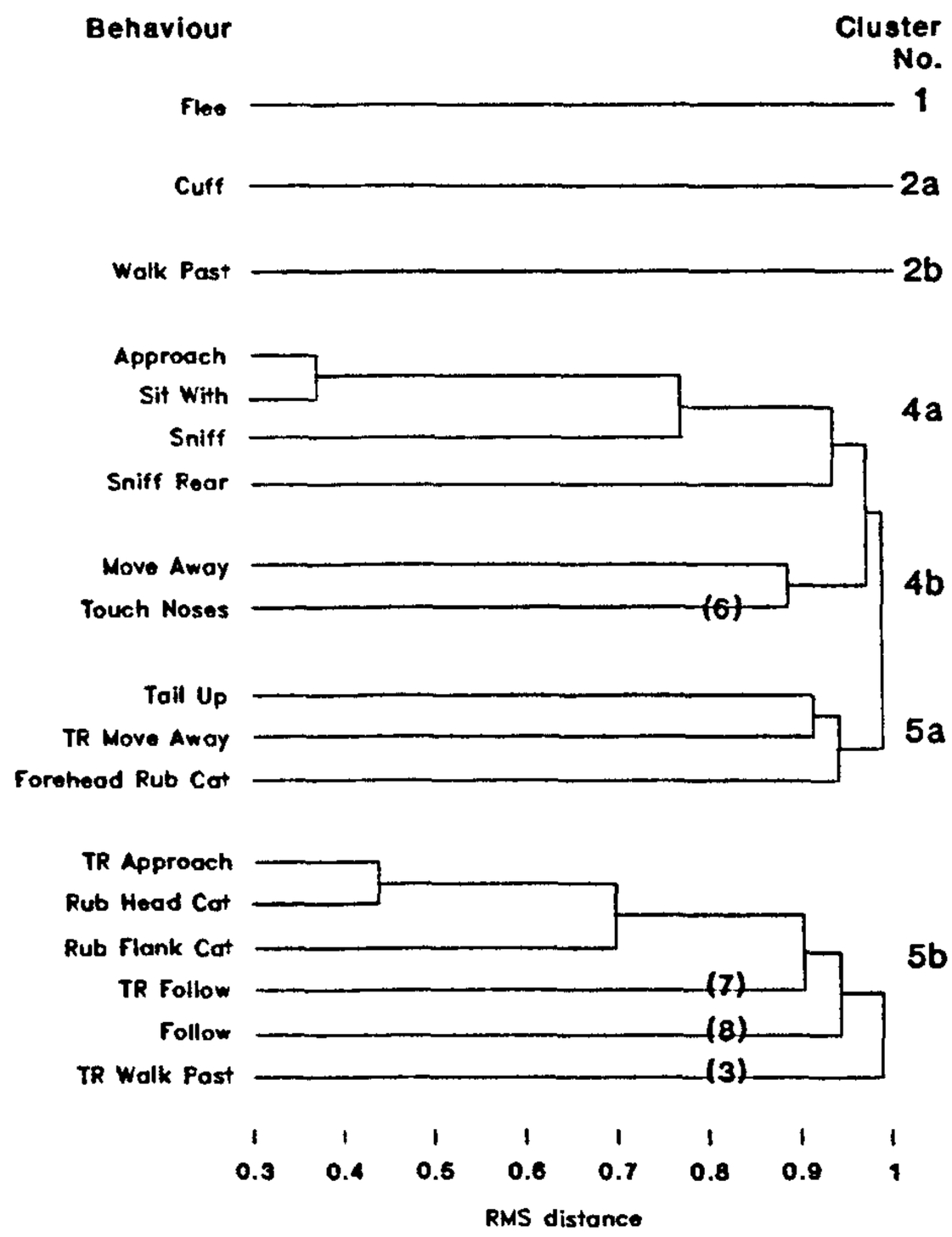
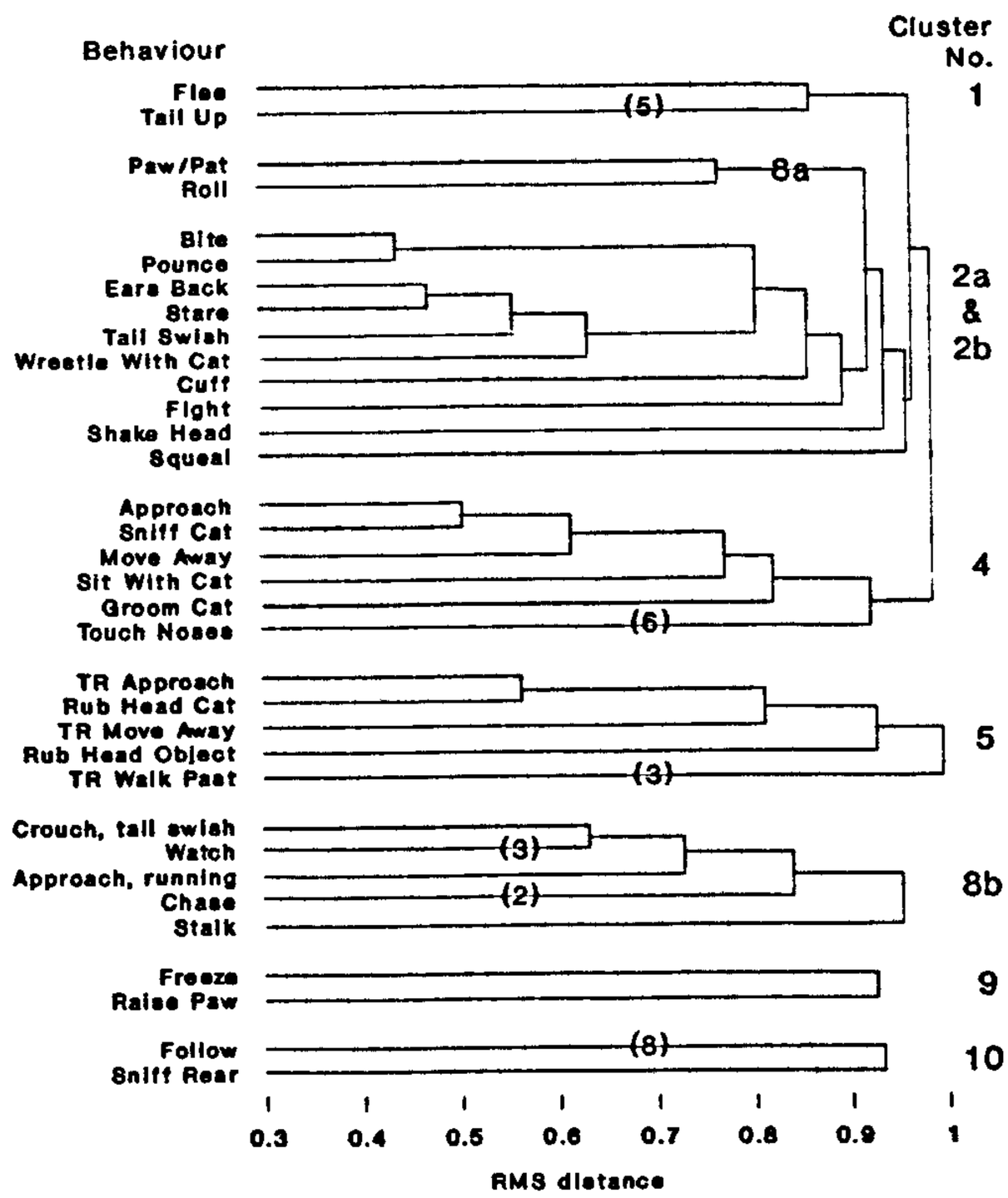


Figure 3.1.3. *Links between behaviour patterns observed in the University colony from Average Linkage Cluster Analysis. Numbers in parentheses refer to cluster numbers at Chilworth (Figure 3.1.1).*



fighting in a confined environment. Cluster 4 again links Approach (tail down), Sniff and Sit With as well as the allogrooming (Groom Cat) observed at Chilworth.

Cluster 5 contains the affiliative tail-raised and rubbing behaviour patterns grouped similarly to both the other colonies, although rubbing in this case was restricted to head rubbing, with flank and tail rubbing virtually absent. Clusters 8a and 8b both contain what appear to be play patterns. The difference appears to be that Pat and Roll in cluster 8a are contact play patterns which often lead to play aggression, hence the link to cluster 2, the aggressive cluster. Stalk, and Crouch with Tail Swishing in cluster 8b, on the other hand, are more "intention to play" patterns. Such playful approach behaviours rarely resulted in further contact play between the interacting cats as the recipient usually fled before the approaching cat reached it (see Table 3.2.1). This explains why clusters 8a and 8b are not linked. Cluster 9 has just 2 elements, indicative of threat to another cat, not seen in the other colonies. Cluster 10 also contains just 2 elements, Follow and Sniff Rear, an unusual combination reflecting investigatory behaviour. Note that only one vocalisation, Squeal, was recorded for this colony since others could not be heard on video.

3.1.4. Comparison of all three dendrograms

Comparison of the dendrograms from each colony shows many behaviours clustered similarly in all three. Table 3.1.1 represents a summary of the groups of behaviours occurring consistently in each "category". As indicated in the legend, not all behaviour patterns have been included in this table as some clustered differently in one or more of the colonies. The table therefore merely provides a basis for classifying some of the more common behaviour patterns -other patterns will be associated with these in different colonies.

3.2. Ordering of behaviour patterns during interactions

Having established which behaviour patterns individual cats performed in conjunction with others, the next step is to examine how they responded to behaviours performed by their interaction partners.

A transition matrix was compiled for each colony from all the sequences recorded. Initiator and Recipient status were kept separate to see how behaviours flowed between the two. The matrix was then condensed such that any behaviours

Table 3.1.1. *Objective categorisation of behaviour patterns based on cluster analysis of sequences at each colony. Included in each category are those behaviours linked into the same clusters in all three colonies, those occurring in only two colonies but clustered the same in both, plus behaviours occurring in just one colony.*

<u>Affiliative</u> Tail-raised Approach Rub Head Cat Rub Flank Cat Tail-raised Move Away Rub Forehead Cat Rub Tail Cat
<u>Approach/Sit/Allogroom</u> Approach (tail down) Sniff Cat Move Away (tail down) Sit With Groom Cat
<u>Aggression/Play Aggression</u> Cuff Yowl Bite Pounce Ears Back Stare Tail Swishing Wrestle with Cat Fight Shake Head Squeal
<u>Threat</u> Freeze Raise Paw
<u>Submissive/Defensive</u> Flee Ears Flattened Crouch with ears flattened Hiss
<u>Play</u> Pat/paw ┐ contact Roll ┘ play Crouch with Tail Swishing ┐ Stalk ├ intent to play Approach running (tail down) ┘

occurring less than 10 times in total were combined together as "others". This avoided analysis of behaviours that contributed little to the cats' behavioural repertoire. The result was a square matrix for each colony, with rows representing preceding behaviours and columns representing following behaviours.

Transitions between behaviour patterns were examined using first-order Markov chain analysis following the method proposed by Slater in 1973 using Chi-Squared tests. Starting and finishing behaviours (behaviour patterns preceded or followed by nothing) were analysed separately since only certain behaviours could start or finish a sequence. This left a matrix of behaviours occurring in the middle of a sequence. All chi-squared calculations included Yates' correction for small sample sizes, thereby reducing the number of Type 2 errors.

Analysis of such a small number of sequences is open to errors and it would be wrong to try to construct a hypothetical sequence from start to finish based on these simple first-order chain calculations. For the same reason only transitions significant at $P < 0.001$ were considered further. Table 3.2.1 in Appendix 2 shows, for each colony, all transitions significant at $P < 0.001$. Comparison of all three sets of results shows that some transitions occur commonly in more than one of the colonies - these are shown in Table 3.2.2.

Any behavioural transition playing a constant and integral part in cat communication would be expected to be seen commonly in all colonies. However, due to the reduced behavioural repertoire of the smallest (Knowle) group, relatively few significant behavioural transitions could occur in common between all three colonies.

The second part of Table 3.2.2 shows those behaviour transitions, not common to all three colonies, that were common to both the Chilworth and the University colonies -with their much larger sample sizes they had more behaviours in common, and therefore provide a more detailed illustration of which transitions were not unique to particular groups. As two free-ranging semi-feral populations, the Chilworth and Knowle colonies may have had specific transitions in common not seen in the more confined University colony. To examine this possibility, the third part of Table 3.2.2. shows those patterns, not common to all three colonies, that were common to both the Chilworth and Knowle colonies.

The transitions from Initiator to Initiator patterns and Recipient to Recipient patterns were also included in the within-individual analysis described in section 3.1.

Table 3.2.2. *Transitions between behaviour patterns occurring significantly more than expected (P<0.001) i) in all three colonies, ii) in just the Chilworth and University colonies and iii) just the Knowle and Chilworth colonies.*

i) TRANSITIONS OCCURRING SIGNIFICANTLY IN ALL THREE COLONIES	
PRECEDING BEHAVIOUR PATTERN	FOLLOWING BEHAVIOUR PATTERN
None (Start)	Approach Initiator Tail-raised Approach Initiator
Follow Initiator	Approach Initiator
Move Away Recipient	Tail-raised Approach Initiator
Move Away Initiator	None (End)
Move Away Recipient	None (End)
Cuff Initiator	Move Away Recipient
Approach Initiator	Sniff Initiator Sniff Rear Initiator
Tail-raised Approach Initi ator	Rub Head Cat Initiator

ii) TRANSITIONS OCCURRING SIGNIFICANTLY IN CHILWORTH AND UNIVERSITY COLONIES ONLY	
PRECEDING BEHAVIOUR PATTERN	FOLLOWING BEHAVIOUR PATTERN
Approach Initiator	Tail-Up Initiator
Chase Initiator	Flee Recipient
Cuff Initiator	Crouch Recipient Flee Recipient
Move Away Initiator	Watch Recipient
Sit With Cat Initiator	Move Away Recipient
Flee Recipient	Chase Initiator
Move Away Recipient	Approach Initiator Follow Initiator
None (Start)	Walk Past Initiator
Tail-raised Move Away Initiator	None (End)
Tail-raised Move Away Recipient	None (End)

Table 3.2.2. *(contd.) Transitions between behaviour patterns occurring significantly more than expected (P<0.001) i) in all three colonies, ii) in just the Chilworth and University colonies and iii) just the Knowle and Chilworth colonies.*

iii) TRANSITIONS OCCURRING SIGNIFICANTLY IN CHILWORTH AND KNOWLE COLONIES ONLY	
PRECEDING BEHAVIOUR PATTERN	FOLLOWING BEHAVIOUR PATTERN
Rub Head Cat Initiator	Rub Flank Cat Initiator
Tail-raised Follow Initiator	Tail-raised Approach Initiator
Cuff Recipient	Move Away Initiator
Move Away Recipient	Tail-raised Follow Initiator
None (Start)	Tail-raised Walk Past Initiator

The following discussion of Table 3.2.2. will therefore concentrate where possible on the Initiator to Recipient and Recipient to Initiator behaviour pattern transitions. Most transitions common to all three colonies are concerned with the beginning and ends of interactions. As Table 3.2.2.(i) shows, the commonest start to a behavioural interaction was an approach by the initiator cat either with or without the tail raised. It is interesting to note that neither forms of approach were followed significantly more often by an immediate response by the Recipient - the Initiator was more likely to perform another behaviour before the Recipient responded.

The position of the tail seems to be of fundamental importance in determining what happened during the rest of the interaction. Tail-raised approaches were followed significantly often in all three colonies by a head rub by the Initiator on the Recipient cat. "Ordinary" approaches (with the tail held in the normal position) were not followed by an above average level of rubbing of any sort or by either cat in any of the colonies. Such tail lowered approaches led significantly often in all three cases to investigatory sniffing (of the head/body or rear of the recipient) by the Initiator. However they also led significantly often to a large number of other behaviours specific to the individual colonies including some of the aggressive patterns (Table 3.2.1, Appendix 2). In two of the colonies an ordinary approach was significantly often followed by the Initiator raising its the tail on reaching the Recipient, but only in the university colony did this subsequent tail-raising stimulate headrubbing (Table 3.2.1, Appendix 2).

Aggression in the form of Cuffing by the Initiator was significantly likely to be followed by the Recipient moving away (tail lowered) in all three colonies. In the University and Chilworth colonies it was also likely to be followed by a Crouch or Flee by the Recipient. A Flee by the Recipient in turn was most likely to induce the Initiator to give chase.

An interesting result from the University and Chilworth colonies is that Sit With Cat by the Initiator to the Recipient was, in both cases, significantly often followed by the Recipient moving away. That it was the Recipient and not the Initiator that ended the interaction in this way illustrates the fact that both partners were not always equally willing to interact with each other.

A tail lowered Move Away by the Initiator was watched by the Recipient significantly more than expected in both the University and Chilworth colonies. A Move Away by the Recipient, on the other hand, was followed by an Approach or

Follow by the Initiator (i.e., the Initiator would pursue a retiring Recipient but not vice versa). The watching of a retiring Initiator by the Recipient suggests that the Recipient may have expected to receive further behaviour patterns from the Initiator. These two transitions suggest that the initiating cat tended to be the most persistent interactor within a pair of cats throughout the course of that interaction.

Within the same two groups, the raising of the tail on moving away had an entirely different effect on the interaction partner. A Tail-raised Move Away by either the Initiator or Recipient cat ended the interaction in a significant number of cases.

Of the transitions common to only the Knowle and Chilworth colonies, the moving away of the Initiator in response to a Cuff from the Recipient, and the tail-raised following of the Recipient by the Initiator following the Recipient's Move Away, were the only two significant inter-individual transitions not also seen in the University group. It seems unlikely that these arose due to any aspect of the free-ranging abilities of the Knowle and Chilworth groups because they did not result in the interacting cats distancing themselves from each other any further than would be possible in the University colony.

3.3. Discussion

The association and use of behaviour patterns by individuals during interactions show many constant features even among three colonies with such different backgrounds and living conditions.

The production of an objective system of categorising behaviour patterns reduces much of the difficulty of using subjective functional criteria for classifying such patterns. Previous workers such as Kerby (1987) have used this latter method satisfactorily but have noted the difficulties in allocating behaviours subjectively into categories. Comparison of the categories in Table 3.1.1 with those of Kerby reveal many similarities, particularly with respect to Play, Aggressive and Submissive categories. However, there are some discrepancies even within these, e.g., Hiss (termed "Swear" by Kerby) is categorised by Kerby as an Aggressive behaviour pattern, but using the objective method it is clustered with Submissive/Defensive patterns.

Perhaps the greatest area of discrepancy is that the division into Approach/Sit

and Affiliative categories achieved by the objective method is combined into a more general "Greeting Behaviour" category by Kerby.

Although not necessarily easier to use, the objective method makes some important distinctions regarding tail positions, vital to a deeper understanding of the cat communication signals investigated in this thesis. Many elements of cat behaviour observed by Kerby in her breeding groups were obviously missing in these neutered groups, e.g., mating and parental behaviours. This may mean that the remaining behaviours are associated in a different way by neutered cats - this is, however, difficult to quantify.

Although it has provided a useful core set of behaviour categories applicable to all three neutered colonies (Table 3.1.1), the analysis also revealed that differences exist between the groups of cats, not only in the number of behavioural elements used, but also, to a certain extent, in the way they used them.

This raises the possibility of "dialects" of behaviour arising within different colonies of cats. Individuals in different colonies may have different interpretations of what particular behaviour patterns mean. This could occur via genetic influences on behaviour, due to the restricted gene pool of feral colonies or, perhaps especially in the case of neutered cats, learned in response to changes within the colony.

The possibility of such dialects arising raises an important implication for pet domestic cats and their owners. With so many individuals housed in separate, often one-cat groups, cat-owner relationships are likely to develop very individual characteristics. This may explain the origin of some of the idiosyncratic uses of behaviour patterns described, albeit anecdotally, by many owners when questioned about their cats (S.E. Lowe, personal communication).

A close look at the sequencing of behaviour patterns within interactions between cats has highlighted the importance of the tail-raised display in suggesting what happens subsequently. At the start of an interaction it indicates whether head rubbing may occur and at the end when associated with a move away by either interactor it inhibits the interaction being pursued any further.

Head rubbing, possibly involving some olfactory communication between cats via the scent glands on the head, is regarded by most authors as the cats' most intense form of greeting (Dards, 1979, Kerby, 1987). Head rubbing on another cat leaves an individual very vulnerable to attack by the recipient cat - such rubbing therefore generally only occurs when the Initiator is confident that a hostile reaction will not be

received (i.e. when the animals are very familiar with one another and/or the Initiator knows it has given an unambiguous signal).

It would seem, therefore, that the position of the tail of the initiating cat at the very moment it initiates the interaction indicates its intentions to the recipient. Such a clear signal as the raised tail is unlikely to be misread by a Recipient hence the frequency of successful head rubs achieved by Initiators following a tail-raised approach. Approaching with the tail down, however, is far more difficult for a Recipient to interpret, hence the much larger number of behavioural transition types that followed such approaches.

During an interaction between two cats the close association between tail-raised and rubbing behaviour patterns is thus maintained both within each cats contribution to the interaction (as seen from the dendrograms), and between the two animals (from the sequence analysis). Such a rigorous "code of behaviour" suggests that these behaviour patterns may be central to the understanding of cat communication. For this reason these patterns were studied experimentally in more detail, described in Chapter 7.

CHAPTER 4

The Knowle Hospital Colony

Exbury courtyard at Knowle Hospital. The observation area with BW2 (far right) and TW1 (far left) present.

CHAPTER 4 - THE KNOWLE HOSPITAL COLONY

4.1. Results

4.1.1. Patrols of Hospital

Sixty-nine individuals were identified during the patrols of the hospital grounds. Observations of social interactions were restricted to a single courtyard area (Exbury) of the hospital. Patrol data enabled easy identification of any visitor to the yard, and provided information on how far it had travelled from its core area.

4.1.2. Interactions of courtyard group

A total of 404 interactions were recorded from the observation vehicle in Exbury courtyard. Of these, 376 occurred between the five most frequent attenders of the yard: BW1, BW2, T1, TW1 and TW2. 23 interactions involved a sixth cat, TW3, who was recorded as present in the yard on 35 occasions (from the scan data); three interactions involved TW4, three involved B1, and two involved BW4 -these latter three individuals were only occasional visitors to the yard observed on six, two and nine occasions respectively. Although the behaviour of the less frequent visitors is important to consider, only the five core members of the group provided enough interactive data to analyse statistically. From the information provided by the vet on examination of these cats, they can be described as follows:

BW1: Male, black & white, approx. 9 years old.
BW2: Female, black & white, approx. 8 years old.
T1: Female, tabby, approx. 5-6 years old.
TW1: Female, tabby & white, approx. 9 years old.
TW2: Male, tabby & white, approx. 7 years old.

With only 5 individuals in the group, analysis of the social interactions could only meaningfully be carried on at an individual or dyadic level, since any sex class generalisations could be over-influenced by a single individual. Nevertheless, characteristics of the colony have been included where possible.

4.2. Uniformity of the data set

With the study having spread over almost a year, it was important to establish before proceeding any further that the data gathered could be regarded as a single data set, (i.e., that the data did not reflect any changes within the colony over the year such that it should be divided into smaller sections for analysis). No changes in the number of animals occurred over the study. Although one cat, BW1, showed a fairly intermittent attendance at the site, this was consistent throughout the year. More subtle changes in the type of behaviour being used by the animals might have occurred, however, so the Kolmogorov-Smirnov (K-S) test was used on the data to find out whether interaction length and/or frequencies of any behaviour patterns changed radically over the study period.

The data was divided into ten consecutive sections, each containing as nearly as possible an equal number of interactions (40 or 41). The K-S test was then run to compare the total number of behaviour patterns that occurred in each section with the expected values calculated from the overall total. The results are shown in Figure 4.2.1.

There was no significant change in number of patterns over the 10 sections ($P>0.05$), indicating that the average number of behaviour patterns in each interaction stayed constant throughout the study. The K-S test was then performed on each of the 15 commonest behaviour patterns. These patterns and their K-S test results are shown in Table 4.2.1.

Out of the behaviour patterns tested, only one showed a significant change in frequency during the study (Move Away Recipient, $P < 0.01$), the other 14 showing no deviation from expected ($P>0.05$ in all cases). Given the number of tests performed, the significant change may have been due to a Type 1 error.

From this it was concluded that no substantial overall change in behavioural quality occurred during the study and, since no change in group composition occurred either, the data set from the study could be considered as a whole.

Figure 4.2.1. *Observed and expected total numbers of behaviour patterns occurring in ten consecutive sectors containing approximately equal numbers of interaction sequences.*

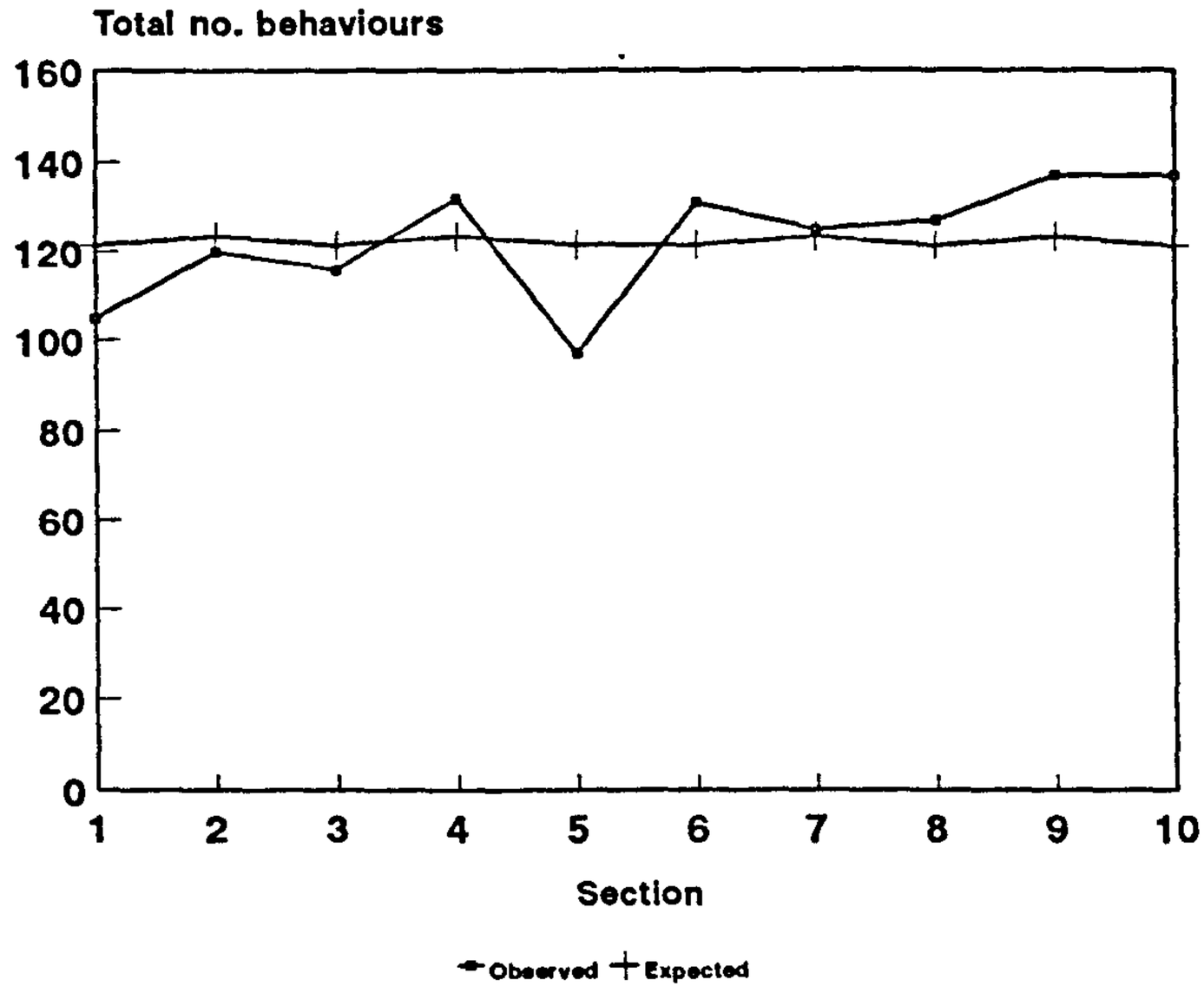


Table 4.2.1. *Results of Kolmogorov-Smirnov tests on the 15 behaviour patterns that occurred > 20 times in total when considering Initiator and Recipient patterns separately. (Data was divided into 10 sections each containg approximately equal numbers of interactions).*

Behaviour pattern	K-S significance level
Approach Initiator	P>0.2
Tail-raised Approach Initiator	P>0.2
Follow Initiator	P>0.05
Sniff Cat Initiator	P>0.2
Sniff Rear Initiator	P>0.2
Rub Head Cat Initiator	P>0.05
Rub Flank cat Initiator	P>0.2
Sit With Cat Initiator	P>0.2
Tail-raised Walk Past Initiator	P>0.2
Cuff Initiator	P>0.2
Move Away Initiator	P>0.2
Touch Noses Both	P>0.2
Tail Up Recipient	P>0.15
Cuff Recipient	P>0.2
Move Away Recipient	P<0.01

Table 4.3.1. *Results of 15 minute scans taken during watches on Exbury courtyard at Knowle Hospital (February - October 1989).*

Cat	No. scans present	No. scans <1m from one or more cats	No. scans < 1m / No. scans present with each possible partner			
			BW2	T1	TW1	TW2
BW1	44	25	5/35	18/40	5/43	8/38
BW2	89	33	-	16/73	9/89	16/74
T1	108	61		-	35/103	18/93
TW1	129	45			-	17/108
TW2	113	37				-

4.3. Scan data

A total of 518 scans were taken from February to October 1989. Unfortunately this did not cover the whole study period, and the scan data is only representative of the second half of the study. For each cat it was calculated : on how many scans it was present; on how many scans it was present with each other cat; on how many scans it was less than one metre away from another cat; and on how many scans it was less than one metre away from each possible partner. These results are shown in Table 4.3.1.

Of all the dyads, BW1 and T1 showed the highest degree of close proximity to each other, a reflection perhaps of the high rate of interactions by BW1 to T1, illustrated in Figure 4.4.1. As Table 4.3.1.shows, T1 actually spent a much greater amount of time in close proximity to TW1 than to BW1 (35 scans compared to 18 scans). The fact that BW1 was less often available to associate with T1 (BW1 available on 40 scans compared to TW1 on 103 scans) makes his association with her stronger than that of TW1.

4.4. Evidence for sociality within the group.

As described in Chapter 1, in a non-social situation where interactions occurred randomly between individuals, it has been suggested (Macdonald et al, 1987) that the number of interactions between each possible pair of animals should be in direct proportion to the amount of time they were available to interact. Overall *rates* of interaction (irrespective of direction) should therefore be the same between all pairs of cats. This does not allow for variation between individuals in overall interactivity and is not therefore an accurate assessment of sociality. Nevertheless, looking at the overall rates and frequencies of interactions between pairs does give a basic idea of whether sociality might exist.

In the Knowle colony there were ten possible dyads of the five cats - all of these interacted at some point during the study. Spearman rank correlations were carried out on time available for interaction (time present together), total number of interactions (number of interactions), and rate of interaction per hour present together (interaction rate) for all ten possible dyads.

There was no correlation ($r=-0.42$, $P=0.21$, $n=10$) between number of interactions and time present together, and a significant negative correlation between

interaction rate and time present together ($r=-0.77$, $P=0.02$, $n=10$).

The null hypothesis of a non-social system predicts a positive correlation between number of interactions and time present together, and no correlation between interaction rate and time present together. It seems likely, therefore, that the flow of interactions within this group was not random and was greatly affected by the identity of the individuals involved. Of particular interest is the tendency for pairs that were present together for less time to interact at a significantly higher rate than those available for more time.

Looking at the flow of interactions within the colony in more detail, the rate at which each individual initiated interactions to each other individual was calculated and is represented in Figure 4.4.1. Asymmetries were tested by chi-squared tests.

4.5. Analysis of individual behavioural styles

Having established that some form of social structure existed within the groups' interactions, it is possible to compare the repertoire of behaviours performed and received by each cat to see how each animal fitted into the the colony's social organisation. Two matrices were constructed, one of behaviours performed and the other of behaviours received by each cat. Behaviours occurring less than 20 times were omitted leaving 12 behaviour patterns for analysis. Table 4.5.1 shows the resulting matrices. A G-test was performed on each of these matrices to test for heterogeneity within the colony. In both cases there was significant heterogeneity within the matrix ($P<0.001$). Tests of homogeneity were then carried out on all pairwise combinations of individuals to see where the heterogeneity occurred. In the case of behaviour patterns performed, these tests showed all 5 cats had a unique behavioural profile apart from T1 and TW1 which were not significantly different ($P>0.05$). Patterns were received differently by all cats, including this pair.

Principal Components analysis of the same matrices enables some interpretation of *how* the cats differed in their behavioural profiles. These graphs are included as Figures 4.5.1 (Behaviour patterns performed) and 4.5.2 (Behaviour patterns received). BW1 appeared to be a high performer of Sit With, and to a lesser extent, Tail Up and Move Away. BW2, the most interactive cat, showed a strong tendency to perform the affiliative tail-raised and rubbing behaviours and also with the Approach and Sniff behaviours. T1 and TW1 are negatively associated with most

Figure 4.4.1. *Relative rates (indicated by the width of the arrows) at which the five core members of the group initiated interactions with one another, corrected for the time that each pair was present together in the observation area. Significant asymmetries in the flow of interactions within pairs are indicated by * (P<0.05); ** (P<0.01); and *** (p<0.001).*

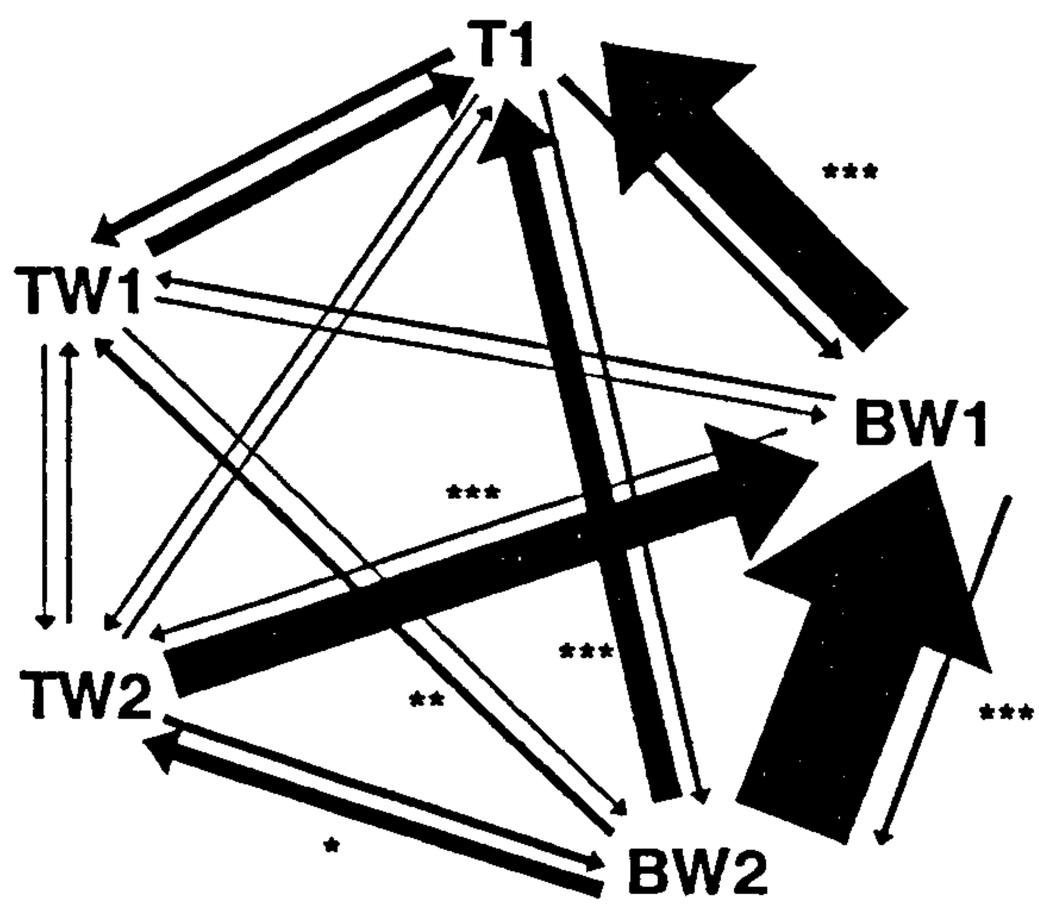


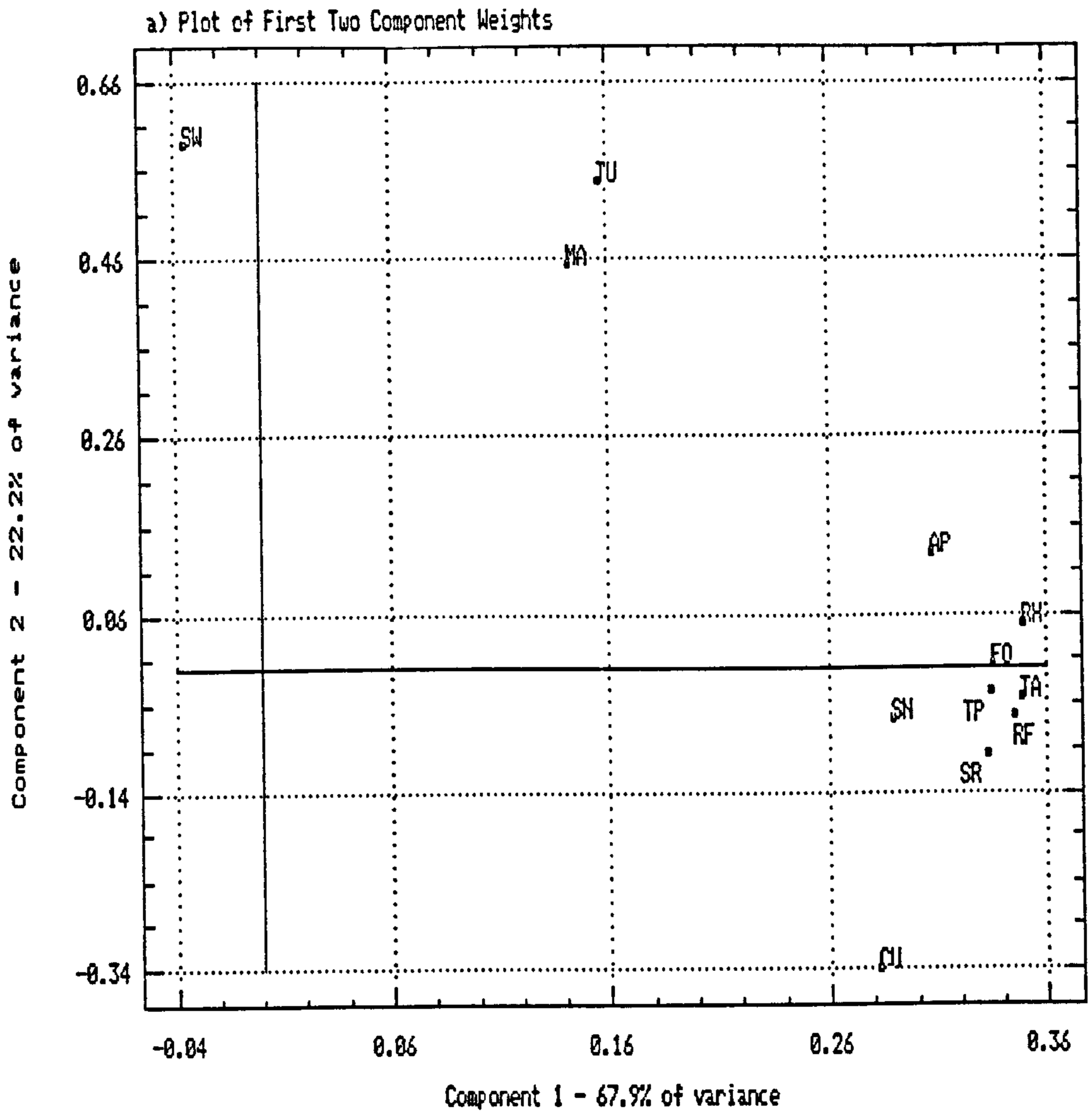
Table 4.5.1. *Matrices of the total number of each behaviour pattern performed and received by the five cats during the study period. Patterns are written as two-letter codes - full descriptions of these are included in Appendix 1. Patterns that occurred <20 times in total were omitted.*

CAT	AP	TA	FO	TU	SN	SR	RH	RF	SW	TP	CU	MA	TOT
	PERFORMED												
BW1	33	16	7	19	8	4	30	4	40	7	2	53	223
BW2	47	103	18	13	30	13	98	28	18	22	32	40	462
T1	23	2	2	4	6	5	2	0	13	1	12	30	100
TW1	27	1	5	4	9	2	2	0	21	6	12	17	106
TW2	40	29	3	12	24	5	22	1	28	3	5	24	196
	RECEIVED												
BW1	37	89	15	12	24	10	76	19	27	16	13	25	363
BW2	14	5	1	14	7	3	19	2	12	3	7	77	164
T1	63	43	17	8	26	7	36	10	60	17	8	22	317
TW1	29	3	1	3	7	4	2	0	12	2	8	9	80
TW2	18	7	0	11	6	2	21	2	6	1	27	30	131

Explanation of Principal Components Analysis

Table 4.5.1 above was used in the Statgraphics package to create the PCA graphs 4.5.1 and 4.5.2. Two principal components were extracted in each case (proportion of variance explained on the graphs). These two components represent underlying trends in the types of behaviour performed and received by each cat. So in each case the top graph represents the contribution of individual behaviour patterns to derived components, and the bottom graph represents the positions of the cats on the same derived components.

Figure 4.5.1. a & b. *PCA on behaviour patterns performed by the Knowle cats. Components 1 and 2.*



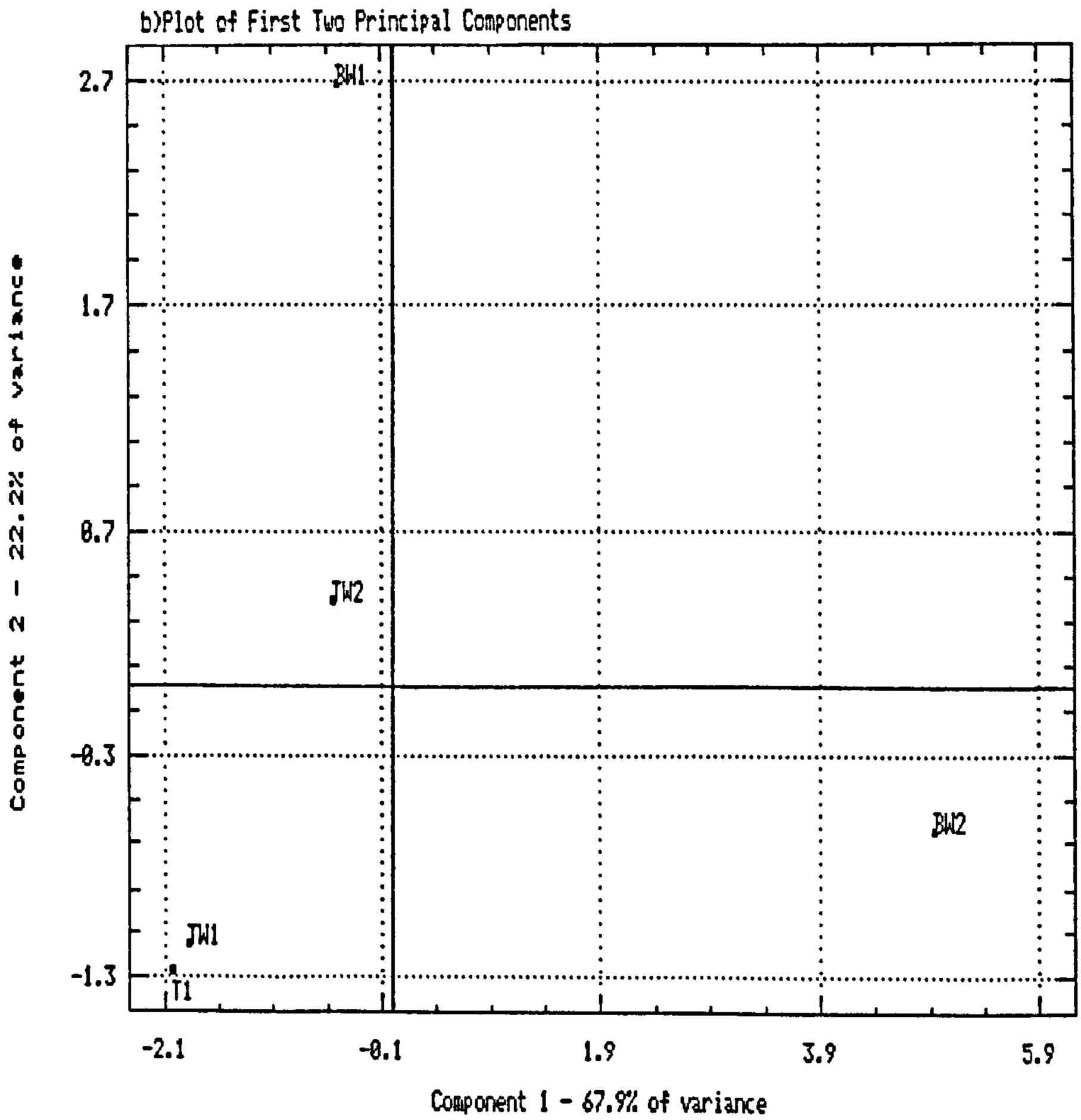
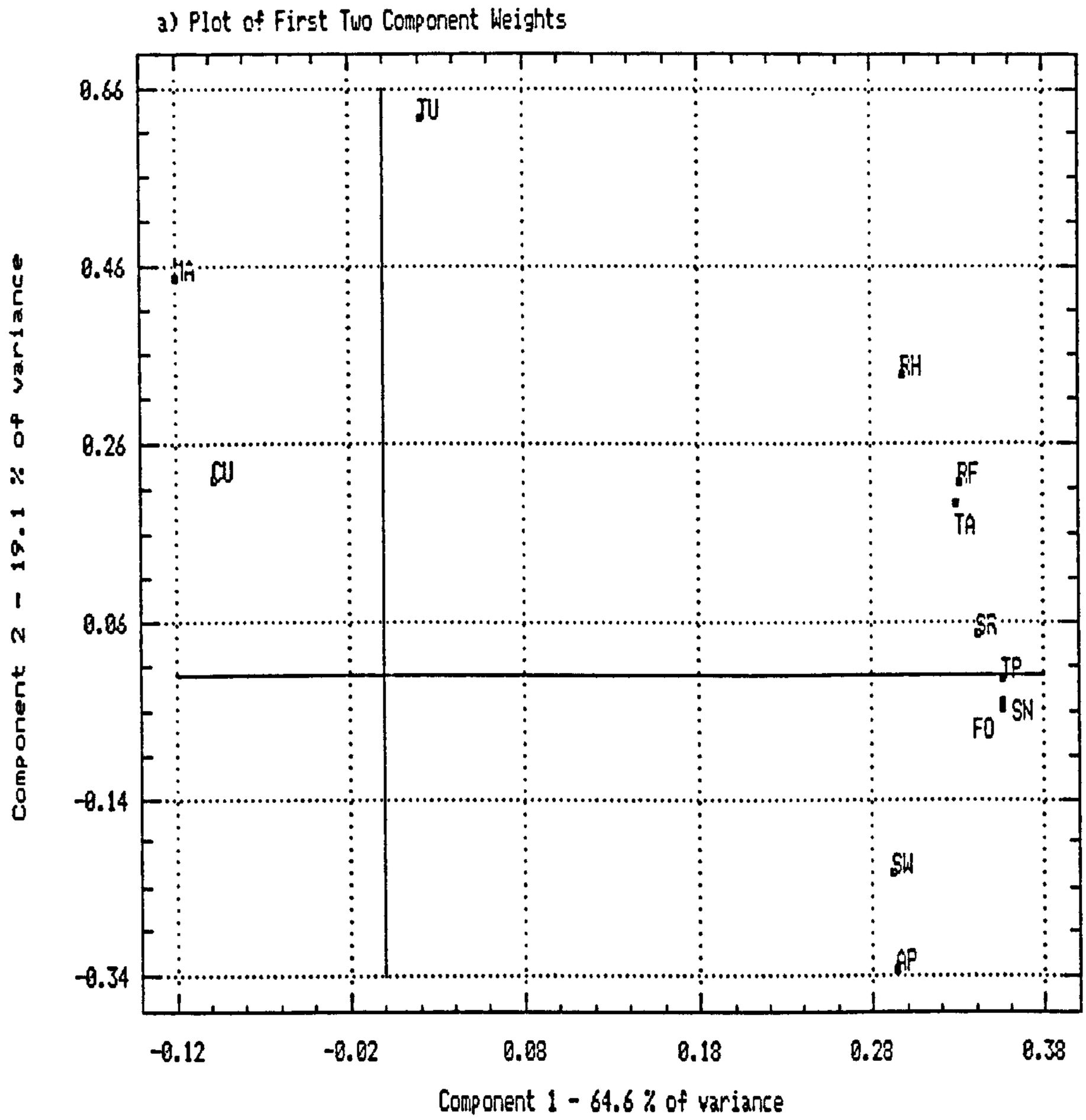
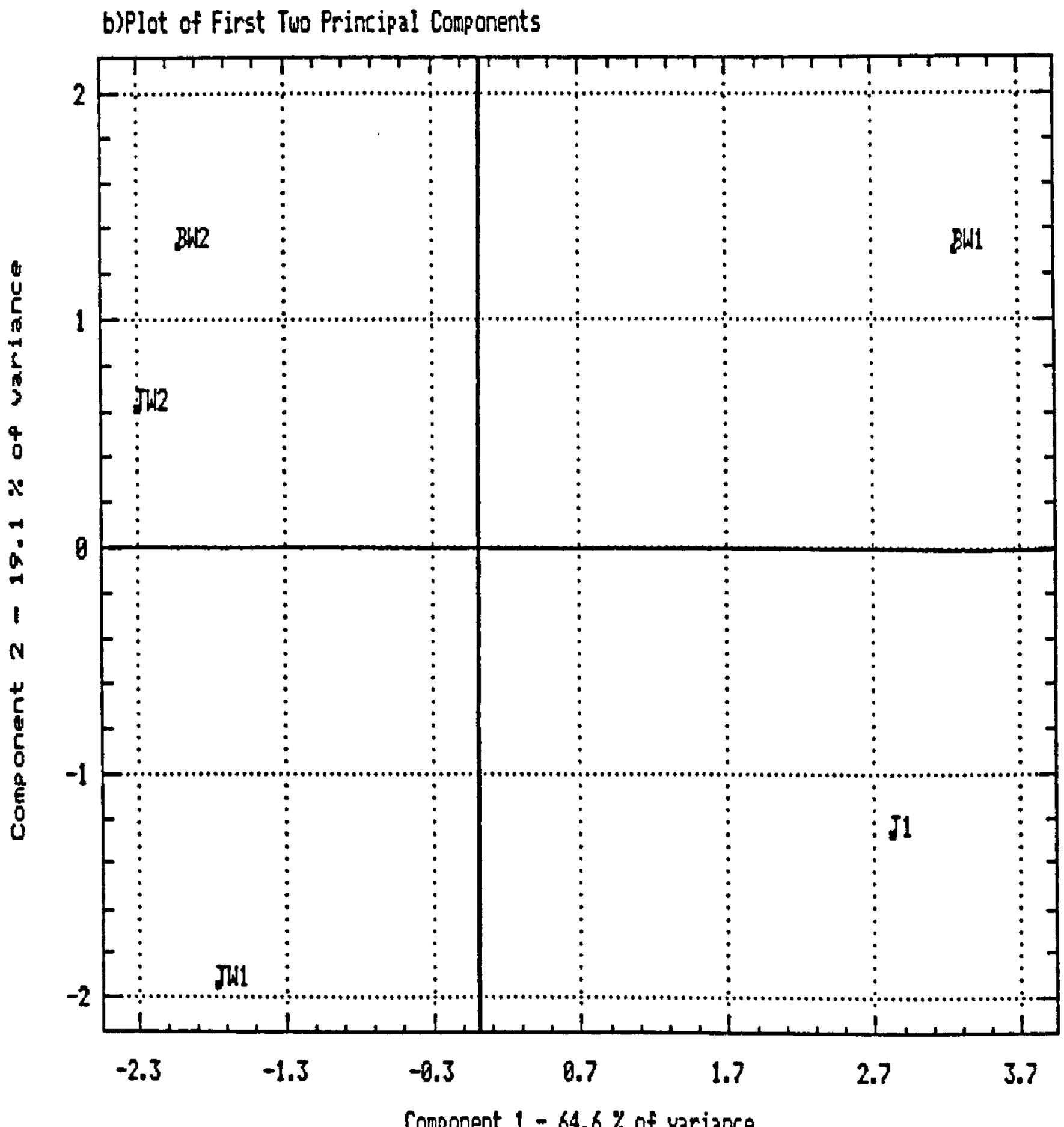


Figure 4.5.2. a & b. *PCA on behaviour patterns received by the Knowle cats. Components 1 and 2.*





of the behaviour patterns, reflecting their low overall interactivity. TW2 showed no tendency to perform any particular pattern (Figure 4.5.1). Looking at patterns received (Figure 4.5.2), BW2 and TW2 received most of the Cuffs and Moves Away from other cats. BW1 seemed to receive most of the affiliative behaviours, whilst T1 received most of the Approach/Sniff/Sit With behaviours. TW1, again shows up as negative on receiving all behaviour patterns, reflecting her low interaction rate.

4.6. Analysis of dyadic relationships

A more detailed picture of how the cats directed their repertoire of behaviour towards different individuals, and therefore of the complexity of the social structure, can be gained from performing the same G-tests and PCA on the matrix of behaviour patterns performed between dyads shown in Table 4.6.1. Each dyad is represented twice, once for each direction of the pattern performed.

A G-test on this matrix showed significant heterogeneity within the colony ($P<0.001$). In order to see where differences occurred between and/or within pairs of cats, selective unplanned pairwise tests of homogeneity were performed (Sokal & Rohlf, 1981). The results of these tests are shown in Table 4.6.2 and Figure 4.6.1 represents these results visually.

Principal Components analysis carried out on the same matrix (Figures 4.6.2 and 4.6.3) reveals which behaviours were characteristic of particular relationships. BW2 showed a tendency to cuff TW2 and T1 a tendency to cuff BW1. BW1 directed his Approach and Sit With behaviours towards T1, whilst BW2 directed her affiliative rubbing behaviours towards BW1. BW1 in response seems to have performed mainly Tail Up and Move Away patterns. TW2 did not apparently single out any particular recipient for specific behaviour patterns, supporting his lack of association with any particular pattern in the individual analysis. These relationships are discussed further in the following summary.

4.6.1. Summary of individual and dyadic characteristics

T1 appeared subjectively to have a high status within the colony suggested by her high proportion of received to initiated interactions (Figure 4.3.1). She responded differently during interactions with the female TW1 compared to interactions with the male BW1, showing a tendency to cuff the latter. Of all the other cats, TW1 was the

Table 4.6.1. *Matrix of behaviour patterns performed between dyads. Patterns occurring less than 20 times in total were omitted, as well as any dyad whose total behaviour count (directions combined) totalled less than 50. Patterns are included as two-letter codes - full descriptions can be found in Appendix 1.*

PAIR	AP	TA	FO	TU	SN	SR	RH	RF	SW	TP	CU	MA	TOT
BW1BW2	3	1	0	9	1	1	13	2	4	1	1	33	69
BW2BW1	15	69	13	8	12	6	59	18	9	15	2	18	244
BW1T1	27	14	7	1	5	1	2	0	32	4	0	6	99
T1BW1	2	0	0	0	0	1	1	0	0	0	9	4	17
BW1TW2	1	1	0	9	1	1	14	2	3	1	1	12	46
TW2BW1	18	20	2	4	12	3	15	1	17	1	1	3	97
BW2T1	10	27	5	3	13	4	32	10	6	7	0	9	126
T1BW2	4	0	1	0	3	2	0	0	3	0	2	17	32
BW2TW2	14	6	0	2	3	1	7	0	3	0	21	10	67
TW2BW2	7	4	0	5	3	0	6	0	5	2	2	16	50
T1TW1	15	2	1	3	3	2	1	0	10	1	0	5	43
TW1T1	24	1	5	4	7	2	1	0	20	6	7	6	83
TOTAL	140	145	34	48	63	24	151	33	112	38	46	139	973

TABLE 4.6.2. *Results of selective unplanned pairwise tests of homogeneity (Gh) with William's correction on behaviour patterns performed within dyads. Each cat's behavioural profile towards a particular partner is compared with a) that partner's behaviour to the cat (indicated with an asterisk) and b) the cat's behaviour to each other possible partner e.g., BW1 to T1 was compared with T1 to BW1 and with BW1 to BW2 and BW1 to TW2.*

PAIR A	PAIR B	Gh VALUE	SIG. LEVEL
* BW1BW2	BW2BW1	86.4	P<0.01
BW1BW2	BW1T1	97.5	P<0.01
BW1BW2	BW1TW2	5.9	N.S.
BW2BW1	BW2T1	7.7	N.S.
BW2BW1	BW2TW2	97.8	P<0.01
* BW1T1	T1BW1	48.0	P<0.01
BW1T1	BW1TW2	77.9	P<0.01
T1BW1	T1BW2	17.9	N.S.
T1BW1	T1TW1	32.0	P<0.05
* BW1TW2	TW2BW1	48.2	P<0.01
TW2BW1	TW2BW2	32.1	P<0.05
* BW2T1	T1BW2	60.6	P<0.01
BW2T1	BW2TW2	78.8	P<0.01
T1BW2	T1TW1	23.7	N.S.
* BW2TW2	TW2BW2	23.6	N.S.
* T1TW1	TW1T1	10.3	N.S.

Figure 4.6.1. *Schematic diagram of behavioural repertoires performed between dyads. Pairs whose overall behaviour pattern count totalled less than 50 were omitted. The circles by each cat denote the different behavioural repertoires exhibited towards partners. Thus, where two arrows leave the same circle that cat performed the same repertoire of behaviours to two partners. Generally the repertoires performed were different to those received, however two relationships, T1-TW1 and TW2-BW2 were reciprocal. T1 showed a complicated pattern, performing the same repertoire to TW1 as to BW2, the same to BW1 as to BW2 but not the same to TW1 as to BW1.*

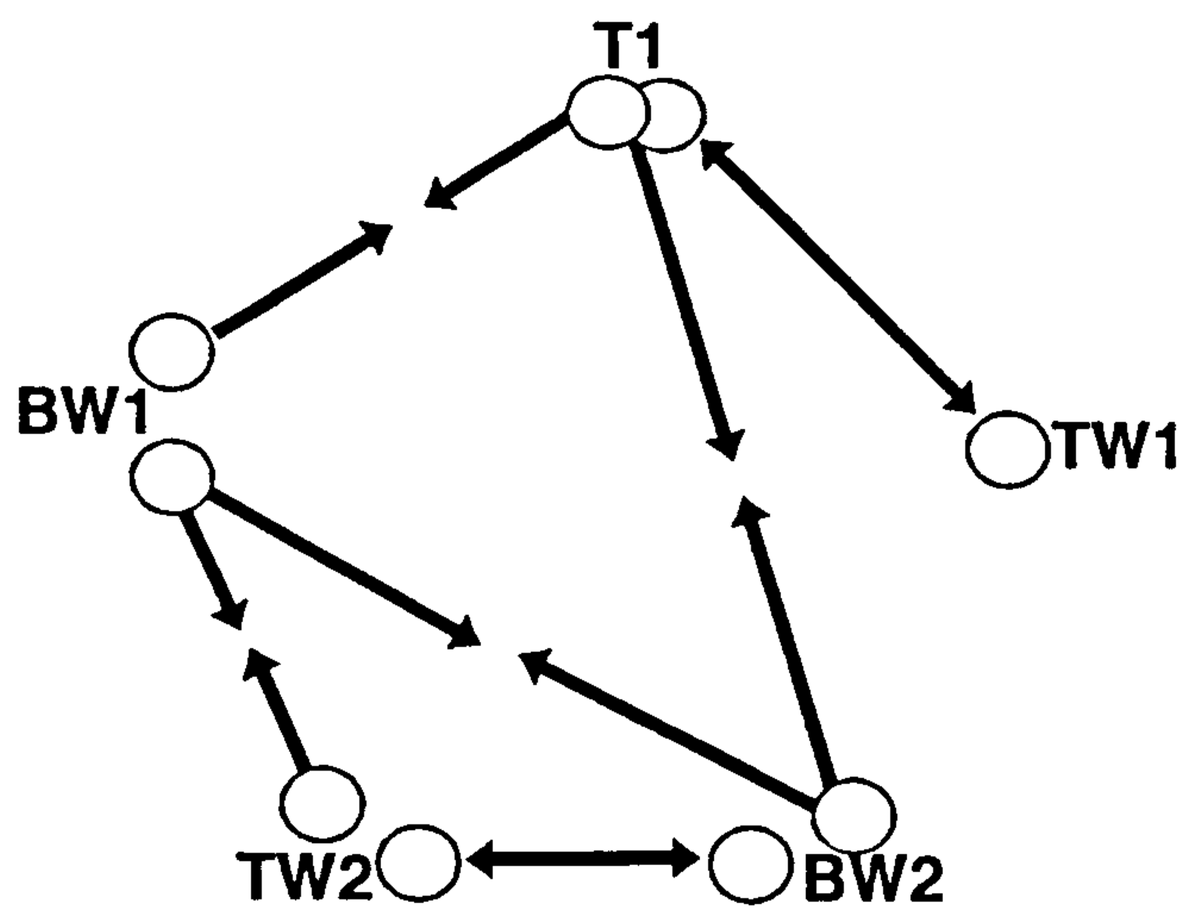
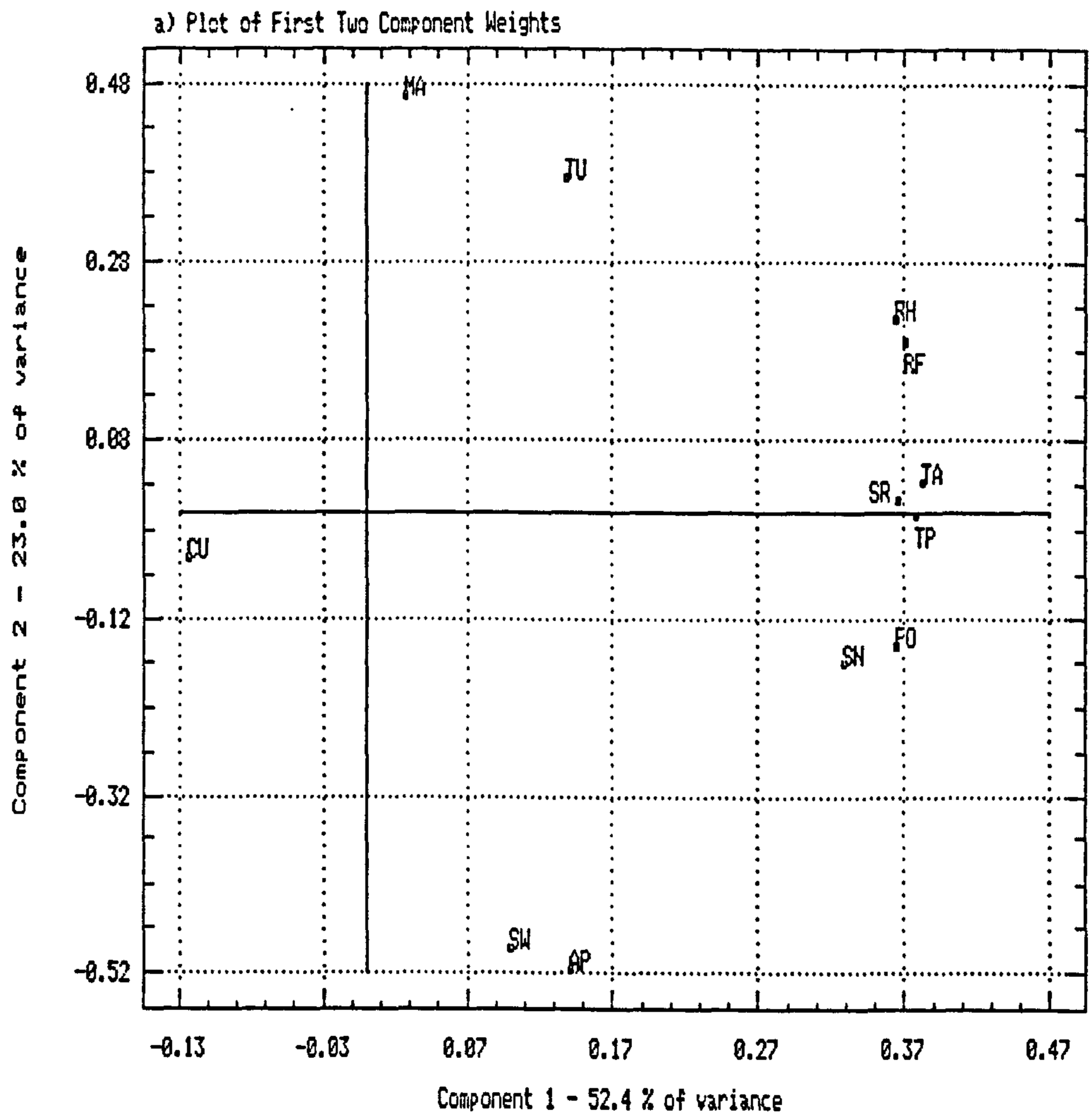


Figure 4.6.2. a & b. *PCA on behaviour patterns performed between dyads at Knowle. Components 1 and 2.*



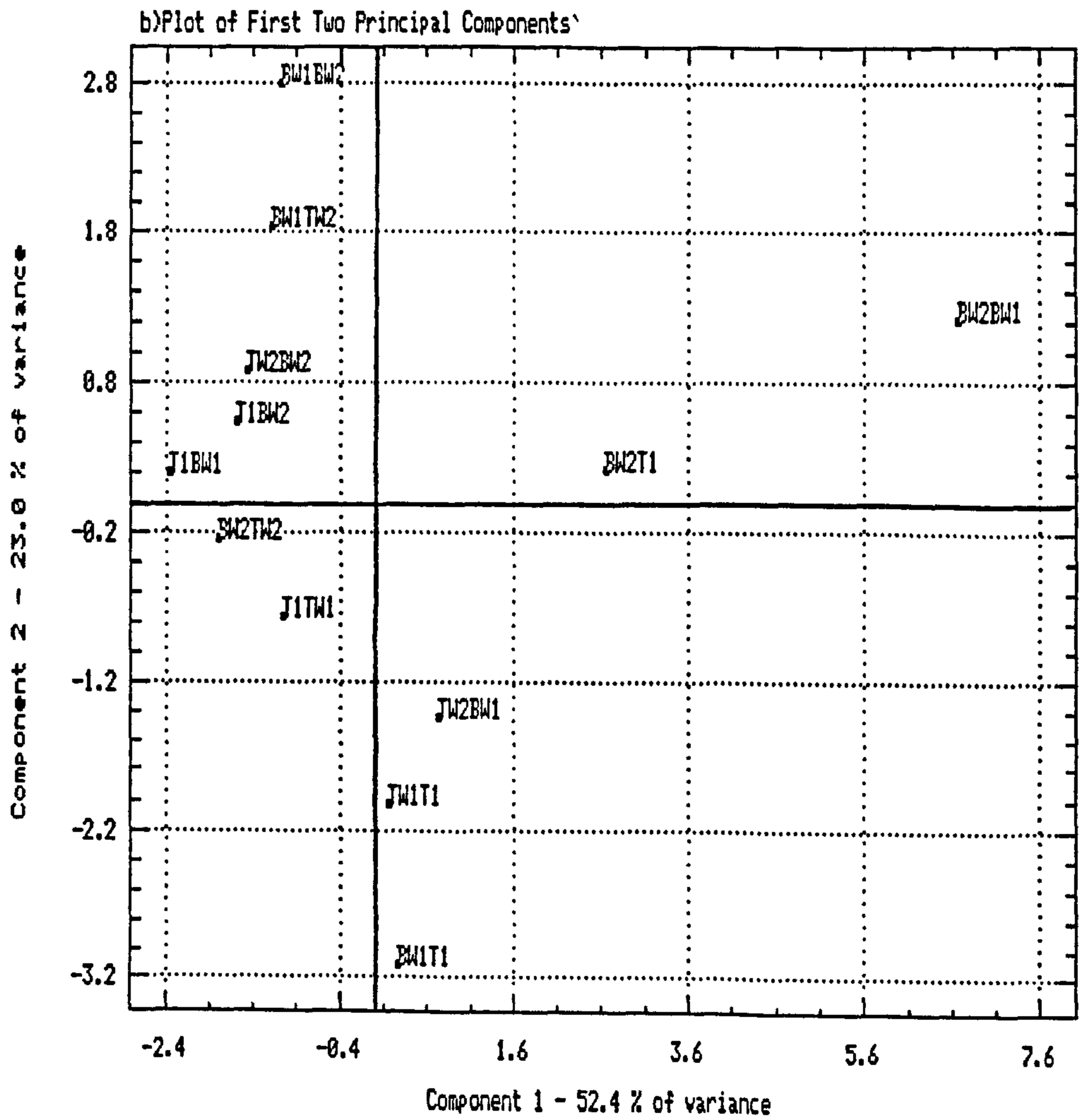
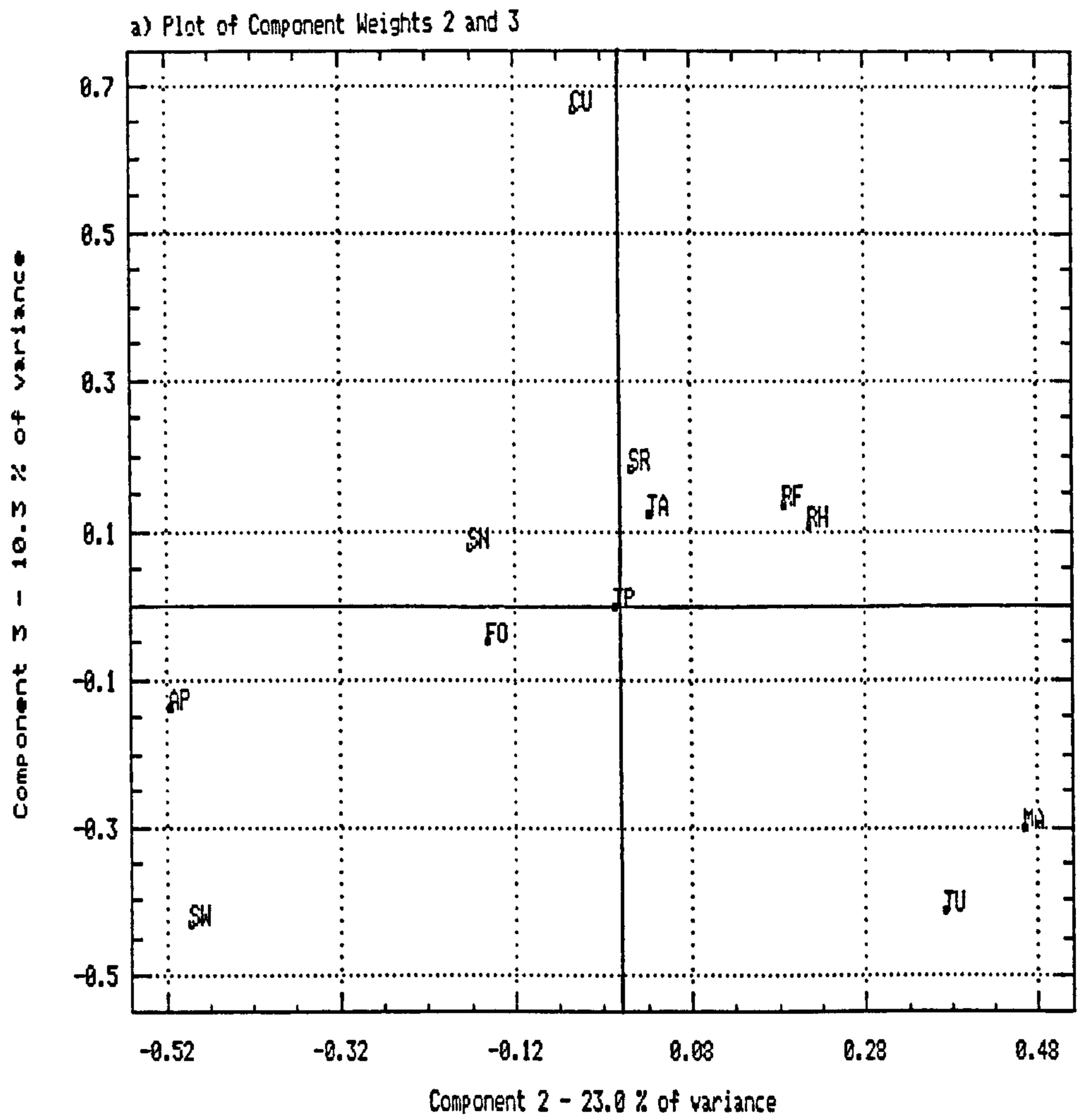
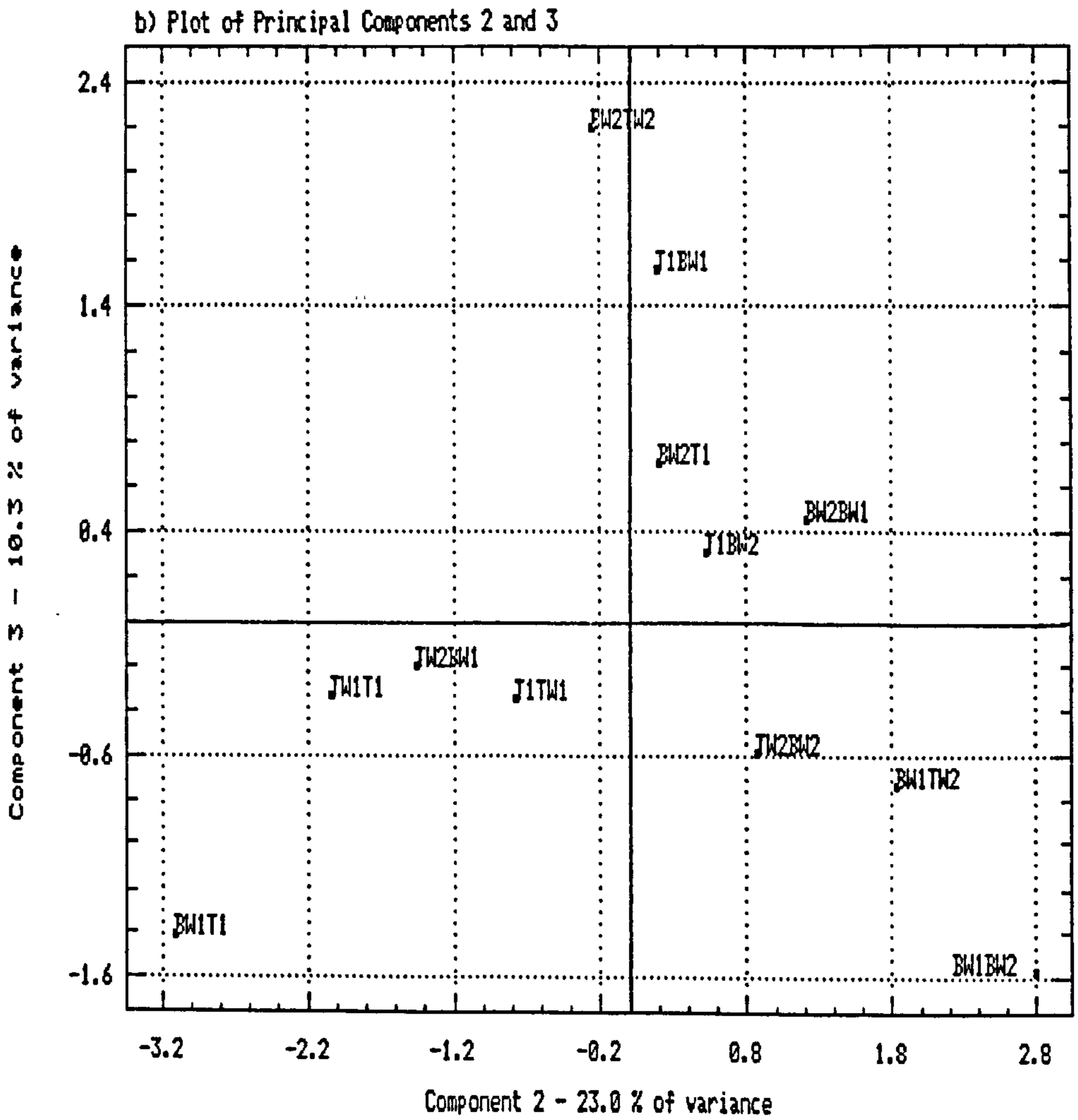


Figure 4.6.3. a & b. *PCA on behaviour patterns performed between dyads at Knowle. Components 2 and 3.*





only one to show a reciprocal relationship with T1, reflected in their similar behavioural profiles (section 4.4). These two females spent more time together than any other pair of cats (Table 4.3.1) but BW1 spent proportionally more time with T1 due to his low attendance at the site (Table 4.3.1). When present, BW1 received high rates of interaction from BW2, mostly in the form of Affiliative (see Chapter 3) tail-raised and rubbing patterns. He showed less inclination to interact with her in response, moving away frequently and preferring to direct his interactions, mostly containing Approach/Sit patterns, towards T1.

Looking at the other females, BW2 showed a different behavioural repertoire towards T1 than she showed to either male (Figure 4.6.1), and little interaction at all with the female TW1. TW1, whilst interacting on a regular although not overly frequent basis with T1, rarely interacted with any other member of the group (Figure 4.4.1).

Of the two males in the group, BW1 and TW2, BW1 appeared (subjectively) to be the more dominant. He was the larger of the two and his dominance may have been reflected in the significantly asymmetric flow of interactions between him and TW2, with TW2 being the greater initiator (Figure 4.4.1). This relationship showed little evidence of aggression, a feature discussed further in the next section. That the two males held different statuses within the group is suggested by the different relationships held by the females with the different males. Whilst performing a high rate of affiliative patterns towards BW1 with little reciprocation, BW2 showed a much high level of Aggression in the form of cuffing towards TW2, in a generally reciprocal relationship (Figure 4.6.1). BW2 and TW2, despite being of different sexes, appeared to hold roughly equal status within the group, reflected in the use of the same behavioural repertoire by BW1 towards both TW2 and BW2 (Figure 4.6.1). T1, whilst responding to BW1's frequent approaches with a high level of cuffing, was rarely involved in any interaction with TW2 (Figure 4.4.1).

Overall there appears to be some form of hierarchical structure within the group, represented in the flow of interactions and behaviour patterns of the cats. This comprises a dominant male BW1, who, possibly because of his infrequent attendance in the core area, showed an apparent subordinate attitude to the female T1, a net recipient of interactions from all four other cats. This female shared an exclusive amicable relationship with the female TW1. The female BW2 and male TW2 both showed a preference for interacting with the male BW1, who, although initiating to

both of them less often, rarely responded with aggression, this being higher between BW2 and TW2.

4.7. The behaviour

Following a study of a colony of similar size to this in Devon, Macdonald et. al (1987) reported that the pattern of head rubbing behaviour was markedly asymmetrical, and flowed predominantly from younger, possibly subordinate individuals, to older ones, and from adult females to males. In their study interactions were not defined in the same way as in the current one where interactions are defined as the whole sequence of behaviours that occur between the interactors, until one of them ends it (see Chapter 2 for more detailed explanation).

As mentioned in the previous section, it is possible that the cat receiving the most interactions (as defined for this study) in proportion to the number it performs may hold a dominant position within the group. It may receive a higher proportion of certain patterns as an indicator of this.

To see how the flow of behaviours related to the overall flow of interaction initiations illustrated in Figure 4.4.1, Spearman Rank Correlations were run on the proportion of each behaviour initiated to received compared with the proportion of interactions initiated to received. As might be expected, Approach behaviours (both with and without the tail raised) produced significant positive correlations ($r=1.0$, $P<0.0001$), i.e., cats that received most interactions also received the most approaches. Sniff Cat showed a similar pattern ($r=1.0$, $P<0.0001$) and the only other behaviours to show a significant correlation were Rub Head Cat ($r=1.0$, $P<0.0001$) and Rub Flank Cat ($r=1.0$, $P<0.0001$). The distribution of the most frequent of these rubbing types, Rub Head, and Sniff, are illustrated in Figures 4.7.1 and 4.7.2. Figure 4.7.3 illustrates the distribution of Cuff, the most common aggressive pattern, which showed no correlation with the proportion of interactions initiated to received.

The lack of association of the flow of cuffing with the overall flow of interactions can be seen by comparison of Figures 4.7.3 and 4.4.1. Aggression in the form of cuffing, normally seen in breeding colonies mainly amongst the males, occurred in this group mainly in female-male pairs, in particular T1 (female) to the male BW1, and the female BW2 to the male TW2. Rubbing flowed mainly from the female BW2 to the male BW1 and female T1, possibly indicating a subordinate status

Figure 4.7.1. *Relative rates (indicated by the widths of the arrows) at which members of the group head rubbed on one another, corrected for the time that each pair was present together in the observation area. Significant asymmetries in pairwise relationships are indicated by stars: * (P<0.05); ** (P<0.01); *** (P<0.001).*

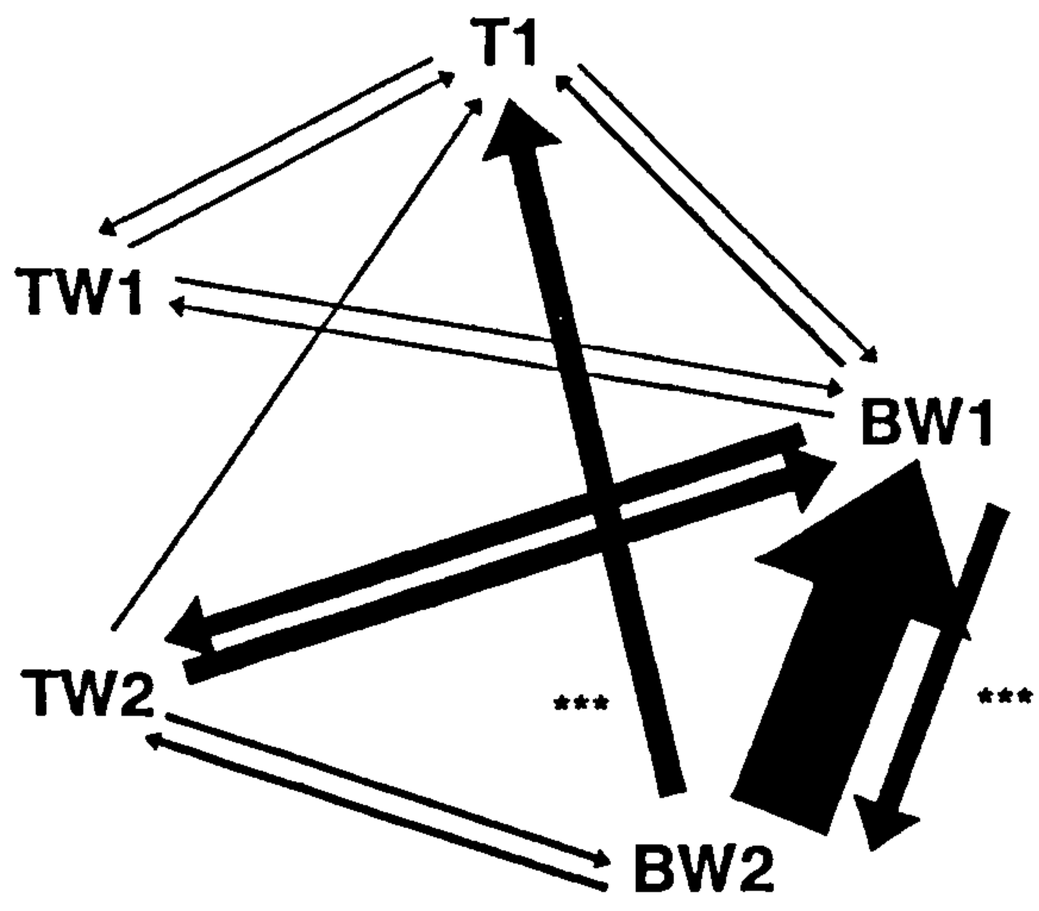


Figure 4.7.2. *Relative rates (indicated by the widths of the arrows) at which members of the group sniffed one another, corrected for the time that each pair was present together in the observation area. Significant asymmetries in pairwise relationships are indicated by stars: * (P<0.05); ** (P<0.01); *** (P<0.001).*

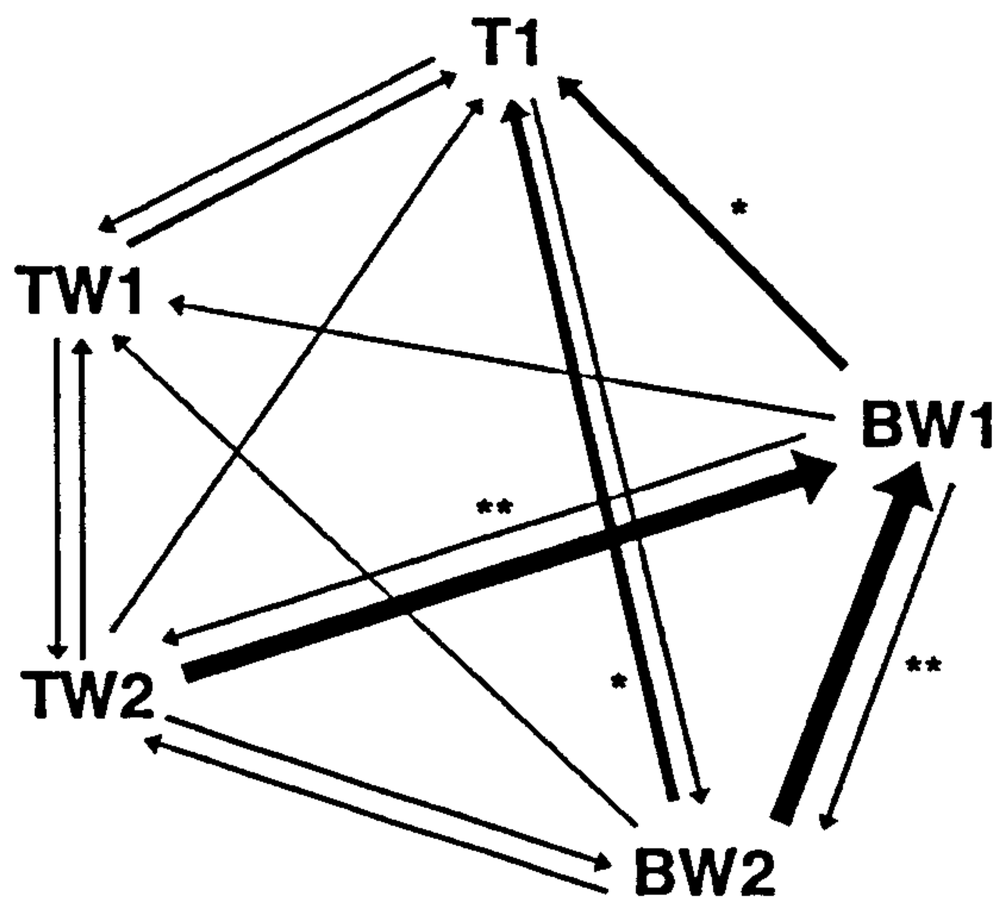
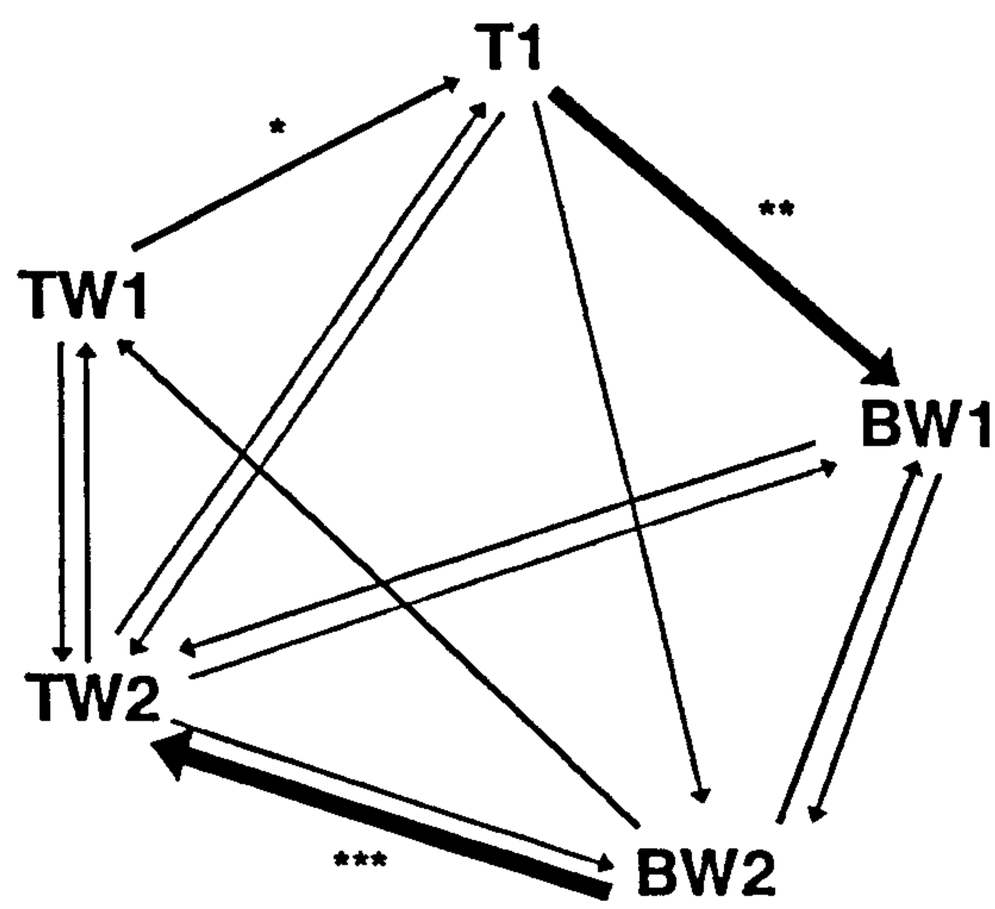


Figure 4.7.3. *Relative rates (indicated by the widths of the arrows) at which members of the group cuffed one another, corrected for the time that each pair was present together in the observation area. Significant asymmetries in pairwise relationships are indicated by stars: * (P<0.05); ** (P<0.01); *** (P<0.001).*



to these two cats, as observed by females in breeding colonies (Macdonald et. al, 1987).

4.8. Interactions with cats outside of the group

Within Exbury courtyard, 25 interactions occurred between members of the core group and one of the occasional visitors to the yard: TW3, B1 and BW4. 20 of these involved TW3. The role of TW3 in the group was always unclear - she was never a regular enough attender to be classed as part of the group but frequently wandered in and out of the yard during watches. During the 20 interactions in which she was involved, Tail-raised Approaches occurred only twice, rubbing never at all, whilst aggression was represented by just four Cuffs and one Stare by one or other of the interactors. Of the 5 interactions involving B1 or BW4, only one, involving B1, contained any aggression, and this was mild. BW4 interacted only twice, both times with BW2, and both initiated by BW2. B1 interacted with TW2 on two occasions, each initiating one interaction. T1 initiated one interaction with B1 - this involved T1 stalking and staring at B1 combined with the use of the Tail Up signal.

4.9. Discussion

The results from this colony show that, even within a group containing only five individuals, a social structure of considerable complexity exists. With such small numbers of individuals, it is easy to visualise the relationships between the cats in detail and to suggest a possible hierarchical structure to the society, with a dominant male BW1 and a dominant female T1. As a group, pairs of cats present together for less time interacted at a higher rate than those together for longer. This implies that interactions may occur more intensely between cats that have not seen each other for some time, e.g., when one returns to the core area.

The close resemblance of the distribution of head rubbing to the overall flow of interactions (Figure 4.4.1) suggests that this behaviour pattern may be one of the most representative of the underlying social structure. Sniff Cat, also, showing a similar pattern, may be another such representative behaviour but the lower numbers of observations involved make it a less rigorous example. Obviously, with only five individuals, any such correlation must be treated as tentative unless supported by

similar conclusions from other colonies.

Possibly the higher interaction rate between pairs present together less often is accompanied by an increased rate of head rubbing, which may be a form of greeting between cats meeting after a period of separation.

A feature of this colony, not present in the others studied, was visits from cats external to the group. The low amount of aggression combined with the low use of tail-raised and rubbing behaviours shown between the core group members and these cats suggests that, whilst not indicating any strong affiliations, neither were feelings towards intruders overtly aggressive (i.e., a tolerance towards visitors existed). Whether this was due to familiarity and perhaps some degree of relatedness to these cats cannot be determined. Possibly the regular provision of large amounts of food in the yard by hospital staff meant that occasional visitors posed no threat to the residents.

Calhoon & Haspel (1989) suggest that resting places rather than food are the limiting factors in urban feral cat populations. The five core members of this group frequented regular resting places within the yard, either perched inside the basement openings in the walls, or on sunny window ledges. Only one of the visiting cats (BW4) ever used any of these resting places - he used one of the basement openings on six out of his nine visits. The lack of hostility shown towards him as a result suggests that he was familiar to the others, possibly a related male who had dispersed to a new area when younger.

CHAPTER 5

The Chilworth Colony

The study site at Kennels Farm, Chilworth.

CHAPTER 5 - THE CHILWORTH COLONY

The study of the Chilworth cats was complicated by the disappearance of two of the females cats at different points in the study, as described in section 5.1. The statistical analysis of the data was correspondingly complicated and used a number of the techniques outlined in Chapter 2. Firstly the data was examined and divided into three periods for analysis (section 5.1). Each period was then analysed in detail, looking firstly for evidence of sociality (section 5.2) and then at the characteristics of individuals (section 5.3). Due to the division into three periods, interpretation of this analysis is complicated - Figure 5.3.3 summarises the main features and changes within the group over the study period. All three periods were combined (section 5.4) for analysis of characteristics of the colony as a whole.

The eleven cats present at various stages of the study were:

BE - female, tortoiseshell & white, disappeared at end of period 2

BL - female, black & white, present throughout

DA - female, black & white, present throughout

DU - male, grey & white, present throughout. Appeared younger with less development of head region than GI or GH (typical of juvenile male).

GE - female, tortoiseshell & white, present throughout

GH - male, black & white, present till end, though absent for much of period 3. Large development of head region typical of mature entire tom cats.

GI - male, ginger, present throughout. Large development of head region typical of mature entire tom cats.

HO - female, tortoiseshell & white, present throughout

PE - female, black & white, present throughout

SI - male, black & white, present throughout. Appeared younger with less development of head region than GI or GH (typical of juvenile male)

SM - female, black & white, disappeared at end of period 1.

5.1. Formation of subsets of data

A total of 574 interactions, containing a total of 2216 behavioural components were recorded throughout the entire study. After 159 interactions the first cat SM disappeared, and after a further 186 interactions the second cat BE disappeared. Figure 5.1.1 illustrates this. It seemed possible that the disappearance of these two individuals might have affected the behaviour of the remaining cats. A preliminary G-test was therefore performed simply comparing the totals of each type of behaviour performed by the whole colony in the three arbitrary periods created by the disappearance of the cats. This showed a highly significant difference ($p<0.001$) in the proportions of each behaviour type performed in each period. Comparing each of the periods with each other, the first differed significantly from the second ($P<0.001$), the second from the third ($p<0.001$) and the first from the third ($p<0.001$). It appears therefore that the behaviour of the colony changed in some way over the period it was studied. It would be wrong, however, immediately to assume that the disappearance of the two females was responsible for this as the changes could have been gradual, or indeed have occurred suddenly at any points before or after the breakpoints created by the cats disappearing, and still have produced a significant difference between the periods tested above.

A more detailed examination of when and what changes occurred in the colony's behaviour was therefore required to determine whether subsets of the data should be analysed separately. The method selected for examining this was the Kolmogorov-Smirnov One Sample test (henceforth referred to as the K-S test).

The interactive data from the whole study was divided into 10 equal sectors, each containing, as closely as possible, the same number of interactions (57 or 58). Figure 5.1.2 illustrates this division into sectors in relation to Figure 5.1.1.

A K-S test was carried out initially on the total number of behaviour patterns in each of these 10 sectors to see whether or not the length of interactions was the same in each sector. This produced a significant result, indicating that interactions were not in fact of constant length but gradually got longer, the point of greatest divergence from expected being between sectors 6 and 7 (Figure 5.1.3).

K-S tests were then performed on 20 key behaviour patterns (with initiator or recipient status kept separate) selected such that each cluster from the dendrogram of linked patterns at Knowle (Figure 3.1.2) as described in Chapter 3 was represented by one or more patterns that had occurred over 20 times in total. The theoretical

Figure 5.1.1. *The timing of the disappearance of the two females SM and BE with respect to the start and end of the study and time of year. The number of interactions that occurred between each disappearance is indicated (int).*

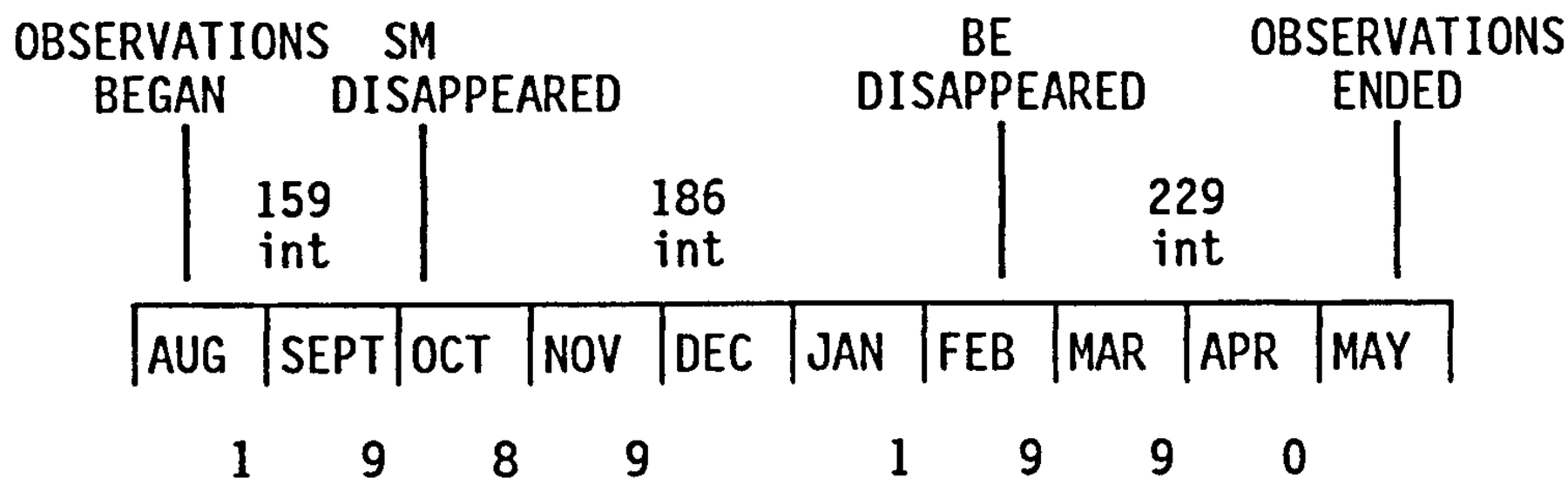


Figure 5.1.2. *Division of study period into sectors containing approximately equal numbers of interactions (int) in relation to start and end of study, disappearance of SM and BE, and time of year.*

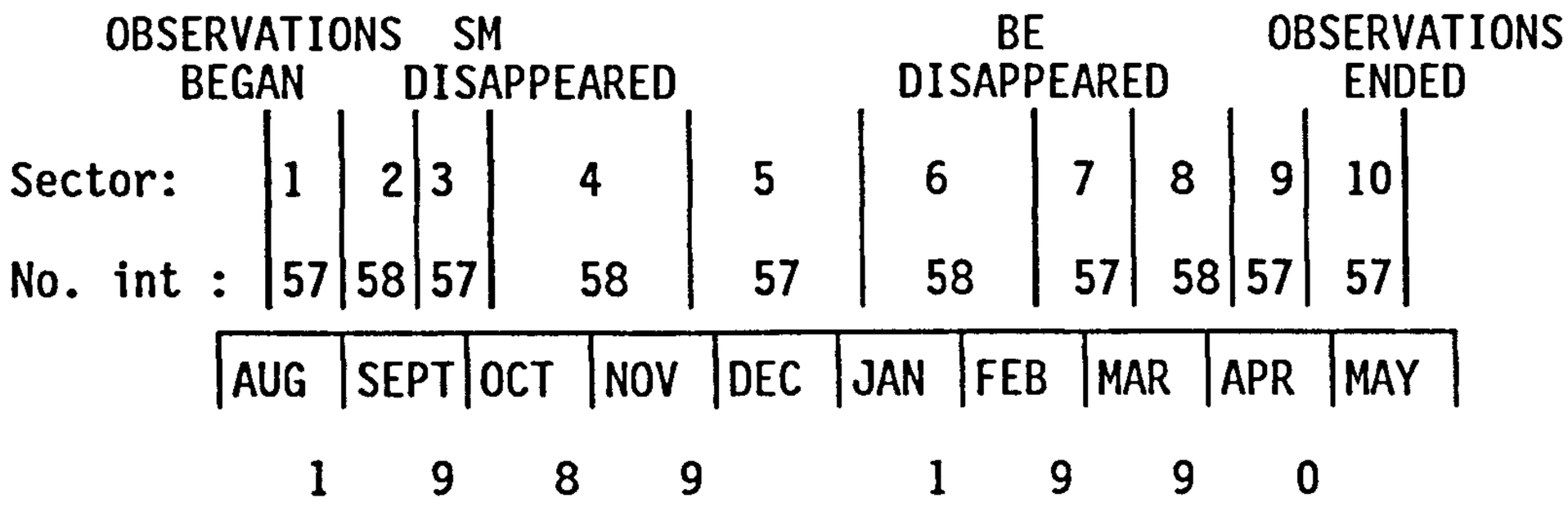
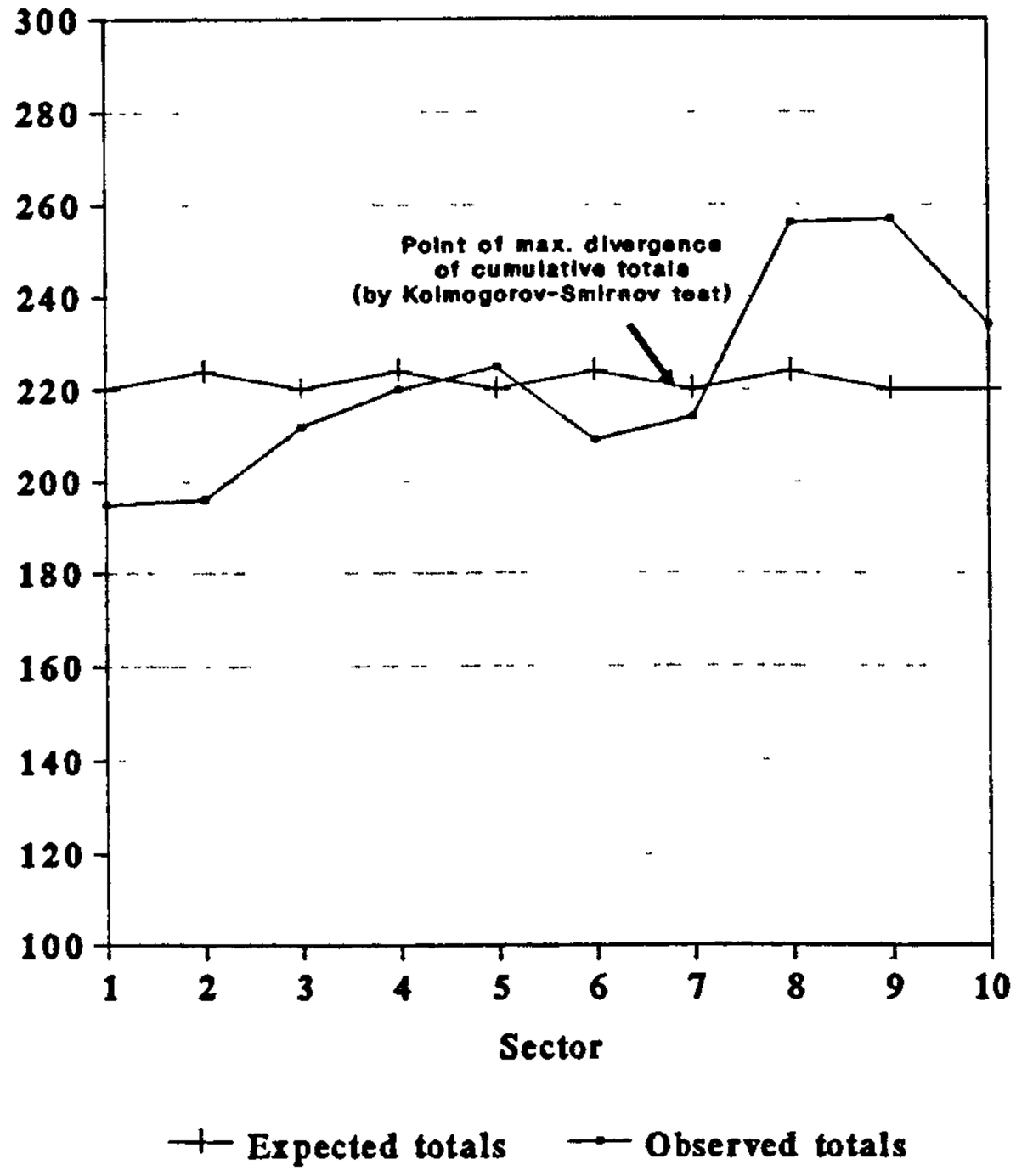


Figure 5.1.3. *The total number of behaviour patterns observed in each sector at Chilworth compared to expected totals.*



distribution with which each behaviour type was compared was based on the actual distribution of total number of behaviours in each sector as shown by Figure 5.1.3 (rather than assuming equal numbers in each sector), since this had been shown to vary. Nine of these behaviours were found to be significantly different from the expected distribution - these are represented in Table 5.1.1. Four of the most common behaviour patterns are illustrated in Figure 5.1.4.

The K-S points of greatest divergence from the expected for these four patterns are at the ends of sector 3 and sector 6, which corresponds with the disappearance of the two cats. However, as Table 5.1.1 shows, not all the behaviour patterns changed significantly at the same points, so to produce a composite picture Principal Components Analysis was performed on all 20 patterns tested by K-S.

The plot of the first two Principal Components (Figure 5.1.5) shows that sectors 1 to 10 form a roughly circular pattern reading clockwise - a feature common in data divided into temporally consecutive samples. As a measure of similarity between sectors the Euclidean distance between each pair of consecutive sectors was calculated from the graph. The greatest distance between any two consecutive sectors is sectors 3 to 4, and the next largest distance is between sectors 6 and 7.

A combination of this Principal Components Analysis and the K-S plots shows that the quality of behaviour at Chilworth changed gradually throughout the study. The greatest changes in the behaviour of the group as a whole seem to have occurred around the ends of sectors 3 and 6, which may or may not be linked with the disappearances of SM and BE respectively. If the data set was analysed as a whole, allowing for the loss of these individuals would be very complicated. It would probably involve dropping these two cats from the analysis altogether -which would be highly undesirable if their leaving had indeed influenced the behaviour of the rest of the group. With this in mind and with the backing of the K-S tests and Principal Components analysis, it was decided for further analysis to split the data set into the three periods shown at the beginning of this section, marked by the disappearance of each cat.

Table 5.1.1. *The nine behaviour patterns whose distributions were shown by K-S analysis to be significantly different from expected. For each pattern it is indicated the sector that marked the point of greatest divergence from the expected.*

Behaviour pattern	Sector marking K-S point of max. divergence from expected
Approach Initiator	3
Cuff Initiator	3
Move Away Recipient	6
Rub Head Cat Initiator	4
Sit With Cat Initiator	5
Tail-raised Approach Initiator	3
Tail-raised Move Away Initiator	8
Tail-raised Walk Past Initiator	3
Walk Past Initiator	3

Figure 5.1.4. *Distribution of four of the most common behaviour patterns shown by K-S analysis to have changed significantly during the study at Chilworth. The K-S points of greatest divergence from the expected values when cumulative values are compared are indicated.*

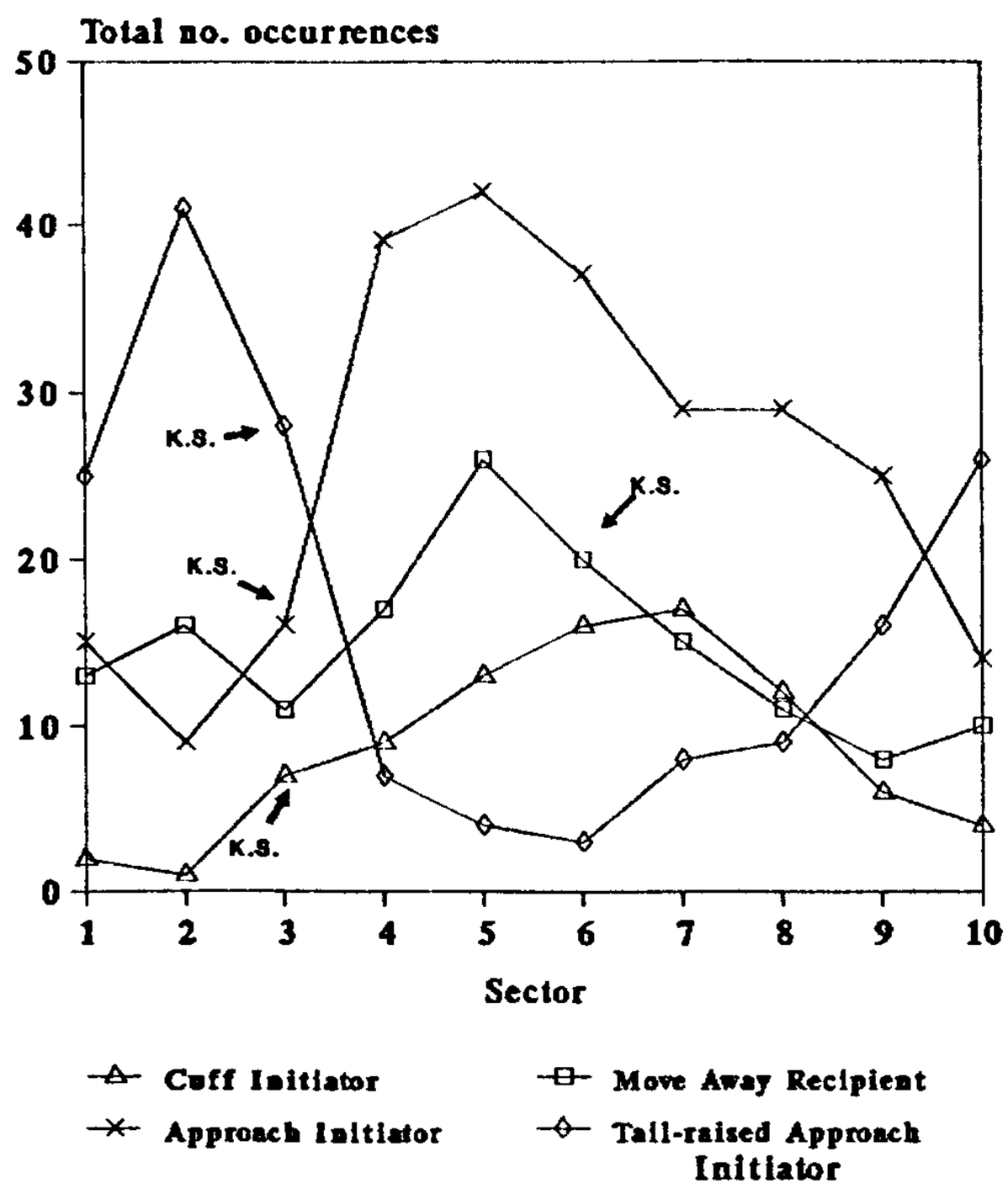
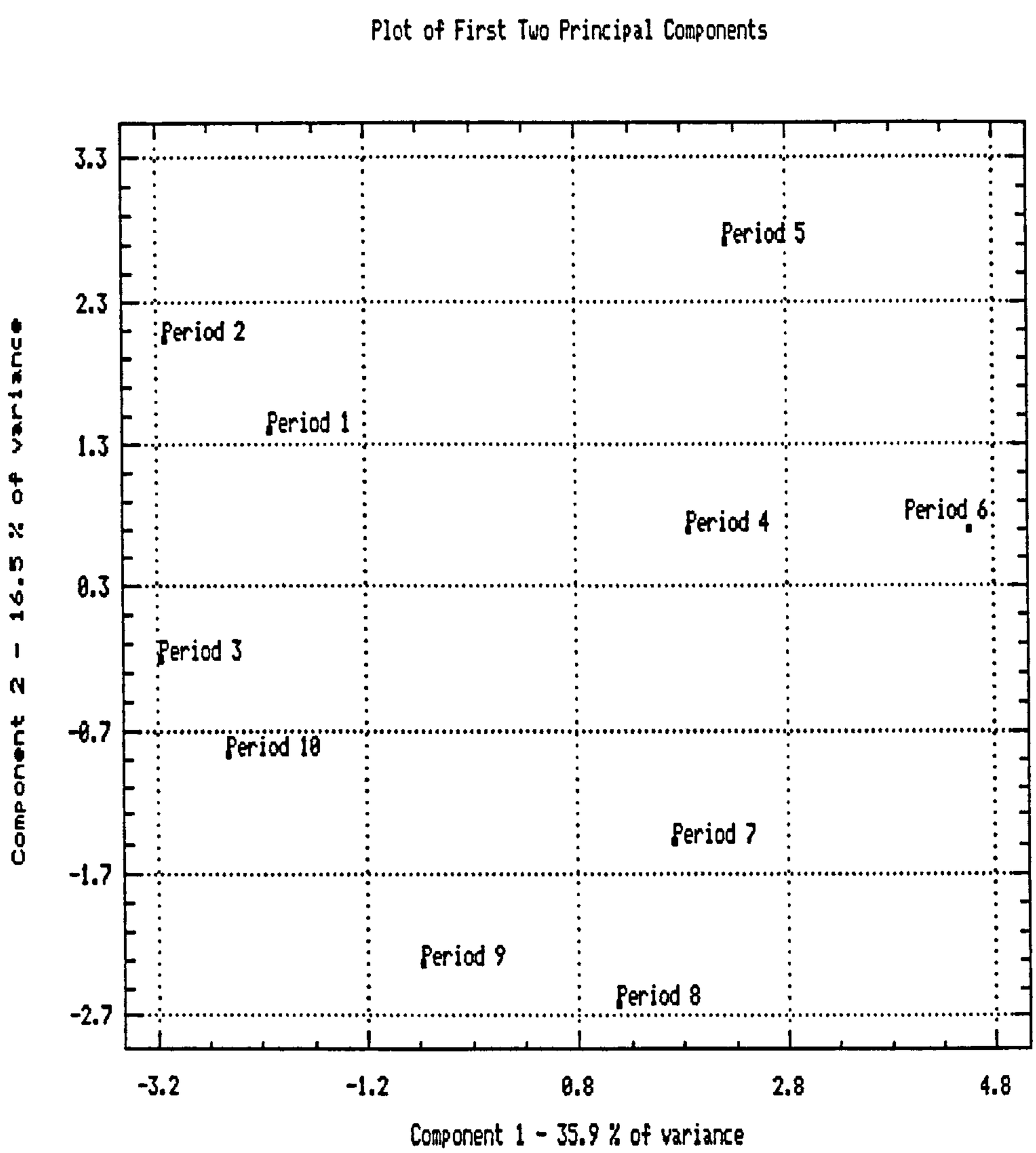


Figure 5.1.5. *PCA on behavioural differences between the ten sectors at Chilworth. Components 1 and 2.*



5.2. Evidence for sociality within the group

Before looking in any detail into the interactions that occurred within each period, it was necessary to gain some evidence that the interactions within the group were socially based, i.e., that the cats were not just interacting randomly as they happened to meet one another. As described in Chapter 1, if no individual variation existed, such a random system of interacting should result in the number of interactions between each possible pair of animals being in direct proportion to the amount of time they were available to interact. The corresponding *rates* of interaction should be the same for every pair of cats and should therefore be independent of time available. This does not, however, allow for individual differences in interactivity (i.e., any evidence of sociality found in this way might be due to certain individuals interacting at a higher rate than the rest of the colony). However, it is useful to gain some indication of the possible social nature of the interactions before looking at individuals in detail.

The members of the group and the quality of their interactions changed significantly over the study period, so, on dividing the data into three periods for detailed analysis, it is logical to examine the relationship between the time pairs of cats were present together, the number of interactions they performed and the rate at which they performed them for each period, to see if sociality was also changing within the group.

Data was included from all the cats present in each period except the female DA in Period 1 and the male GH in Period 3, each of which was present in those periods for less than a quarter of total scans taken. For each possible pair of cats in each period the following variables were calculated: time present at the study site together and therefore available for interaction (time present together was defined as the number of scans on which both cats were present, irrespective of their distance from each other); number of interactions between them (irrespective of direction of interaction); and rate of interaction (corrected for time available for interaction). Pairs that never interacted were omitted as their inclusion would bias the data too much.

Rank correlations on these variables showed, in Period 1, no association between the number of interactions and the amount of time cats were present together ($r=0.01$, $P=0.94$, $n=34$), and a significant negative correlation between interaction *rate* and time present together ($r= -0.42$, $P=0.01$, $n=34$). The same

relationships were present in Period 2, with no correlation between number of interactions and time present together (r=0.04, P=0.80, n=34), and a negative correlation between interaction rate and time present together (r= -0.41, P=0.02, n=34). In period 3 the relationship between these variables were different, with a significant relationship between interactions and time together (r=0.65, P=0.00, n=23), and a marginally significant positive relationship between interaction rate and time present together (r=0.38, P=0.07, n=23).

Periods 1 and 2 displayed the same pattern of positive indicators of sociality as were present at Knowle (section 4.3, Chapter 4) with cats not interacting with others according to how often they encountered them, and with pairs attending the site together for less time interacting at a higher rate than those attending for more time together. Period 3 indicates that cats were interacting more according to how often they met partners, however the marginal significance of the positive correlation of interaction rate and time present together suggests that cats available to interact for more time interacted at a higher rate. Rather than being asocial, therefore, the group appeared to be interacting in a different way, possibly due to a reorganisation of the social structure.

5.3. Characteristics of individuals

With some evidence of sociality within the group, it was then possible to look in detail at the individuals involved in the interactions. Demonstration that each cat performed a different proportion of behaviour patterns, and more especially that each cat received a different proportion of patterns to every other cat would provide further evidence of sociality within the group, indicating that cats were seeking out particular individuals with which to interact.

5.3.1. Interactions - analysis of individual behavioural styles

For each of the three periods two matrices were compiled, one of the behaviour patterns performed by each cat, and one of the behaviour patterns received by each cat. Behaviours occurring less than 20 times in a period were omitted, as was any cat whose behaviours performed and received totalled less than fifty. This was to allow the inclusion of cats that performed few but received a lot of behaviours (or vice versa) whilst eliminating cats who generally participated little in interactions during

that particular period. Thus, for each period, a slightly different set of cats and behaviours was analysed, although there was considerable overlap. The three matrices of patterns performed are included in Table 5.3.1. and the matrices of patterns received are in Table 5.3.2.

The G-test for R X C tables (with Williams' correction), (Sokal & Rohlf 1981) was employed to test each matrix for heterogeneity. All six matrices were significantly heterogeneous at $P<0.01$ and for all except the patterns received in Period 1, this significance extended to the level of $P<0.001$.

For each matrix unplanned pairwise tests of homogeneity were used (Sokal & Rohlf, 1981) with Williams' correction to test for differences between pairs of cats, such that every cat was tested against every other for homogeneity. The results for periods 1,2 and 3 are shown in Tables 5.3.3, 5.3.4. and 5.3.5 respectively. Where obvious similarities or differences could be seen within groups of cats, tests could be carried out on subsets of cats to see if they were homogeneous. Unfortunately, as examination of tables 5.3.3 -5.3.5 reveals, the situation was generally more complicated than this with no obvious subsets of cats emerging from the pairwise tests. The cats apparently differed from one another with respect to different behaviours according to the individuals involved.

Median linkage cluster analysis was used where appropriate to give some suggestion of which cats might be closest together behaviourally and groups could be tested for homogeneity on this basis. In some of the matrices, especially in the later two periods, nearly all the cats were different from all the others and no clear homogeneous groups could be found.

To provide some visual help to the interpretation of this data, Principal Components Analyses were performed on the six matrices. The results of these are included in Appendix 3. Thus through a combination of G-tests on the whole matrices, pairwise tests and group tests within these matrices and Principal Components Analysis of the matrices, the following descriptions of the colony during the three periods emerged.

Table 5.3.1. *Totals of each behaviour pattern performed by each cat during each period of the study. Patterns occurring < 20 times in a period were omitted, as was any cat whose patterns performed and received totalled < 50. Patterns with numbers in parentheses were not included in the analysis for that individual period but were included for the analysis of all three periods combined. Behaviour codes are described in Appendix 1.*

	BEHAVIOUR PATTERNS																
	AP	SN	MA	RH	TU	WP	ST	CU	TP	TA	RF	SW	SR	CH	FL	TM	WA
PERIOD 1																	
BE	2	2	5	8	2	(1)	(0)	(1)	4	8	6	1	2	-	-	-	-
BL	3	3	6	13	4	(0)	(2)	(1)	4	21	7	6	1	-	-	-	-
DU	6	5	16	21	5	(1)	(1)	(0)	7	30	6	7	1	-	-	-	-
GH	14	11	12	7	3	(2)	(2)	(3)	5	9	4	2	5	-	-	-	-
GI	0	5	15	1	0	(2)	(3)	(1)	0	0	0	0	8	-	-	-	-
PE	6	3	5	23	7	(1)	(0)	(2)	6	9	1	4	1	-	-	-	-
SI	2	0	4	6	8	(3)	(1)	(0)	1	5	2	0	3	-	-	-	-
SM	4	0	12	8	0	(0)	(0)	(3)	5	17	3	0	3	-	-	-	-
PERIOD 2																	
BE	10	5	17	7	6	5	1	1	(3)	(6)	(3)	6	-	0	4	-	-
BL	2	1	16	0	1	1	2	1	(0)	(4)	(1)	1	-	0	0	-	-
DU	30	8	29	3	19	13	0	9	(6)	(0)	(0)	6	-	5	7	-	-
GE	4	5	15	1	1	0	2	3	(0)	(3)	(2)	2	-	0	7	-	-
GH	39	10	13	22	3	4	4	12	(1)	(0)	(5)	3	-	0	0	-	-
GI	1	3	3	0	0	1	9	1	(0)	(0)	(0)	0	-	0	0	-	-
HO	16	3	7	0	1	3	2	22	(0)	(0)	(0)	0	-	11	0	-	-
PE	12	5	15	2	0	0	0	20	(0)	(1)	(0)	5	-	4	12	-	-
SI	11	3	12	4	1	3	0	1	(1)	(3)	(1)	2	-	0	0	-	-
PERIOD 3																	
DU	30	5	24	20	31	16	8	7	11	26	7	(4)	-	-	-	23	16
GE	1	5	9	0	2	1	0	0	1	2	0	(0)	-	-	-	0	3
GI	3	1	2	0	0	6	10	1	0	0	0	(0)	-	-	-	0	4
HO	35	13	21	4	3	9	6	29	9	9	2	(2)	-	-	-	1	4
PE	23	13	21	22	14	7	3	15	5	19	7	(5)	-	-	-	6	3
SI	2	3	19	28	4	1	8	0	2	26	14	(0)	-	-	-	9	8

Table 5.3.2. *Totals of each behaviour pattern received by each cat during each period of the study. Patterns occurring < 20 times in a period were omitted, as was any cat whose patterns performed and received totalled < 50. Patterns with numbers in parentheses were not included in the analysis for that individual period but were included for the analysis of all three periods combined. Behaviour codes are described in Appendix 1.*

	BEHAVIOUR PATTERNS																
	AP	SN	MA	RH	TU	WP	ST	CU	TP	TA	RF	SW	SR	CH	FL	TM	WA
PERIOD 1																	
BE	5	3	5	9	3	(3)	(0)	(0)	3	8	4	2	2	-	-	-	-
BL	4	5	18	6	3	(2)	(1)	(1)	4	7	3	0	8	-	-	-	-
DU	1	1	8	19	5	(1)	(2)	(8)	1	6	1	1	4	-	-	-	-
GH	2	2	11	10	4	(1)	(4)	(2)	5	18	8	7	1	-	-	-	-
GI	6	6	9	11	4	(1)	(1)	(0)	8	27	6	5	1	-	-	-	-
PE	5	6	9	17	4	(2)	(0)	(1)	3	5	0	2	4	-	-	-	-
SI	5	3	6	10	1	(1)	(1)	(0)	3	10	3	0	1	-	-	-	-
SM	6	3	9	5	6	(0)	(0)	(1)	2	15	4	3	3	-	-	-	-
PERIOD 2																	
BE	26	9	15	11	3	6	0	12	(3)	(1)	(3)	7	-	0	0	-	-
BL	17	9	6	14	4	1	0	4	(0)	(0)	(2)	1	-	0	0	-	-
DU	9	2	11	1	2	2	0	21	(0)	(4)	(1)	1	-	5	5	-	-
GE	18	3	11	1	3	7	1	15	(2)	(0)	(1)	6	-	8	0	-	-
GH	7	3	27	3	6	0	7	2	(2)	(3)	(2)	5	-	0	7	-	-
GI	13	3	12	0	1	0	4	0	(4)	(6)	(1)	1	-	0	0	-	-
HO	2	0	16	0	0	4	1	4	(0)	(0)	(0)	0	-	0	16	-	-
PE	25	10	20	4	11	6	5	5	(0)	(1)	(0)	3	-	4	2	-	-
SI	8	4	9	5	2	4	2	7	(0)	(2)	(2)	1	-	3	0	-	-
PERIOD 3																	
DU	27	11	26	13	13	7	9	14	8	22	8	(3)	-	-	-	7	5
GE	13	4	2	1	5	6	1	7	1	0	0	(6)	-	-	-	2	1
GI	7	4	4	0	1	1	3	2	3	3	0	(2)	-	-	-	2	8
HO	1	0	18	3	3	0	9	6	0	3	2	(0)	-	-	-	3	6
PE	18	6	23	14	17	6	5	7	6	23	5	(2)	-	-	-	14	10
SI	29	16	20	20	13	16	8	15	8	32	15	(0)	-	-	-	12	7

Table 5.3.3. *Results of unplanned pairwise tests of homogeneity with Williams correction (Gh) on Period 1 matrices in Tables 5.3.1 and 5.3.2 -behaviour patterns performed and received by each cat.*

Pair	Patterns performed		Patterns received	
	Gh value	Significance level	Gh value	Significance level
BE - BL	5.1	N.S.	12.4	N.S.
BE - DU	6.6	N.S.	11.7	N.S.
BE - GH	11.7	N.S.	7.5	N.S.
BE - GI	38.3	P<0.01	5.5	N.S.
BE - PE	12.4	N.S.	9.4	N.S.
BE - SI	10.6	N.S.	4.1	N.S.
BE - SM	11.6	N.S.	3.7	N.S.
BL - DU	3.0	N.S.	17.0	N.S.
BL - GH	26.4	P<0.05	25.6	N.S.
BL - GI	61.4	P<0.01	27.1	P<0.05
BL - PE	13.3	N.S.	14.1	N.S.
BL - SI	17.6	N.S.	11.2	N.S.
BL - SM	20.6	N.S.	14.4	N.S.
DU - GH	25.1	N.S.	20.7	N.S.
DU - GI	60.1	P<0.01	27.7	P<0.05
DU - PE	13.3	N.S.	8.6	N.S.
DU - SI	20.3	N.S.	14.6	N.S.
DU - SM	17.2	N.S.	16.7	N.S.
GH - GI	35.6	P<0.01	5.7	N.S.
GH - PE	24.2	N.S.	26.0	N.S.
GH - SI	21.5	N.S.	12.1	N.S.
GH - SM	26.3	P<0.05	8.0	N.S.
GI - PE	57.0	P<0.01	24.0	N.S.
GI - SI	38.0	P<0.01	7.3	N.S.
GI - SM	45.2	P<0.01	6.9	N.S.
PE - SI	14.4	N.S.	12.9	N.S.
PE - SM	29.2	P<0.05	16.0	N.S.
SI - SM	19.6	N.S.	8.5	N.S.

Table 5.3.4. *Results of unplanned pairwise tests of homogeneity with Williams correction (Gh) on Period 2 matrices in Tables 5.3.1 and 5.3.2 -behaviour patterns performed and received by each cat.*

Pair	Patterns performed		Patterns received	
	Gh value	Significance level	Gh value	Significance level
BE - BL	17.4	N.S.	10.5	N.S.
BE - DU	18.8	N.S.	40.6	P<0.01
BE - GE	17.6	N.S.	26.1	N.S.
BE - GH	34.0	P<0.01	54.4	P<0.01
BE - GI	32.4	P<0.05	33.1	P<0.01
BE - HO	69.6	P<0.01	71.0	P<0.01
BE - PE	45.8	P<0.01	26.1	N.S.
BE - SI	8.3	N.S.	14.0	N.S.
BL - DU	24.9	N.S.	45.8	P<0.01
BL - GE	11.6	N.S.	40.5	P<0.01
BL - GH	35.4	P<0.01	46.8	P<0.01
BL - GI	14.7	N.S.	30.1	P<0.05
BL - HO	34.3	P<0.01	70.3	P<0.01
BL - PE	30.7	P<0.05	23.3	N.S.
BL - SI	14.8	N.S.	17.6	N.S.
DU - GE	28.9	P<0.05	16.7	N.S.
DU - GH	64.7	P<0.01	47.5	P<0.01
DU - GI	45.5	P<0.01	39.9	P<0.01
DU - HO	54.3	P<0.01	31.7	P<0.05
DU - PE	47.1	P<0.01	37.3	P<0.01
DU - SI	18.1	N.S.	18.1	N.S.
GE - GH	45.1	P<0.01	58.0	P<0.01
GE - GI	19.8	N.S.	32.0	P<0.05
GE - HO	46.9	P<0.01	57.9	P<0.01
GE - PE	17.6	N.S.	24.8	N.S.
GE - SI	22.1	N.S.	10.4	N.S.
GH - GI	32.9	P<0.01	20.1	N.S.
GH - HO	57.7	P<0.01	36.7	P<0.01
GH - PE	67.0	P<0.01	29.7	P<0.05
GH - SI	13.1	N.S.	32.5	P<0.05
GI - HO	30.9	P<0.05	43.5	P<0.01
GI - PE	40.5	P<0.01	18.6	N.S.
GI - SI	28.0	N.S.	24.8	N.S.
HO - PE	36.1	P<0.01	59.9	P<0.01
HO - SI	41.3	P<0.01	43.3	P<0.01
PE - SI	35.4	P<0.01	8.8	N.S.

Table 5.3.5. *Results of unplanned pairwise tests of homogeneity with Williams correction (Gh) on Period 3 matrices in Tables 5.3.1 and 5.3.2 -behaviour patterns performed and received by each cat.*

Pair	Patterns performed		Patterns received	
	Gh value	Significance level	Gh value	Significance level
DU - GE	31.5	P<0.05	31.0	P<0.05
DU - GI	49.3	P<0.01	26.1	N.S.
DU - HO	84.6	P<0.01	40.8	P<0.01
DU - PE	31.9	P<0.05	11.4	N.S.
DU - SI	68.0	P<0.01	8.0	N.S.
GE - GI	30.0	P<0.05	23.0	N.S.
GE - HO	24.6	N.S.	54.9	P<0.01
GE - PE	26.5	N.S.	39.0	P<0.01
GE - SI	34.1	P<0.01	33.1	P<0.05
GI - HO	37.2	P<0.01	33.8	P<0.05
GI - PE	58.5	P<0.01	24.9	N.S.
GI - SI	58.5	P<0.01	30.7	P<0.05
HO - PE	39.6	P<0.01	38.4	P<0.01
HO - SI	136.0	P<0.01	55.9	P<0.01
PE - SI	63.7	P<0.01	15.9	N.S.

<u>Period 1 - SM present</u>

8 cats included in analysis -BE,BL,DU,GH,GI,PE,SI and SM.

Behaviour patterns performed

The pairwise tests of homogeneity (Table 5.3.3.) indicate that GI is different to all the others with respect to patterns performed. The remaining seven cats show heterogeneity as a group ($P<0.05$), but testing all possible groups of six revealed that variations within this seven cannot be ascribed to a single individual. The pairwise tests suggest that any heterogeneity within the group not due to GI may be due to SM's differences compared to GH and/or PE or BL's differences to GH (all significant at $P<0.05$).

Examination of the PCA graphs of the first two weights and components (Figures 5.3.1 a & b, Appendix 3) suggests that GI differs from the rest of the cats due to his relatively high performance of Sniff Rear (SR) combined with his relatively low performance of most other patterns. From the same graphs and also those showing the second vs. third weights and components (Figures 5.3.1 c & d, Appendix 3), it also appears that GH's differences to other cats (mentioned above) are stronger than those of SM. He differs in his use of Approach (AP) rather than Tail-raised Approach and also in his use of Sniff (SN).

Behaviour patterns received

Of all the matrices analysed (see Table 5.3.2) this one showed the least significant heterogeneity ($P<0.01$ compared to $P<0.001$ for all the others). This was reflected in the pairwise tests (Table 5.3.3) with only two comparisons, GI vs BL and GI vs DU, showing significant differences. Not surprisingly tests of subsets of the matrix revealed no single source of the heterogeneity within the whole matrix.

The first and second weights and components of the PCA analysis (Figures 5.3.1. e & f, Appendix 3) pull out GI, BL, DU, and GH from the others, the first three supporting the findings of the pairwise tests. The third component (Figure 5.3.1. g & h) pulls out BL even further. From these graphs it appears that GI differs in being a higher recipient of Tail-raised Approaches (TA) and Tail-raised Walk pasts (TP); DU in being a recipient of Tail-Ups (TU) and Head Rubs (RH); BL a recipient of Move Away (MA) and Sniff Rear (SR); and GH possibly a recipient of Sit With (SW).

<u>Period 2 - SM absent</u>

Nine cats could be included in the analysis - BE, BL, DU, GE, GH, GI, HO, PE and SI.

Behaviour patterns performed

The pairwise tests of homogeneity (Table 5.3.4) indicate a great deal more heterogeneity between cats than in the previous period. Median linkage cluster analysis was used to give some clues as to which groups of cats to test as possibly homogeneous. A number of homogeneity tests were carried out and a pattern gradually emerged. SI, BL, GE, BE, and GI were found to form a homogeneous group. The other four cats PE, HO, GH, and DU were all significantly different both from each other and from the homogeneous group with regard to behaviours performed.

PCA supports this conclusion. Plots of the first two weights and components (Figures 5.3.1. i & j, Appendix 3)) separates DU and GH, whilst the third component (Figures 5.3.1 k & l) separates PE and HO from the others. DU performs a group of 4 behaviours more frequently than the others: Walk Past (WP); Tail-Up (TU); Sit With (SW); and Move Away (MA). GH has a high level of Rub Heads (RH); HO has a high level of Cuff (CU) and Chase (CH) ; whilst PE has a high level of Flee (FL). To a lesser extent, GI is pulled out slightly as being a performer of Stare (ST).

Behaviour patterns received

Even more heterogeneity exists between pairs looking at behaviours received (Table 5.3.4) with only SI emerging as fairly similar to most of the others. PCA (Figures 5.3.1. m & n, Appendix 3) shows just how widely spaced the cats are with regard to their behavioural reception and SI only emerges as similar to any of them through being fairly "average" in his behaviour. Looking at the third component (Figure 5.3.1 o & p) as suggested by the scree diagram shows a few associations do exist. BL appears to be a recipient of Head Rubbing (RH), HO is a recipient of Flee (FL); DU, PE, GE and, to a lesser extent SI receive Cuffs (CU) and Chase CH); GH receives Stare (ST) and Move Away (MA); and BE receives Approaches (AP)-tail down and Sit Withs (SW).

<u>Period 3 - BE absent</u>

Six cats were included in this analysis - DU, GE, GI, HO, PE and SI.

Behaviour patterns performed

Pairwise tests of homogeneity (Table 5.3.5) show that all except two combinations of cats are significantly different to each other with respect to behaviours performed in this period. Even the two non-significant pairs HO vs GE and PE vs GE are bordering on significance. PCA (Figures 5.3.1. q & r, Appendix 3) on the matrix separates out GI and GE as performing almost all behaviours at a low rate. GI is also, to a certain extent, positively associated with Stare (ST). HO is pulled out as performing a high level of Cuff (CU) and to a lesser extent Sniff (SN), PE Approaches (AP) and Moves Away (MA), DU does Tail Ups (TU), whilst SI is associated with Tail-raised Approaches (TA), Rub Heads (RH) and Rub Flanks (RF).

Behaviour patterns received

This is probably the most difficult matrix of all to interpret, with approximately half the pairwise tests (Table 5.3.5) showing differences between cats, with the significant ones not always involving the same cats. In the PCA, with over 70 % of the variance being explained by the first component, only the first two components can be used for explaining the results (Figures 5.3.1 s & t, Appendix 3). With such a wide spread of cats it is difficult to find any specific relationships. GI, HO, and GE seem to be negative on most behaviours, DU and SI are possibly recipients of the various Tail raised and Rubbing behaviours, whilst PE tends to receive Move Away (MA) and Stare (ST).

<u>All three periods combined</u>

Though useful as an indication of the behavioural styles of each cat in each period of the study, the above descriptions are somewhat disconnected and is hard to gain an overall picture of which cats are doing and receiving what during the study. The reason, as discovered earlier, is that the behaviour of the group as a whole was changing gradually. To find out whether this was due to a change in all the cats' behaviour, or due to certain individuals, and if so, which ones, analysis of the three

periods together was required.

The "Behaviours Performed" and "Behaviours Received" matrices were still treated as separate but the data for all three periods was combined to produce a single matrix of each type. As mentioned earlier, the three periods were not completely compatible in terms of the cats and behaviours analysed. All cats included in the individual matrices were included in the overall matrix, suffixed with a 1, 2 or 3 to indicate what period its data was for. Therefore some cats would appear three times in the matrix, some twice and some only once. Not all behaviours included in the original three matrices were included, however, since continuity between periods had to be established. Only behaviours that had been analysed individually in two or three of the periods were included and where necessary, data that had been omitted for an individual period was replaced for the overall analysis. The resulting matrices were therefore modified forms of Tables 5.3.1 and 5.3.2 (see Table legends for details).

Analysis of these two matrices was as for the individual periods, by G-tests and PCA on the whole matrices. Not surprisingly, the G-tests showed both matrices to be significantly heterogeneous ($P<0.001$). Within each matrix selective unplanned pairwise tests of homogeneity could then be carried out comparing each cat with itself in any other period. The results of these tests are shown in Table 5.3.6. A combination of this and examination of the corresponding PCA graphs (Figures 5.3.1. u -x, Appendix 3) shows which cats changed most between different periods in terms of behaviours performed and received and with respect to which behaviours in particular. The fact that some cats appear only once whilst others appear throughout the study confuses the picture slightly, but the fact that a cat had insufficient data to be included in the analysis itself indicates that that cat's behaviour had changed. Where statistical significance is stated this is $P < 0.05$.

DA - Female. Although present throughout the study, DA interacted very infrequently with other cats and in no period did she produce enough data to permit inclusion in the analysis.

SM - Female. Present for the first period only, SM appeared to have a similar behavioural repertoire and indeed to receive a similar set of behaviours as BE (see below) in the same period

Table 5.3.6. *Results of selective unplanned pairwise tests of homogeneity with Williams correction (Gh) on combined matrices in Tables 5.3.1 and 5.3.2 -behaviour patterns performed and received by each cat. Each cats patterns performed and received is compared with those performed and received in each other period.*

Behaviours Performed

Pair tested	G-value (with Williams corr)	Significance level
BE1 - BE2	15.1	N.S.
BL1 - BL2	32.4	P < 0.05
DU1 - DU2	111.6	P < 0.01
DU2 - DU3	61.2	P < 0.01
DU1 - DU3	47.8	P < 0.01
GH1 - GH2	32.0	P < 0.05
GI1 - GI2	11.9	N.S.
GI2 - GI3	5.4	N.S.
GI1 - GI3	23.1	N.S.
PE1 - PE2	65.1	P < 0.01
PE2 - PE3	51.6	P < 0.01
PE1 - PE3	23.1	N.S.
SI1 - SI2	22.4	N.S.
SI2 - SI3	44.8	P < 0.01
SI1 - SI3	20.0	N.S.
HO2 - HO3	21.0	N.S.
GE2 - GE3	12.1	N.S.

Behaviours Received

BE1 - BE2	30.4	P < 0.05
BL1 - BL2	34.4	P < 0.01
DU1 - DU2	34.5	P < 0.01
DU2 - DU3	34.6	P < 0.01
DU1 - DU3	31.7	P < 0.05
GH1 - GH2	30.6	P < 0.05
GI1 - GI2	31.8	P < 0.05
GI2 - GI3	8.7	N.S.
GI1 - GI3	27.1	N.S.
PE1 - PE2	39.2	P < 0.01
PE2 - PE3	40.2	P < 0.01
PE1 - PE3	22.3	N.S.
SI1 - SI2	23.7	N.S.
SI2 - SI3	15.2	N.S.
SI1 - SI3	15.3	N.S.
HO2 - HO3	22.0	N.S.
GE2 - GE3	7.8	N.S.

BE - Female. This female was present for the first two periods only. Regarding behaviours performed, although the quantity of behavioural elements almost doubled between the first and second periods the proportions of different patterns used remained statistically the same. Looking at behaviour patterns received, again the quantity doubled from the first to the second period but the proportions of different patterns also changed significantly. PCA shows that compared to period one she received much more Cuffing (CU), more Approach (AP), Sniff(SN) and Move Away (MA) and less Rub Heads (RH), Rub Flanks (RF), Tail-raised Approach (TA) and Tail Up (TU).

BL - Female. Although present at the site throughout the entire study period, this female's activity in the third period was too low for inclusion in the analysis. Comparing periods one and two the behaviour patterns she performed changed both in quantity (in this case *decreasing* by 50 %) and in proportion to one another - she performed far more Move Aways (MA) and less Rub Heads (RH), Rub Flanks (RF), Tail-raised Approaches (TA) and Tail Ups (TU)in period 2. The quantity of behaviour patterns she received did not change although the proportion of different patterns did, with less Move Aways (MA) and Tail-raised Approaches (TA) and more Approach (AP), Rub Heads (RH) and Sniff (SN).

GE - Female. Although present for all three periods of the study, this female was not interactive enough in the first period for her data to be included in the analysis. From period 2 to period 3 the quantity of behaviour patterns she performed decreased by almost 50 % but the proportion of different patterns remained statistically the same. Over the same time the quantity of behaviour patterns she received decreased by 30 % and the proportions of different patterns remained the same.

HO - Female. Although present throughout the study this female produced insufficient data for analysis in the first period. From period 2 to period 3 there was no change in the proportions of different patterns performed or received. The actual number of patterns performed increased threefold between the two periods and the number received increased by 50 %.

PE - Female. This female was present and interactive enough throughout the study for data for all three periods to be included. From period 1 to period 2 the quantity of behaviour patterns performed did not alter but the proportions of different patterns changed significantly with much more Cuffing (CU) and less Rub Heads (RH), Tail-raised Approach (TA), and Tail Up (TU). From period 2 to period 3 the quantity of behaviour patterns performed increased 2.5 times and the proportions of different patterns changed significantly again with less Cuffing (CU) and Move Away (MA) and more Rub Heads (RH), Rub Flanks (RF), Tail-raised Approach (TA) and Tail Up (TU). Behaviour patterns performed in period three were in the same proportions as in period 1, indicating that her behaviour changed temporarily during the middle period and returned to its former state in the last period.

Behaviour patterns received by PE increased both quantitatively (40%) and in proportion to one another from periods 1 to 2 with more Approach (AP), Move Away (MA) and Tail Up (TU) and less Rub Heads (RH). From periods 2 to 3 there was a 50 % increase in quantity of behaviours received and proportions of different patterns changed significantly again, with less Approach (AP) and Sniff (SN) and more Rub Heads (RH), Tail-raised Approaches (TA) and Tail Up (TU). Behaviour patterns received in period 3 were in the same proportions as in period 1.

SI - Male. Present throughout the study SI exhibited a slight increase in quantity but no significant changes in proportions of different patterns performed between periods 1 and 2. Between periods 2 and 3 his quantity of behaviour patterns performed increased almost 3 times and also changed in proportion to one another with less Approach (AP) and more Rub Heads (RH), Rub Flanks (RF) and Tail-raised Approach (TA).

There was no change in the number of behaviours received between periods 1 and 2, but between periods 2 and 3 the total increased fourfold. There were no significant changes in proportions of different patterns received by SI throughout the whole study.

DU - Male. Present for all three periods, DU increased his total number of behaviour patterns performed by 20% from period 1 to period 2 and the proportions of different patterns changed significantly, with more Walk Past (WP), Approach

(AP), Move Away (MA), Tail Up (TU) and Cuff (CU), and less Rub Heads (RH), Rub Flanks (RF) and Tail-raised Approaches (TA).

From period 2 to period 3 quantity increased by 50% and proportions of different patterns altered significantly again, with less Cuffing (CU), Approach (AP), Sniff (SN) and Move Away (MA) and more Stare (ST), Rub Heads (RH), Rub Flanks (RF), Tail-raised Approach (TA) and Tail Up (TU).

Total number of behaviour patterns received stayed the same from period 1 to 2, but proportions of patterns changed significantly with much more Cuffing (CU) and to a lesser extent Approach (AP) being received and less Rub Heads (RH). Period 3 compared with period 2 shows that the quantity of behaviour patterns received increased three times and the proportions of different patterns changed once more to less Cuffing (CU), and more Rub Heads (RH), Rub Flanks (RF), Tail-raised Approach (TA), Tail Up (TU), Stare (ST) and Tail-raised Walk Past (TP).

GH - Male. Due to his infrequent attendance in the last period only data for periods 1 and 2 were analysed for this male. Period 2 compared with period 1 shows a 50 % increase in quantity of behaviour patterns performed by GH and a significant change in the proportions of different patterns with more Cuffing (CU), Approach (AP) and Rub Heads (RH) and less Tail-raised Approaches (TA). Quantity of behaviour patterns received did not alter between the two periods but proportions of different patterns altered significantly with more Move Aways (MA) and less Rub Heads (RH), Rub Flanks (RF) and Tail-raised Approaches (TA).

GI - Male. Present throughout the study, this male performed very few behaviour patterns in any period, and those he did perform did not change in proportion to one another from one period to the next. He received far more behaviour patterns in the first period compared with the second (a fifty per cent drop) and the proportions of these patterns changed significantly, with more Approach (AP) and Move Away (MA) and less Tail-raised Approach (TA) and Rub Heads (RH) in the second period. From period 2 to period 3 there was a slight further decrease in total patterns received but no changes in the proportions of different patterns.

5.3.2. Proximity - analysis of proximity between pairs of cats

A total of 216 scans were taken throughout the whole study period, 35 of these being in period 1, 87 in period 2 and 94 in period 3. For each cat in each period it was calculated: on how many scans it was present; on how many scans it was present with each other cat; on how many scans it was less than one metre away from another cat; and on how many scans it was less than one metre away from each possible partner. Where two cats were less than one metre apart they are referred to as close to one another. When observed at the site on the same scan, regardless of whether they were close, they are referred to as present together.

The cats showed various degrees of attendance at the site and different tendencies to be close to other individuals. This varied from frequent attendance but rare association to less frequent attendance but a high proportion of close associations when present.

For each period indices of association between all pairs of cats were calculated by dividing the number of scans a cat was close to each possible partner by the number of scans it was present with each of those partners. Average linkage cluster analysis was performed on the resulting proportions. Cats showing a very low attendance at the site (less than one quarter of scans recorded in a period) or a very low proportion of close associations were omitted from this analysis. The cluster analysis results were then used to produce dendrograms of close associations between individuals for each period. These are shown in Figures 5.3.2 a,b & c.

These Figures illustrate the changes in associations that occurred between individuals across the three periods and thus can be used to interpret the behavioural changes described. They will be discussed in the following summary section in relation to the interactive data.

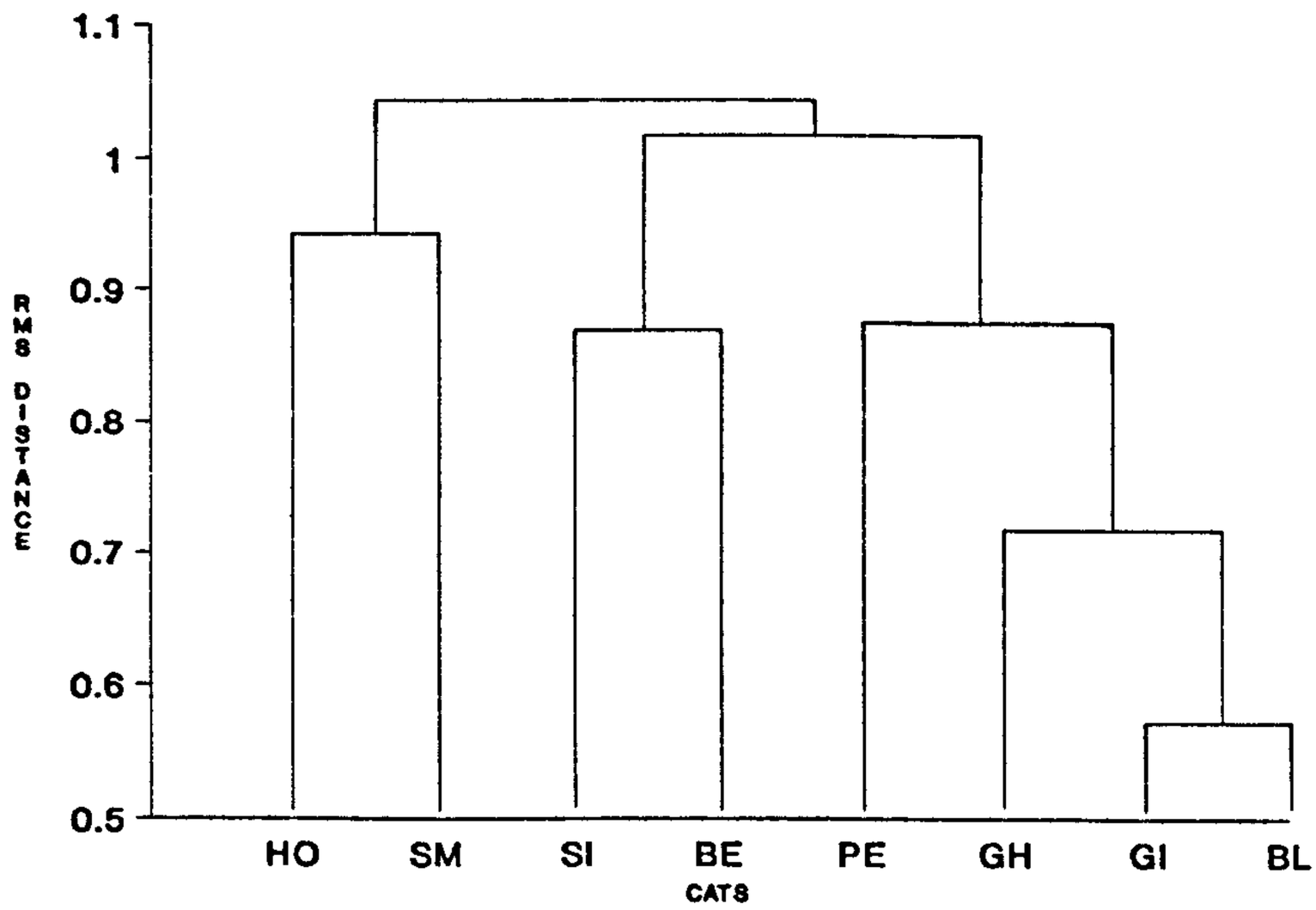
5.3.3. Summary of individual and dyadic characteristics

The analysis of the behaviour and proximity characteristics of the different cats within and between periods at Chilworth produces a detailed picture of what went on within the colony during the year following neutering. Figure 5.3.3 summarises these results.

In period one, the cats on the whole behaved fairly similarly, apart from the

Figure 5.3.2. *Dendrograms of close associations between cats at Chilworth based on average linkage cluster analysis*
Cats whose lines join nearer the bottom of each dendrogram showed a higher preference for each others company in that period than those joining nearer the top.

a) Period 1 (DU and DA omitted due to insufficient data - see text)



b) Period 2 (HO omitted due to insufficient data - see text)

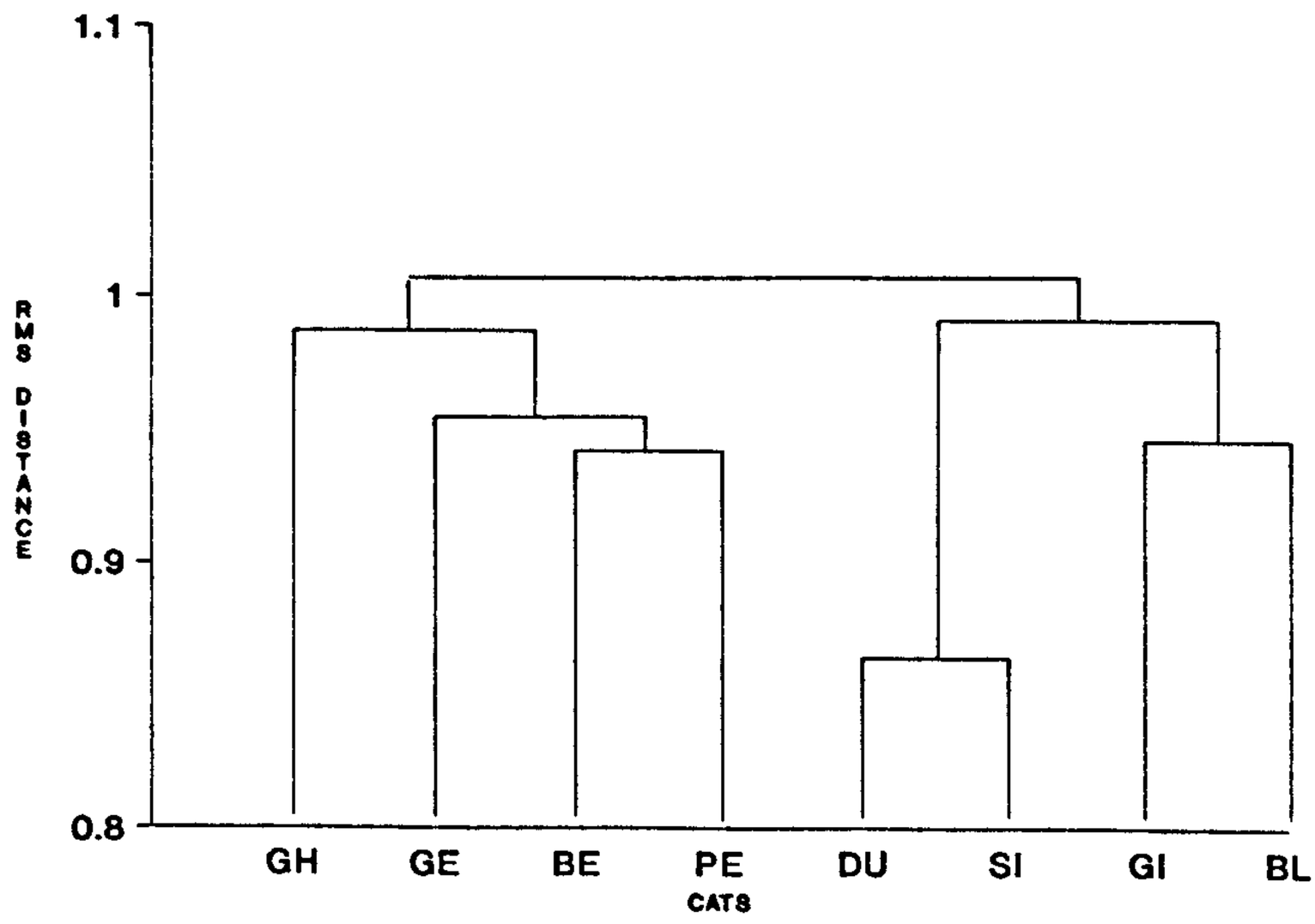


Figure 5.3.2. (contd.) *Dendrograms of close associations between cats at Chilworth based on average linkage cluster analysis Cats whose lines join nearer the bottom of each dendrogram showed a higher preference for each others company in that period than those joining nearer the top.*

c) Period 3

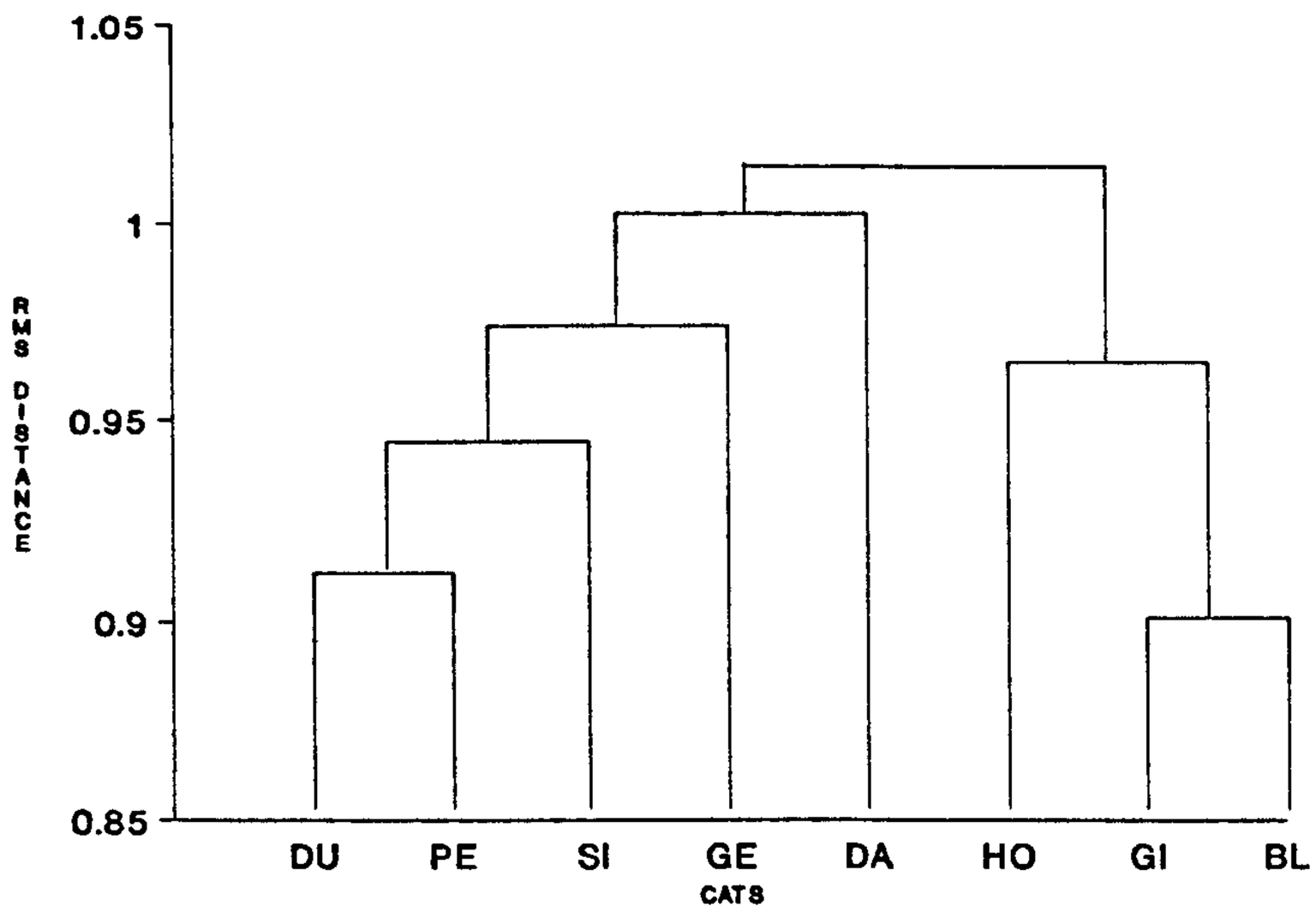


Figure 5.3.3. *Summary of main characteristics of individuals and inter-individual relationships during the study period at Kennels Farm, Chilworth.*

	1989	PERIOD 1
AUG		Period characterised by high levels of affiliative behaviour.
		Mature male GI net recipient of interactions, particularly Tail-raised Approaches.
SEPT		GI and female BL exhibited high frequency of close proximity.
		- - - - - - -SM DISAPPEARED- - - - - - - - - - -
OCT		PERIOD 2
		Period characterised by change in overall quality of interactions, becoming much less affiliative and more aggressive in nature.
NOV		Female HO became especially aggressive to others, particularly DU (male) and PE (female).
		Mature males GI and GH hostile towards one another (staring frequently), apparently due to competition for female BL.
DEC		GI and BL showed less close proximity compared to period one.
JAN	1990	The two young males, SI and DU exhibited more close proximity than in period one
		Females PE and HO, and males DU and GH became highly individualist in their behaviour
FEB		- - - - - - -BE DISAPPEARED- - - - - - - - - - -
		PERIOD 3
MAR		Period characterised by infrequent attendance of mature male GH - thought to be gradually dispersing from the group.
		Reduced hostility between GI and GH and increased close proximity between GI and the female BL.
APR		The two young males, SI and DU formed a strong affiliative association, along with the female PE.
MAY		

male GI who mostly refrained from interacting. Generally, affiliative behaviour patterns, particularly from cluster 5 of the colony's behaviour dendrogram (Fig 3.1.1) were common and aggression was low.

At the beginning of Period 2, a great change in behaviour seemed to have occurred, with some cats, namely PE, HO, GH, and DU becoming much more individualistic in their behaviour compared to the others. Generally the colony as a whole seemed to become more aggressive and less affiliative with the tail-raised and rubbing patterns typical of affiliative encounters being much less common. It seems possible that this change in behaviour was due to the rapid increase in aggression by the female HO. From a generally low rate of activity in period one she suddenly became involved in interactions (whereas the others were already fairly interactive). HO's contribution to interactions involved about 50 % aggressive behaviours. This increase in aggression was received by a spread of cats, most notably DU and PE, and may account for their sudden change in behaviour - presumably retaliation or avoidance of HO. HO's increasing unfriendliness from periods one to two is reflected in the dendrograms of close proximity between cats. From period one where her degree of association with any cat was extremely low, the proportion of scans she was close to another cat in period two was too low to be included in the analysis.

The change in behaviour of GH (the large black and white male), as well as bearing a possible effect from HO, is reflected in that of GI (the large ginger male) and BL (a black and white female). It appears from the repertoires of behaviour patterns performed and received by these three that in period one BL and GI interacted a great deal with each other, with BL initiating most patterns. This relationship is reflected in the association dendrogram for period one, GI and BL exhibiting close proximity on a large proportion of scans (Figure 5.3.2.a). During period two GH affiliated himself with BL (exhibiting a great deal of Rub Heads) and she simultaneously interacted less with GI. The weakening of the GI-BL association is reflected in the proximity dendrogram for Period 2 compared to that of Period 1 - although GH himself rarely rested close to BL (Figure 5.3.2.b). At the same time GI emerged as a performer and GH a recipient of Stare (ST), suggesting some hostility between these two large males, possibly with respect to access to BL. This may explain why neither male rested close to BL for any length of time during this period. During period three GH became a very infrequent visitor to the site (possibly due to competition with GI) and GI and BL showed an increased level of close proximity

once more (Figure 5.3.2.c), although not to the same degree as in period one.

Possibly due to HO's aggression, close proximity between cats was generally weak during the apparently tense period 2, only the two young males DU and SI exhibiting some preference for resting together. During period three, although HO still exhibited a great deal of aggression, these two young males, SI and DU, and the female PE seemed to be less affected by her behaviour and had apparently formed an affiliative association between themselves. This involved tail-raised and rubbing behaviour patterns typical of the affiliative cluster in Figure 3.1.1 and was reflected by an association of these three cats on the cluster analysis of close proximity on scans (Figure 5.3.2.c). Though himself becoming more affiliative, the weaker of the two young males, SI, experienced little change in behaviours received from the other two, suggesting that PE and DU received most of this affiliative behaviour.

Throughout the study certain females seemed to remain much more aloof from the rest of the group, both behaviourally and by physically distancing themselves, thus maintaining a much more solitary way of life. DA was probably the most extreme example, rarely seen at first and never entering into interactions until the last period and even then at a rate too low to be analysed. GE, though present for a large percentage of the time, exhibited little tendency to rest with or associate with other cats. BE associated and interacted with others but showed a much more stable pattern of behaviour up to her disappearance at the end of Period 2. Finally, SM, the first female to disappear, seemed to be behaviourally very similar to BE at the start - whether their characters would have diverged in later periods had she survived can only be speculated on.

The Chilworth story is quite obviously not a simple one -the complexity of the changes in relations (and in some cases personality) suggests that the group was living as a social unit and not simply a structureless aggregation of cats around a food source. Whether these changes occurred as a result of neutering, the disappearance of certain individuals, the gradual habituation of the cats to humans or the new site, ageing of the animals or simply changing of the seasons, is impossible to decipher. Throughout the study the male GI appeared subjectively to be the dominant individual, mainly due to the large development of the head characteristic of intact males. Objectively, this may have been reflected in his low rate of initiating interactions in comparison to the number he received. He received a high rate of Affiliative and Approach/Sit categories of behaviour, although these fluctuated

during the study.

The first two periods (especially the second) showed evidence of competition between GI and the other large male GH, particularly with respect to the female BL. This conflict was a possible cause of the marked absence of GH for most of Period 3 of the study.

The increase in aggression observed in the female HO during the second period following the disappearance of SM is similar to that observed by Kerby (1987) in one of her females. She noted that this female became unusually aggressive following the death of her mother. It is possible therefore, that HO may have been closely related to SM and her increased aggression was a reaction to her disappearance.

Period 3 showed signs of a different form of sociality within the group, with both the number of interactions and the rate of interaction more dependent on the availability of pairs than previously.

Despite its complicated nature, this detailed analysis of the individual and dyadic relationships shows that, though it may have had an effect, neutering did not apparently destroy the sociality of these animals. It may have allowed and even encouraged affiliations between individuals that would never have associated amicably in an intact state e.g. the two males SI and DU.

5.4. Analysis of sex/class characteristics

In one of her study colonies, Kerby (1987) showed that cats which attended the core area frequently ("Central" animals) exhibited different proximity and interactive characteristics from those which attended the site less often ("Peripheral" cats). This was different for males and females. With a similar range of attendance at the site by the Chilworth cats it seemed logical to perform a similar investigation of the colony characteristics of this group.

Kerby divided males and females into the two categories based on whether they attended the core area of the site for more ("Central") or less ("Peripheral") time than the average for that sex. This was attempted for the Chilworth cats but produced unsatisfactory results, with small sample numbers in each category and many cats falling on the borderline between Central and Peripheral. A different method of analysis was therefore employed, maintaining the continuous scale of attendance and correlating this with the various interactive and proximity variables being considered.

The aim of the analysis was to test whether a neutered cat's role in this farm society was related to its sex, to the amount of time it spent in the core area and/or to the amount of time it spent in close proximity to others (i.e. to identify any characteristics typical of "Central" or "Peripheral" male and female cats). Characteristics considered were attendance at the site; proportion of time observed less than 1 metre from nearest neighbour; overall interaction rate; and ratio of initiated to received interactions.

All three periods were combined for analysis and, due to different levels of attendance and disappearance of certain individuals between periods, the attendance scores for each cat for each period were kept separate, suffixing the cats name code with the period number as appropriate. All cats were included except those present for less than one quarter of the total scans in each period since in these cases there was insufficient behavioural data to produce reliable rates or, for proximity data, reliable proportions. This eliminated DA from period 1 and GH from period 3, leaving 28 records of attendance and behaviour:
BE1,BL1,DU1,GE1,GH1,GI1,HO1,PE1,SI1,SM1,BE2,BL2,DA2,DU2,GE2,GH2,GI2 HO2,PE2,SI2,BL3,DA3,DU3,GE3,GI3,HO3,PE3,SI3.
Using the data in this way opens the analysis up to possible errors since each cat code is not strictly a replicate, cats appearing three times in some cases. However, since it seemed to be the only possible method of examining the study period as a whole, where significant effects were found a visual examination of the data concerned was carried out to ensure that it was not an effect produced by any one cat or period.

5.4.1. Attendance and proximity to others

An approximation of the time spent at the site was calculated for each cat for each period by multiplying the number of scans each cat was recorded as present by 15 minutes - this being the interval between the scans. This, termed the attendance score, assumes that if a cat was present at the site on a scan that it remained there for the next 15 minutes. This creates a possible overestimation of the amount of time animals actually spent at the site but such an overestimate would, if anything, tend to diminish differences in their attendance in the core area.

The resulting attendance scores were analysed by ANOVA on sex and period. No difference between sexes was found ($P=0.6696$) but there was a significant difference between periods ($P=0.0001$), attendance being higher in Periods 2 & 3

compared to Period 1 (Table 5.4.1.). Proximity scores were calculated for each cat by dividing the number of scans it was recorded < 1 m from one or more other cats (i.e. "close") by the total number of scans it was recorded present for each period. These were then analysed by ANOVA on sex and period. There is a significant difference between the sexes (P=0.0299) with females spending less time close to others than males (Table 5.4.1.). There is also a significant difference between the periods (P=0.001), with a higher level of close proximity in Period 1 compared to Periods 2 and 3.

Looking at proximity scores in more detail, as for the cluster analysis of associations, each possible dyad was given a proximity score for each period by calculating the number of scans they were observed close to each other by the number of scans they were both present in the core area and therefore available to sit close to each other. Each dyad was then classified as a male-male, male-female (or female-male, since no directional component is involved with proximity data) or female-female association. Proximity was then analysed by ANOVA on the above classification and by period. Period 1 showed a higher level of proximity than the later periods (P=0.009) but there was no significant difference between the three possible categories of association (P=0.2255), i.e. no tendency for either sex to sit with a cat of the same or different sex (Table 5.4.2).

A Spearman rank correlation was run on attendance vs. proximity scores for the whole colony over the three periods and then for the sexes separately (Table 5.4.3). The whole colony showed a negative correlation between presence in the core area and frequency of close proximity to others, driven by the males (i.e., males frequenting the site less often ("Peripherals") were more likely to sit close to another cat). Visual examination of the data suggested that this negative relationship was not being driven by any one individual but that it may have been due to the greater amount of proximity in relation to attendance in period 1. A similar plot of the whole colony supports this, suggesting that the cats were possibly more "friendly" in Period 1. This seems logical bearing in mind the high level of affiliative behaviours observed in Period 1.

Table 5.4.1. *Arithmetic means of variables analysed by ANOVA on sex and period. For each variable and for sex and period separately, means followed by the same letter are not significantly different at P=0.05 using transformed data.*

	MALES	FEMALES	Period 1	Period 2	Period 3
PRESENCE (hours)	11.6 a	12.1 a	6.3 a	13.6 b	17.0 b
PROXIMITY (proportion of scans present)	0.32 b	0.27 a	0.43 b	0.15 a	0.20 a
INTERACTION RATE (sequences/hr)	5.8 b	2.9 a	5.8 a	3.0 a	3.1 a
INITIATION RATE (sequences/hr)	3.2 a	1.4 a	3.1 a	1.6 a	1.5 a
PROPORTION OF SEQUENCES INITIATED	0.45 a	0.48 a	0.46 a	0.47 a	0.48 a

Table 5.4.2. *Arithmetic means of variables analysed by ANOVA on sex of partner. For each variable means followed by the same letter are not significantly different at P=0.05 using transformed data.*

	F-F	M-M	F-M or M-F	
PROXIMITY (scans < 1m as proportion of total possible)	0.05 a	0.08 a	0.07 a	
INTERACTION RATE (sequences/hr)	0.26 a	0.97 b	0.86 b	
	F-F	M-M	F-M	M-F
INITIATION RATE (sequences/hr)	0.13 a	0.48 b	0.40 b	0.46 b

Table 5.4.3. *Spearman Rank Correlation Coefficients (r) and corresponding significance levels (P) of variables tested against presence in the core area and close proximity to others.*

		PRESENCE		PROXIMITY	
		Corr. coeff.(r)	Sig. level (P)	Corr. coeff.(r)	Sig. level (P)
PROXIMITY	Colony	-0.386	0.045	-	-
	Males	-0.664	0.036	-	-
	Females	-0.216	0.387	-	-
INTERACTION RATE	Colony	-0.333	0.083	0.824	0.000
	Males	-0.736	0.020	0.773	0.015
	Females	0.012	0.961	0.799	0.001
INITIATION RATE	Colony	-0.1194	0.5349	0.4906	0.0108
	Males	-0.4556	0.1497	0.3508	0.2673
	Females	0.1229	0.6231	0.4828	0.0534
PROPORTION OF SEQUENCES INITIATED	Colony	-0.005	0.978	0.061	0.752
	Males	-0.255	0.421	0.136	0.666
	Females	0.243	0.331	-0.088	0.724

Table 5.4.4. *Spearman Rank Correlations for proportions of each behaviour pattern initiated/received compared to overall interactions initiated/received.*

Behaviour pattern	Correlation coefficient (r)	Significance level (P)
Cuff	0.0940	0.6666
Walk Past	0.2576	0.2378
Stare	-0.2685	0.2546
Tail-raised Walk Past	0.7283	0.0015
Approach, tail lowered	0.8704	0.0000
Move Away	-0.1271	0.5512
Sniff Cat	0.3700	0.0826
Sit With Cat	0.6136	0.0075
Rub Head Cat	0.6489	0.0047
Rub Flank Cat	0.4423	0.0606
Tail-raised Approach	0.0695	0.7503
Tail Up	0.5756	0.0069

5.4.2. Interactions

The rate at which each cat initiated interactions plus its overall interaction rate (based on number of interactions the cat was involved in regardless of initiator or recipient status) were calculated for each cat for each period. These rates were calculated according to the amount of time each cat was present in a period and therefore eliminated any trends due to different attendance by cats. Analysis of overall interaction rate by ANOVA on sex and period showed that females interacted at a lower rate than males (P=0.0114). There was also a suggestion of a higher interaction rate in Period 1 compared to Period 2 (Table 5.4.1). Initiation rates, however, showed no significant differences either between the sexes (P=0.5398) or between periods (P=0.5703).

To examine interaction rates in more detail, each dyad was given an interactivity rate score calculated by dividing the number of interactions performed between the two cats (regardless of initiator or recipient status) by the time they were present at the site together. This was analysed by ANOVA on the male-male male-female female-female classification mentioned above and by period. The earlier suggestion of a difference in interaction rate was not supported here (P=0.6674). There was, however, a significant difference between the possible categories of interaction (P=0.0035), with the female-female interaction rate being significantly lower than the male-female/female-male or male-male rates which were the same (Table 5.4.2).

In order to investigate the difference in interaction rates further, the rate at which cats *initiated* interactions to all possible partners was calculated. This introduced a directional component to the dyads, creating a division between male-female and female-male initiations in addition to the female-female and male-male categories.

This was analysed by ANOVA on the possible categories of partners and by period. No difference between periods was detected. There was a significant difference between the four possible categories of partner (P=0.0042), female-female initiations occurring at a significantly lower rate than female-male, male-female, and male-male initiations, there being no difference between these latter three categories. Thus females had a significant tendency not to interact with other females, whilst males showed no preference for males or females.

Spearman rank correlations were run on initiation rate and interaction rate

against attendance and proximity for the whole colony and for males and females separately - the results of these are shown in Table 5.4.3.

The colony showed a strong positive correlation between amount of time spent in close proximity to another cat and overall rate of interaction. Visual examination of the data suggests this to be a real effect significant in both sexes, although more so in the females. The colony also shows a weak negative association between time spent in the core area and rate of interaction. This is driven by this effect being highly significant in the males, but not evident at all in the females. Examination of the plot of this correlation suggests the effect may be due to a single male DU in period one showing a pattern not mirrored by any of the others. Hence this may not be a general effect.

Initiation rate shows a statistically significant correlation with close proximity to others and this seems to be driven by a weak effect in the females, not reflected by the males (Table 5.4.3). This weak effect appears to be due to differences between Period 1 compared to later periods and is probably not generalisable. There is no clear relationship between time present in the core area and rate of interaction initiation for either sex.

Having established that overall interaction rate differed according to proximity to other cats but that initiation rate probably did not, an examination of the relative contributions of initiated and received interactions to this overall rate was carried out.

The number of interactions initiated as a proportion of the total involving that cat was calculated for each period, and analysed by ANOVA on sex and period. As Table 5.4.1. illustrates, this revealed no significant differences between the sexes ($P=0.7843$) or between periods ($P=0.9927$), and no interaction between the two ($P=0.7770$).

Attendance and proximity were then correlated with the initiation proportions for the whole colony and for males and females separately, but showed no significant associations as shown in Table 5.4.3. Hence the amount of time both males and females spent in the core area or in close proximity to others had no relationship to the proportion of interactions they initiated or received.

5.4.3. The behaviour

a) Proportions of behaviour patterns initiated to received

This analysis was performed to see how, if at all, the overall flow of interactions related to the behaviour patterns used. As with the Knowle colony (section 4.7, Chapter 4), the proportion of each behaviour pattern initiated compared to that received by each cat was calculated. This was done for the 12 commonest behaviours (only those that occurred >20 times were included). These were then correlated with the overall proportion of interactions initiated compared to that received, calculated in the previous section. The results are shown in Table 5.4.4

As Table 5.4.4 shows, proportion of interactions initiated to received correlated significantly with the proportions initiated to received of two of the Approach/Sit category of behaviour patterns (Approach (tail lowered) and Sit With Cat), and, marginally with another pattern in this category, Sniff Cat. It also correlated significantly with three of the Affiliative category of behaviours (Rub Head Cat, Tail Up and Tail-raised Walk Past) and marginally with Rub Flank Cat, also in this category. Three of these correlations are the same as three of the four significant ones for the Knowle colony suggesting some common link between them. These were Approach (tail lowered), Rub Head Cat, and Sniff Cat. Interestingly, Tail-raised Approach, significantly correlated with initiated to received proportions at Knowle, showed no such association in this colony.

That the overall flow of interactions between cats was related to the flow of certain behaviours suggests that cats who were net recipients of interactions were also net recipients of particular behaviour patterns and these behaviours, along with overall initiation to receiving rates, may be indicators of status within the colony. Approach behaviours, with or without the tail raised might be expected to correlate with interaction initiating/receiving since most interactions are initiated by one of these patterns. It is interesting that cats receiving more interactions than they initiate are more likely to receive affiliative and approach/sit behaviours than those receiving less interactions.

Possibly dominant individuals were characterised by receiving more interactions

than they initiated and receiving more affiliative and approach/sit behaviour patterns from subordinate cats. These may represent appeasement behaviours from subordinate cats in a social structure where lower ranking individuals are not challenging the dominant cat for status. Through such behaviour, the social structure is maintained within the group without unnecessary levels of aggression.

b) Rates of behaviour patterns

Rates of performance of 12 of the commonest behaviours (only ones that occurred > 20 times in two or more periods) were calculated for each cat for each period. Since the analysis of quantity of interaction showed differences between males and females, it seemed quite possible that quality of interactions would show similar differences so males and females were investigated separately. Spearman rank correlation coefficients were calculated for the twelve behaviour rates versus attendance in the core area and proximity to others.

Those behaviours that correlated significantly with either attendance or proximity were then put into a partial correlation analysis in order to ascertain whether each correlation was independent or due to correlations between the behaviours themselves. Partial correlation analysis uses the parametric Pearson correlation method - a method not entirely suitable for this data as the plots of each behaviour against attendance revealed a non-normal distribution. For this reason, the behaviours to be put into partial correlation analysis were first ranked as with the Spearman method and a partial correlation carried out on the resulting ranks.

Females:

Attendance in the core area showed a significant positive correlation with the behaviour "Approach" ($P=0.02$) and a weaker one with "Sniff Cat" ($P=0.06$). Partial correlation on these behaviours with attendance showed the association to be more strongly due to Approach rather than to Sniff Cat. This effect was not due to any one individual in particular and was indeed a general trend. Thus females attending the core area more frequently showed a higher rate of Approach behaviour. Close proximity to others in the core area showed strong positive correlations with the all the tail-raised and rubbing behaviours (Tail-raised Walk Past, Tail-raised Approach, Tail-Up, Rub Heads, Rub Flanks) and also with Sit With (all $P<0.05$). Partial correlation analysis of these with proximity showed that, of the tail-raised and

rubbing behaviours, only Tail-raised Walk Past showed a real correlation with proximity, the others merely showing strong correlations amongst themselves, as previously shown by the cluster analysis of behaviour patterns (Figure 3.1.3). Sit With independently showed a strong correlation with close proximity, as might be expected.

Males:

With there being a possible negative correlation between attendance and proximity in the case of the males, these variables might be expected to exhibit opposite relationships with particular behaviours. This was the case with "Move Away" which was negatively correlated with attendance (P=0.06) and positively correlated with proximity (P=0.01). Also "Sniff Cat" exhibited the same pattern. Partial correlation of Move Away and Sniff Cat with both attendance and proximity showed Sniff Cat to be the stronger correlate with attendance and Move Away with proximity, the two behaviours themselves being strongly correlated as shown by the cluster analysis previously (Figure 3.1.3). This effect was not due to any one cat, suggesting that in general males attending the core area less frequently ("Peripherals") performed higher rate of sniffing other cats. Also males spending more time in close proximity to others performed a higher rate of Move Away. This latter effect may however be an artifact of the negative relationship between attendance and proximity.

5.4.4. Summary of colony characteristics

Most of the characteristics of the group concern differences between the sexes, suggesting that, despite being neutered, these cats were still aware of their own male/female status and were responding to this status in others.

Despite being present in the core area for the same amount of time overall as the males, females spent less of that time in close proximity to others. They interacted at a significantly lower overall rate and initiated interactions at a lower (though not significant) rate than males, but the proportion of interactions initiated by them was not significantly different from males. When they were involved in interactions, females interacted significantly more often with males than with other females. Similarly, females initiated significantly more interactions with males than with other females. This apparent tendency to avoid other females as interaction

partners was not reflected in the proximity data, there being no preference for sitting with either sex.

Males seemed to be generally less fussy about partners. They interacted at a higher rate than females but interactions involved male and female partners equally. They also initiated interactions equally to the same and the opposite sex. Males spent more time in close proximity to others than did females, although again they showed no tendency to be found close to one sex in particular.

Relationships between attendance and interaction variables which might have produced characteristics of "Central" or "Peripheral" cats appeared in many cases to be spurious ones based on differences between periods or to multiple inclusion of one individual. One relationship which does appear to be robust and also makes logical sense is the strong positive correlation between time spent in close proximity to other cats and overall interaction rate (i.e., the more time a cat spends in close proximity to others, the higher its interaction rate). This is apparent in both males and females, despite their other differences.

Analysis of the behaviour patterns revealed few associations of patterns with frequent or infrequent attendance of the core area. Females attending the core area more often generally showed a higher rate of Approach, and there was a suggestion that males attending less often performed a higher rate of investigatory sniffing of other cats. This lack of distinguishing behaviour patterns suggests that, contrary to the intact colony studied by Kerby (1987), "centrality" of individuals may be of less importance within the group in a neutered colony such as this.

What may be more significant in terms of neutered colony characteristics is the apparent different usage of behaviours by males and females. For example, females exhibited a strong positive association between use of affiliative behaviours and close proximity to others, whereas in a similar close proximity situation males apparently concentrated only on moving away. This does not necessarily mean that males and females were using different repertoires of behaviour but this is difficult to test in this group due to the complication of dividing the data into three periods. Males and females may well have been using the same proportions of behaviour in their repertoires, merely using them differently in different contexts (see Chapter 6, University colony, section 6.2.3.(4)).

5.5. Discussion

Of the three colonies studied, the one at Chilworth was the one observed closest to the time of neutering. This may account for the large fluctuations in the colony's behaviour recorded during the period of the study. This was in contrast to the unchanging levels of specific behaviour patterns seen in the Knowle colony which had been neutered several years prior to the study.

Sociality certainly existed but the basis of this appeared to change over the course of the study. At the start, pairs of cats present together for less time interacted at a higher rate than those together for longer, suggesting that interactions occurred more intensely between cats when one or both had been absent from the group for some time. Towards the end of the study this changed to a tendency for pairs together for more time to interact at a higher rate than those together for less time, possibly reflecting a tendency for individuals to be absent from the core area less or to interact with each other less on returning.

The group seemed dominated, although not actively so, by one male GI who was challenged by another, GH. Such a situation is typical between entire males within a breeding group of cats. That it was maintained for 8 months post neutering before GH became an infrequent attender of the core area suggests that neutering had not affected the competition between males at the top of the social hierarchy.

Within the rest of the group changes occurred over the study that may well have been ascribable to neutering. The gradual increase in aggressive behaviour by the female HO, for example, is not a feature typical of intact colonies -females are generally amicable amongst themselves (e.g. Dards, 1976; Kerby, 1987). Similarly the lack of aggression and development of a highly affiliative relationship between the young males SI and DU suggests that neutering had prevented the increase in aggression which generally occurs between intact juvenile males as they become adult and compete for dominance.

Unfortunately, so many variables changed within the colony at this time that neutering is only one explanation for the changes that occurred. Elimination of some of the possible alternative explanations, e.g., that behaviour changed according to the time of year, could only be achieved by studying a similar colony on a much longer term basis, and in particular, both before and after neutering.

Nevertheless, the study, not only revealed details of the social behaviour of

colony-living cats, but also showed that a social structure can be maintained within such a group after neutering. In addition, certain individuals (in particular males with strong dominant (e.g.,GI) or subordinate (e.g.,SI) characteristics), may retain their status within the group following neutering.

CHAPTER 6

The University Colony

Two of the University colony cats - SO performing "Sniff Rear" to OR.

CHAPTER 6 - THE UNIVERSITY COLONY

6.1. Pilot study results

The purpose of the pilot study was to determine the most objective method with which to observe this particular colony. Data was gathered to compare video and direct recording techniques. 25 hours of video were recorded and watched producing 205 interactions, whilst 272 interactions were recorded during the 14 hours of direct observation. This discrepancy in interactions per hour was due to the limited field of view of the camera, not to lower resolution of the video.

The overall totals of each behaviour pattern were calculated for the two sets of data (Table 6.1.1). Comparison of these totals by chi-squared analysis revealed a highly significant difference ($P<0.001$) between the results of the two methods. The highest contributions to chi-square came from behaviours involving a raised tail which had occurred less often during direct observation than during video observation. Aggressive behaviours, particularly Cuff and Ears Back, on the other hand, occurred *more* often when an observer was present.

To test this apparent trend further, the behavioural totals were classified into categories according to the cluster analysis of behaviours observed in the main study of this colony (Figure 3.1.3.). Table 6.1.2.shows the totals for each observation method. Chi-squared analysis of this table also showed a significant difference between methods ($P<0.001$). Breaking this down into 2X2 tables of each behaviour category versus the rest confirmed that the differences between observation methods occurred mainly with respect to Affiliative ($P<0.001$) and also with Aggressive patterns ($P<0.05$). The other five categories showed no significant differences between observation methods. Figure 6.1.1. illustrates the relative proportions of each behaviour category to the total number of behavioural events observed by the two methods.

Conclusions

The presence of an observer affected the behaviour of the cats significantly and suggested that video recording, although more time consuming, was a more objective method. In addition, the results revealed an indication of how cats reacted among themselves to the presence of a familiar human, (i.e., they became less affiliative and more aggressive towards each other). The effects of human behaviour on affiliative

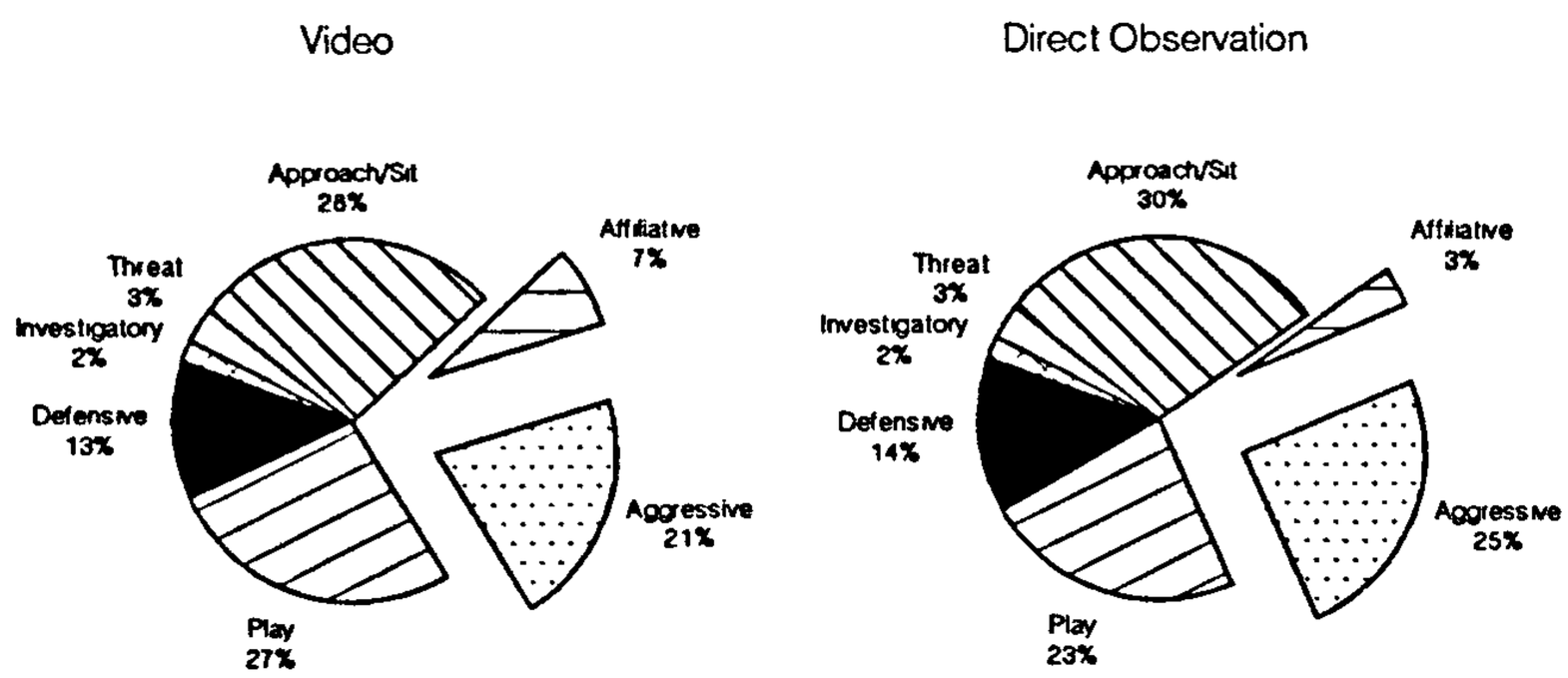
Table 6.1.1. *Totals of each behaviour pattern recorded from direct observation and from video recordings. Patterns totalling less than 10 observations omitted plus all vocalisations as rarely audible on video. Explanations of behaviour codes in Appendix 1.*

	VIDEO	WATCH	TOTAL
AP	77	113	190
TA	21	19	40
AR	68	107	175
TR	18	9	27
FO	9	7	16
TU	57	20	77
SN	45	73	118
SR	7	19	26
RH	6	8	14
RO	14	11	25
SW	10	24	34
WP	17	18	35
CU	28	72	100
RP	8	10	18
PA	11	11	22
PO	17	39	56
SK	2	9	11
GC	9	21	30
CH	69	84	153
AV	9	4	13
FL	107	133	240
CR	11	17	28
CT	25	45	70
BI	7	7	14
MA	85	145	230
TM	23	15	38
WA	39	50	89
ST	77	133	210
TS	21	18	39
TJ	5	5	10
EB	12	38	50
WC	16	31	47
FR	19	32	51
TN	10	30	40
TOTAL	959	1377	2336

Table 6.1.2. *Totals in each behaviour category observed by direct and video recorded methods of observation. Categories taken from cluster analysis (Figure 3.1.3.) of behaviours in main study.*

Category	Video	Direct Observation
Affiliative	60	46
Aggressive	180	338
Approach/Sit	236	406
Defensive	107	190
Play	228	317
Investigative	16	26
Threat	27	42
Total (N=2219)	854	1365

Figure 6.1.1. *Relative proportions of each behaviour category observed by direct observation and from video recordings. Segments cut out from charts indicate significant differences between the two methods.*



behaviour patterns were examined further in the experiments described in Chapter 7.

6.2 Main study results

A total of 157 hours of video tape was recorded and watched, from which 1066 interactions were observed and 628 scans were taken. From the scans an estimation of the amount of time spent by each cat in the field of view of the camera could be calculated, as with the Chilworth data, by multiplying the number of scans each cat was recorded as present by 15 minutes. This could not be interpreted as amount of time present in the core area since the animals had a restricted area over which they could range. The scan information was valuable however, for calculating how much time cats were available for interaction with each other on camera and therefore their rates of interaction, and the proportion of that time they were in close proximity to others. Two female cats, DO and AM, were omitted from the analysis since they appeared in the field of view of the camera for less than ten scans in total. This left 24 cats, 10 female and 14 male, for inclusion in the analysis.

Two valuable pieces of extra information were available for the colony. One was the family tree for all the cats illustrated in Chapter 2 (Figure 2.1.6). From this information an index of relatedness could be calculated for each pair of cats (Crow & Kimura, 1970). These indices are shown in Table 6.2.A. A one-way ANOVA was run on these relatedness scores to test whether male-male, male-female or female-female combinations showed different degrees of relatedness. There was no significant difference ($P=0.6904$).

The second piece of information was a complete veterinary record for each cat, giving details of its birth date and time of neutering. These birth dates and ages at neutering are shown in Table 6.2.B.

6.2.1. Tests for evidence of sociality within group

The first step in analysis as with the Knowle and Chilworth data, was to test the interactive data for evidence of sociality. This involved testing the data against a null hypothesis of a non-social system where, assuming individual variation in interactivity did not exist, the number of interactions between pairs of cats should have occurred in proportion to the amount of time they were available to interact with one another,

Table 6.2.A. Indices of relatedness between individuals in University colony

CAT	SEX	AD M	BO F	BR M	CE M	CL M	FA M	FL F	HE M	HN F	HT F	JA F	MI F	OD M	OR M	PA F	RO M	SM M	SO M	SP F	ST M	SY F	TI M	TW F	WA M
AD	M																								
BO	F	0.313																							
BR	M	0.313	0.500																						
CE	M	0.500	0.313	0.313																					
CL	M	0.500	0.313	0.313	0.500																				
FA	M	0.250	0.094	0.094	0.250	0.250																			
FL	F	0.078	0.094	0.094	0.078	0.078	0.419																		
HE	M	0.063	0.031	0.031	0.063	0.063	0.313	0.372																	
HN	F	0.266	0.281	0.281	0.266	0.266	0.016	0.016	0.062																
HT	F	0.500	0.313	0.313	0.500	0.500	0.250	0.078	0.063	0.266															
JA	F	0.294	0.031	0.031	0.294	0.294	0.294	0.385	0.369	0.060	0.294														
MI	F	0.078	0.094	0.094	0.078	0.078	0.328	0.507	0.281	0.016	0.078	0.294													
OD	M	0.078	0.078	0.078	0.078	0.078	0.063	0.063	0.000	0.047	0.078	0.000	0.063												
OR	M	0.281	0.266	0.266	0.281	0.281	0.063	0.063	0.124	0.297	0.281	0.120	0.063	0.156											
PA	F	0.078	0.078	0.078	0.078	0.078	0.063	0.063	0.000	0.047	0.078	0.000	0.063	0.500	0.156										
RO	M	0.063	0.031	0.031	0.063	0.063	0.313	0.372	0.559	0.062	0.063	0.369	0.281	0.000	0.124	0.000									
SM	M	0.281	0.250	0.250	0.281	0.281	0.094	0.122	0.155	0.297	0.281	0.151	0.216	0.156	0.313	0.156	0.155								
SO	M	0.328	0.313	0.313	0.328	0.328	0.109	0.250	0.063	0.266	0.328	0.044	0.171	0.078	0.281	0.078	0.063	0.313							
SP	F	0.294	0.031	0.031	0.294	0.294	0.294	0.385	0.369	0.060	0.294	0.625	0.294	0.000	0.120	0.000	0.369	0.151	0.044						
ST	M	0.266	0.281	0.281	0.266	0.266	0.016	0.016	0.062	0.500	0.266	0.060	0.016	0.047	0.297	0.047	0.062	0.297	0.266	0.060					
SY	F	0.156	0.141	0.141	0.156	0.156	0.156	0.156	0.093	0.047	0.156	0.088	0.156	0.125	0.109	0.125	0.093	0.063	0.156	0.088	0.047				
TI	M	0.266	0.281	0.281	0.266	0.266	0.016	0.016	0.062	0.500	0.266	0.060	0.016	0.047	0.297	0.047	0.062	0.297	0.266	0.060	0.500	0.047			
TW	F	0.078	0.094	0.094	0.078	0.078	0.328	0.507	0.281	0.016	0.078	0.294	0.632	0.063	0.063	0.063	0.281	0.216	0.171	0.294	0.016	0.156	0.016		
WA	M	0.078	0.078	0.078	0.078	0.078	0.063	0.063	0.000	0.047	0.078	0.000	0.063	0.500	0.156	0.500	0.000	0.156	0.078	0.000	0.047	0.125	0.047	0.063	

)

Table 6.2.B. *Sexes, dates of birth and ages at neutering of the 24 cats included in analysis of University colony. Males and females and the six younger cats listed separately.*

MALES			FEMALES		
Cat	Date of Birth	Age at Neutering (months)	Cat	Date of Birth	Age at Neutering (months)
AD	27/06/87	8.0	BO	11/06/87	24.75
BR	11/06/87	8.5	FL	28/06/87	24.25
CE	27/06/87	8.0	HT	27/06/87	24.25
CL	27/06/87	8.0	JA	13/06/87	24.75
FA	21/02/87	12.0	SY	17/06/87	24.25
HE	13/06/87	8.5	SP	13/06/87	24.75
OR	14/06/87	8.5	TW	02/07/87	24.0
RO	13/06/87	8.5	MI	02/07/87	24.0
SM	17/06/87	8.25			
WA	30/07/87	6.75			
OD	14/06/88	6.0	HN	26/05/88	13.25
SO	26/05/88	6.5	PA	14/06/88	12.75
ST	26/05/88	6.5			
TI	26/05/88	6.5			

and the *rate* of interaction should be independent of time available. Individual variation probably would exist, however, so any indicators of sociality may be due to this. Individual and dyadic characteristics were investigated separately (section 6.2.2).

276 possible dyads could occur from the 24 cats included in the data set for analysis. Of these, only 218 pairs actually interacted. Due to the large number of zero values in this data which would bias the statistical test, for this particular part of the analysis only those pairs of cats which actually interacted were included in the analysis.

Spearman Rank Correlations were performed on the time pairs were available for interaction on screen against the total number of interactions they performed and the corrected rate at which they interacted per hour available to interact. There was no correlation between the time they were available to interact and the overall number of interactions ($r=0.04$, $P=0.54$). There was, however, a significant *negative* correlation between the time they were available to interact and interaction *rate* ($r=-0.43$, $P<0.001$). Comparing these results with the predictions of the null hypothesis suggests that the flow of interactions within this group was not random and was greatly affected by the identity of the individuals. In addition to this there was a tendency for pairs that were available for interaction with each other for less time to interact at a significantly higher rate than those available for more time.

Having gained some evidence for sociality within the group a more detailed exploration of the data could be performed.

6.2.2. Individual and dyadic characteristics

With a large colony such as this, statistical analysis of individual characteristics, and/or relationships between each pair of cats would be difficult to interpret into a useful image of social relationships as has been attempted for the smaller Knowle and Chilworth colonies. Nevertheless, it seems inadequate to analyse and discuss characteristics of the group as a whole without first gaining some insight into the flow of interactions and types of behaviour between the individual members of the group. This section will therefore present the interactive and proximity results for individuals and dyads and discuss it simply by description of the data. This will hopefully reveal some of the more distinctive members of the group and help in subsequent interpretation of the colony's behaviour as a whole.

1. Proximity to others

Proximity scores were calculated for each possible pair of cats by dividing the number of scans they were observed less than one metre apart by the number of scans they were both visible on camera. These proximity scores are shown in Table 6.2.2.a. Average linkage cluster analysis was performed on the scores and the resulting dendrogram is shown in Figure 6.2.2.

The highest level of proximity occurred between two males FA and SM, spending just over 20% of time available together less than one metre apart. Neither of these individuals spent more than 10% of their time that close to any other cat (Table 6.2.2.a). The cat showing the highest overall level of proximity to other cats was OD, spending 36% of his time less than one metre away from one or more cats, and associating more than 10% of time available with PA, ST and TI. Similar levels of association occurred between all possible combinations of these four cats except TI and PA. All four of these cats were from the younger group introduced to the colony later than the original 20 members. Other associations occurring above the level of 10% of possible were between OR and ST, OR and CE, OR and BR, MI and HE, and SO and ST - not very many considering the number of possible combinations of cats. This may reflect the need for individuals to maintain their personal space in a confined environment such as this colony inhabited.

2. Interactions

Overall interaction rate between dyads, irrespective of direction has already been discussed in section 6.2. in relation to time available for interaction - interactions within the group appear to be socially structured.

Table 6.2.2.b. illustrates the rate at which each cat initiated interactions to each possible partner, thus introducing the directional information of the overall interaction rate of dyads.

The highest initiator of interactions was the male SM, followed by the males OD, ST and RO. The highest recipient of interactions was the male TI, followed by the male FA. Another way of looking at this information is to calculate the proportion of initiated to received sequences for each cat (shown in column on far right). The male OD had the highest proportion of initiated to received interactions and the female FL the lowest.

Table 6.2.2.a. Number of scans that pairs of cats were less than one metre apart as a proportion of the total scans on which they were both present

		AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA
CAT	SEX	M	F	M	M	M	M	F	M	F	F	F	F	M	M	F	M	M	M	F	M	F	M	F	M
AD	M	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BO	F	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BR	M	0.00	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CE	M	0.02	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CL	M	0.05	0.00	0.03	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FA	M	0.02	0.00	0.03	0.05	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FL	F	0.04	0.00	0.04	0.00	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HE	M	0.02	0.00	0.04	0.00	0.07	0.03	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HN	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HT	F	0.00	0.02	0.04	0.01	0.04	0.06	0.00	0.03	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JA	F	0.03	0.04	0.00	0.05	0.02	0.03	0.02	0.00	0.00	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MI	F	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.06	-	-	-	-	-	-	-	-	-	-	-	-	-
OD	M	0.00	0.00	0.09	0.07	0.00	0.04	0.09	0.07	0.07	0.02	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-
OR	M	0.03	0.00	0.12	0.11	0.07	0.05	0.03	0.03	0.00	0.04	0.00	0.00	0.10	-	-	-	-	-	-	-	-	-	-	-
PA	F	0.06	0.00	0.03	0.00	0.07	0.06	0.02	0.02	0.00	0.04	0.05	0.00	0.13	0.06	-	-	-	-	-	-	-	-	-	-
RO	M	0.00	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.00	0.02	0.00	0.05	0.04	0.00	0.03	-	-	-	-	-	-	-	-	-
SM	M	0.00	0.00	0.05	0.00	0.08	0.21	0.05	0.05	0.00	0.02	0.00	0.00	0.09	0.10	0.10	0.03	-	-	-	-	-	-	-	-
SO	M	0.03	0.00	0.04	0.06	0.00	0.00	0.00	0.03	0.05	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.06	-	-	-	-	-	-	-
SP	F	0.00	0.00	0.04	0.03	0.03	0.04	0.00	0.08	0.03	0.00	0.03	0.00	0.10	0.00	0.04	0.00	0.07	0.00	-	-	-	-	-	-
ST	M	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.09	0.00	0.00	0.00	0.00	0.13	0.14	0.13	0.00	0.04	0.15	0.06	-	-	-	-	-
SY	F	0.00	0.03	0.04	0.00	0.00	0.04	0.00	0.01	0.02	0.04	0.02	0.00	0.02	0.05	0.07	0.02	0.01	0.00	0.08	0.00	-	-	-	-
TI	M	0.03	0.00	0.06	0.00	0.10	0.04	0.02	0.05	0.00	0.08	0.00	0.00	0.13	0.10	0.08	0.00	0.00	0.09	0.00	0.14	0.07	-	-	-
TW	F	0.00	0.08	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.03	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.03	0.06	-	-
WA	M	0.00	0.00	0.07	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.03	0.00	0.00	-
OVERALL		0.09	0.07	0.24	0.09	0.17	0.22	0.12	0.21	0.05	0.14	0.09	0.09	0.36	0.31	0.32	0.07	0.29	0.15	0.17	0.25	0.15	0.26	0.11	0.05

Figure 6.2.2. *Dendrogram of average linkage cluster analysis of associations between cats in University colony, based on proportion of time available that cats were observed less than one metre apart.*

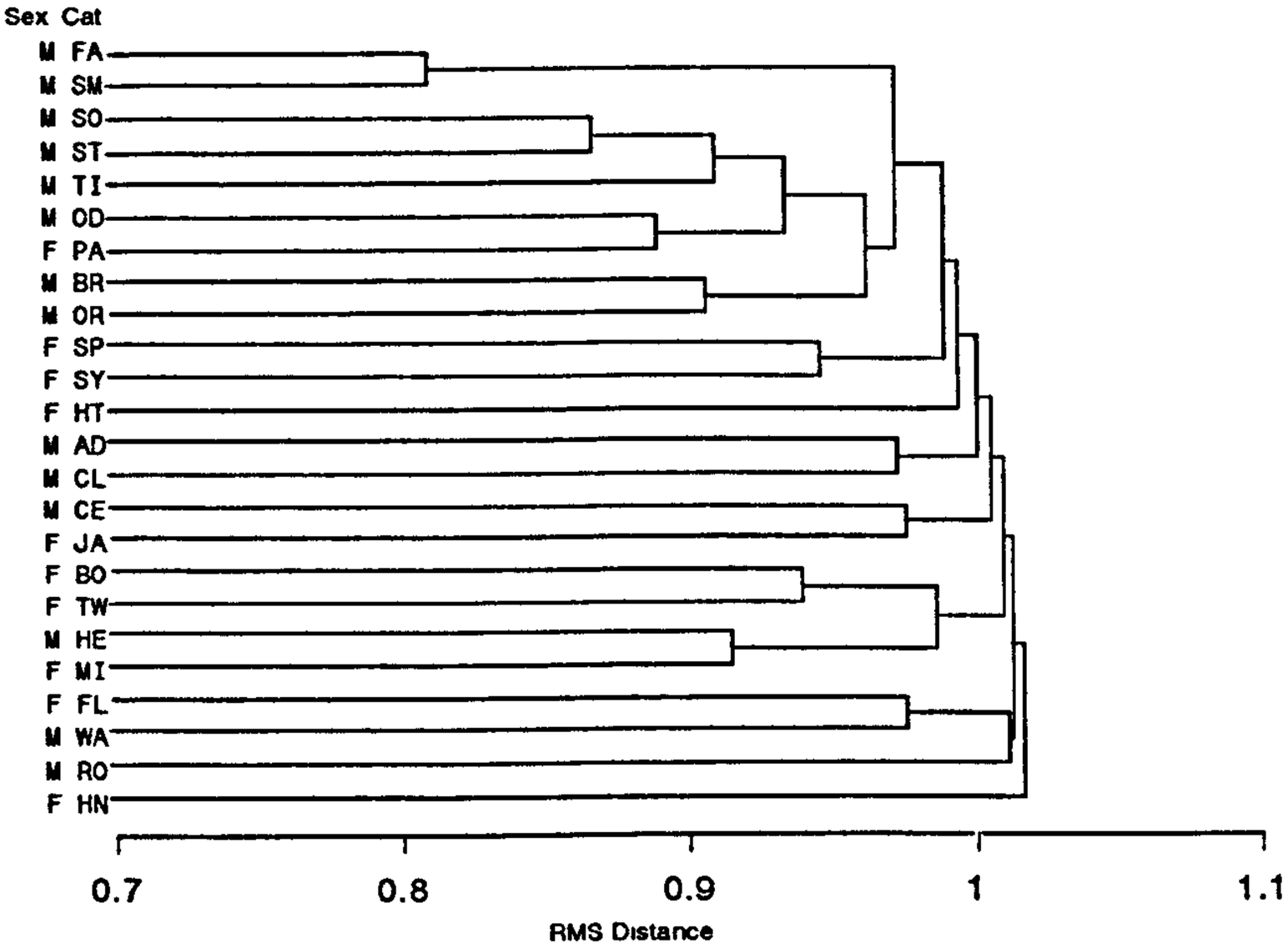


Table 6.2.2.b. Rate (per hour) at which each cat initiated interactions to every other cat - corrected for time pairs were available for interaction

		CAT																									
		AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA	INIT	PROPORTION
CAT	SEX	M	F	M	M	M	M	F	M	F	F	F	F	M	M	F	M	M	M	F	M	F	M	F	M	RATE	INIT/REC
AD	M		0.00	0.00	0.06	0.00	0.09	0.08	0.08	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.07	0.34	0.00	0.00	0.00	0.82	0.00	0.00	0.47	0.35
BO	F	0.12		0.15	0.34	0.00	0.00	0.00	0.00	0.44	0.08	0.35	0.00	0.14	0.00	0.13	0.00	0.11	0.22	0.17	0.00	0.22	0.15	0.00	0.00	0.85	0.31
BR	M	0.10	0.77		0.00	0.00	0.26	0.00	0.26	0.48	0.00	0.00	0.00	0.11	0.15	0.23	0.00	0.10	0.35	0.29	0.00	0.16	0.13	0.00	0.27	1.13	0.67
CE	M	0.19	0.23	0.21		0.16	0.51	0.08	0.19	0.10	0.16	0.10	0.31	0.09	0.14	0.13	2.56	0.24	0.11	0.10	0.36	0.05	0.51	0.21	0.00	1.67	0.65
CL	M	0.90	0.46	0.11	0.16		0.33	0.10	0.09	0.10	0.16	0.17	0.00	0.00	0.14	0.00	0.12	0.65	0.28	0.26	0.00	0.00	0.29	0.00	0.00	1.27	0.73
FA	M	0.17	0.00	0.00	0.00	0.22		0.00	0.11	0.00	0.07	0.00	0.00	1.04	0.19	0.80	0.00	0.65	0.32	0.30	0.22	0.17	1.23	1.87	0.00	1.61	0.35
FL	F	0.00	0.00	0.00	0.00	0.00	0.00		0.26	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.13
HE	M	0.00	0.29	0.00	0.09	0.00	0.21	0.17		0.23	0.10	0.00	0.71	0.10	0.00	0.08	0.16	0.07	0.00	0.31	0.00	0.00	0.50	0.00	0.00	0.76	0.48
HN	F	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.14	0.00	0.12	0.00	0.12	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.19	0.17
HT	F	0.00	0.08	0.00	0.05	0.05	0.07	0.00	0.05	0.00		0.00	0.00	0.00	0.00	0.00	0.09	0.05	0.00	0.00	0.00	0.08	0.00	0.12	0.00	0.23	0.33
JA	F	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00		0.25	0.00	0.00	0.00	0.25	0.00	0.00	0.24	0.24	0.00	0.00	0.31	0.00	0.34	0.36
MI	F	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.33	0.00	0.00	0.20	0.00	0.35	0.00	0.00	0.00	1.47	0.33	0.00	0.63	0.33
OD	M	0.09	0.43	0.11	0.36	0.37	0.87	0.26	0.10	0.14	0.13	0.11	0.67		0.13	1.33	0.32	1.67	2.26	0.00	2.25	0.08	2.40	0.00	0.00	3.61	0.77
OR	M	0.00	1.03	0.00	0.14	0.00	0.19	0.22	0.00	0.20	0.00	0.15	0.00	0.00		0.00	0.00	0.14	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.77	0.34
PA	F	0.00	0.00	0.00	0.13	0.10	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.36	0.13		0.55	0.08	0.12	0.00	0.25	0.00	0.00	0.44	0.00	0.58	0.23
RO	M	0.00	1.33	0.19	0.24	0.24	0.43	0.24	0.48	0.16	0.36	0.50	0.20	0.48	4.89	0.83		0.75	1.25	1.80	0.92	0.29	2.40	0.44	0.92	3.42	0.58
SM	M	0.00	0.00	0.20	0.72	0.00	5.12	0.27	0.07	0.00	0.00	0.29	0.64	0.19	1.38	0.16	0.88		2.67	0.09	1.08	0.12	1.06	0.17	0.00	3.74	0.66
SO	M	0.00	0.22	0.17	0.11	0.41	0.00	0.00	0.00	0.55	0.20	0.00	0.00	0.52	0.00	0.73	0.25	0.61		0.15	0.62	0.00	6.43	0.36	0.00	2.60	0.50
SP	F	0.00	0.33	0.43	0.40	0.13	0.44	0.10	0.00	0.24	0.00	0.36	0.20	0.00	0.22	0.00	0.60	0.28	0.00		0.44	0.21	0.00	0.94	0.00	1.20	0.51
ST	M	0.64	1.33	0.00	0.00	0.00	0.44	0.33	0.35	0.67	0.14	0.00	1.20	0.50	0.29	1.75	1.23	1.08	1.85	0.00		0.42	1.27	0.50	0.00	3.58	0.61
SY	F	0.00	0.22	0.00	0.05	0.14	0.08	0.00	0.17	0.09	0.04	0.00	0.00	0.00	0.20	0.35	0.38	0.12	0.11	0.10	0.21		0.09	0.00	0.00	0.58	0.50
TI	M	0.82	0.15	0.00	0.72	0.00	1.23	0.49	0.30	0.47	0.24	0.29	0.00	0.70	0.39	0.72	0.57	0.82	0.52	0.59	1.27	0.18		0.00	0.50	2.71	0.39
TW	F	0.00	0.67	0.40	0.21	0.00	0.00	0.33	0.19	0.22	0.12	0.00	1.67	0.19	0.00	0.67	0.89	0.00	1.09	0.71	0.50	0.00	1.25		0.00	1.81	0.60
WA	M	0.31	0.00	0.27	0.22	0.00	0.19	0.19	0.00	0.22	0.20	0.16	0.57	0.00	0.00	0.17	0.00	0.00	0.00	0.60	0.00	0.00	0.17	0.00		0.78	0.70
REC RATE		0.86	1.93	0.57	0.90	0.48	3.05	0.68	0.81	0.91	0.48	0.60	1.27	1.10	1.49	2.00	2.47	1.93	2.64	1.17	2.33	0.58	4.24	1.21	0.34		

Within the matrix a number of strong asymmetries in initiation rates within pairs of cats can be seen. The strongest of these are between the males SO and TI initiating to each other at 6.43 and 0.52 interactions per hour present respectively; the males SM and FA at 5.12 and 0.65 initiations/hr; and RO and OR, also males, at 4.89 and 0 initiations/hr respectively.

3. The behaviour

Although useful as a guide to where the strongest relationships existed, interaction and initiation rates give no indication of the nature of the different relationships between pairs of cats (i.e., what types of behaviour are used between particular dyads). Due to the larger number of behaviour patterns observed in this colony in comparison with the previous two, it seemed appropriate to look at the categories of behaviour used, rather than individual patterns as in the other colonies. Behaviour patterns were therefore combined, as for the pilot study, into seven categories (Aggressive, Threat, Defence, Play, Affiliative, Approach/Sit, Investigative), according to the cluster analysis of interactions (Figure 3.1.3).

Having grouped the behaviours in this way, there were two alternative ways of using the data. One method would be to score each category of behaviour only once in an interaction, regardless of how many behaviour patterns the interaction contained representative of that category. This would avoid possible overemphasis on categories containing the most behaviour patterns. The alternative would be to count all occurrences of behaviour patterns in an interaction as single representatives of categories, so that a behaviour category could be represented many times within an interaction. This retains some information on the intensity of a particular category of behaviour within an interaction and was therefore chosen as the most appropriate method of utilising the data.

To see how the flow of different behavioural types related to the overall flow of sequence initiations, Spearman Rank Correlations were run on the proportion of each behaviour category initiated to received for each cat, compared with the proportions of sequences initiated to received. The correlation coefficients and significance levels are shown in Table 6.2.2.c.

Perhaps the most notable feature of this analysis for comparison with the other two colonies is the significant positive correlation of initiated to received interactions with initiated to received aggression and its lack of any association with affiliative

Table 6.2.2.c. *Spearman Rank Correlation Coefficients between proportion of sequences initiated to received and proportions of each behaviour category initiated to received for each cat.*

	Proportion of interactions initiated to received	
	Correlation coefficient (r)	Significance level (P)
Aggresssive	0.46	0.03
Threat	-0.34	0.10
Defence	-0.48	0.02
Play	0.63	0.002
Affiliative	0.11	0.62
Approach/Sit	0.65	0.002
Investigative	0.72	0.001

ratios (i.e., the complete opposite to associations with equivalent behaviours tested for the Knowle and Chilworth colonies). In both these cases, CU, one of the few representative Aggressive behaviours showed no relationship with initiated to received interaction ratios whereas Head Rubbing, one of the strongest representatives of Affiliative behaviours, correlated positively with initiated to received interactions.

Tables 6.2.2.d-j illustrate the rates at which each cat performed each of the seven behaviour categories to each possible partner. Table 6.2.2.k shows the proportion of the overall behaviour category totals for the whole colony performed and received by each cat. A closer examination of these tables helps explain the social dynamics of the University colony.

i) Aggression (Table 6.2.2.d)

As Table 6.2.2.k shows, the male TI both performed and received the highest proportions of the colony's aggressive behaviour patterns. OD and RO, both males, were also high performers of aggression (each contributing over 10% of the total aggression observed), whilst OD and the male SO each received over 10% of the total aggression.

Aggression between these four cats was high except between RO/OD and RO/SO where it was very low in both directions. The most aggressive pair was TI/SO with TI performing more. TI/RO were also highly aggressive with RO being the more aggressive partner. OD/TI had a strong but roughly reciprocal aggressive relationship. The other combination of OD/SO showed approximately equal aggression to each other, although one third less than OD/TI.

Examination of Table 6.2.2.d. shows that high levels of aggression also occurred between the following pairs of cats: RO/OR, RO/PA, RO/ST, TI/MI, TI/ST, OD/ST, OD/SM, SO/SM, FA/SM and ST/PA (irrespective of direction). Within all these pairs asymmetry existed in the amount of aggression performed by each individual. It is perhaps not coincidental that of the 9 cats mentioned, five out of the six younger cats, introduced to the group at a later stage, were high aggressors.

A valuable additional if somewhat anecdotal piece of information regarding aggression in the group was provided when trying to scruff each animal for vaccination by the veterinarian. All cats were approached and scruffed in the same way and responded with varying degrees of aggression towards the handler.

Table 6.2.2.d. Rate per hour at which each cat performed aggressive behaviour patterns towards each other cat - corrected for time pairs were available for interaction

		AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA	INIT
	SEX	M	F	M	M	M	M	F	M	F	F	F	F	M	M	F	M	M	M	F	M	F	M	F	M	RATE
AD	M		0.00	0.00	0.71	0.14	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.69	0.00	1.28	0.00	2.05	0.00	0.15	1.16
BO	F	0.00		0.92	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.14	0.39	0.00	0.53	0.00	0.00	0.00	0.44	0.22	0.00	0.33	0.00	0.80
BR	M	0.00	1.23		0.00	0.33	0.00	0.00	0.00	1.28	0.00	0.00	0.00	0.11	0.00	0.00	0.19	0.00	0.87	0.14	0.00	0.00	0.13	0.00	0.27	1.17
CE	M	0.26	0.00	0.00		0.16	0.00	0.08	0.00	0.10	0.16	0.19	0.00	0.36	0.00	0.00	0.32	0.24	0.11	0.00	0.18	0.00	1.13	0.00	0.00	0.83
CL	M	0.21	0.31	0.33	0.16		0.22	0.00	0.00	0.00	0.43	0.00	0.00	0.09	0.00	0.00	0.24	0.16	0.55	0.13	0.00	0.07	0.00	0.00	0.00	0.82
FA	M	0.00	0.00	0.00	0.00	0.33		0.00	0.11	0.00	0.00	0.00	0.00	0.87	0.00	0.11	0.57	4.09	0.00	0.15	0.67	0.25	2.31	0.27	0.00	2.66
FL	F	0.00	0.00	0.00	0.00	0.00	0.00		0.09	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.20	0.00	0.00	0.20
HE	M	0.08	0.14	0.00	0.00	0.00	0.00	0.09		0.00	0.05	0.00	0.71	0.00	0.00	2.00	0.16	0.00	0.00	0.41	0.00	0.00	1.00	0.00	0.00	1.30
HN	F	0.36	0.22	1.28	0.10	0.00	0.00	0.00	0.11		0.00	0.00	0.00	0.29	0.00	0.00	0.32	0.00	0.36	0.24	0.33	0.00	0.00	0.00	0.22	0.85
HT	F	0.00	0.00	0.00	0.26	0.38	0.00	0.05	0.05	0.00		0.00	0.00	0.19	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.47	0.20	0.65
JA	F	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00		0.25	0.00	0.00	0.00	0.63	0.00	0.00	0.24	0.00	0.00	0.20	0.00	0.00	0.37
MI	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.00	0.00	0.00		0.33	0.00	0.00	0.00	0.16	0.17	2.00	0.00	0.00	6.74	1.00	0.00	2.59
OD	M	0.09	0.57	0.11	0.36	0.09	1.22	0.17	0.00	0.57	0.13	0.00	0.67		0.00	2.31	0.64	5.30	6.61	0.00	5.75	0.00	9.50	0.19	0.00	8.81
OR	M	0.00	0.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	6.67	0.28	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.98
PA	F	0.00	0.00	0.11	0.00	0.00	0.34	0.00	1.83	0.00	0.00	0.00	0.00	2.04	0.00		4.83	0.08	0.85	0.00	7.50	0.61	0.92	0.44	0.00	4.37
RO	M	0.23	1.60	0.19	0.24	0.12	0.71	0.00	0.00	0.48	0.44	0.50	0.20	0.48	12.00	6.48		3.00	0.50	1.00	6.15	0.29	10.86	1.33	0.31	8.85
SM	M	0.00	0.00	0.00	0.16	0.24	4.84	0.00	0.00	0.00	0.00	0.10	0.00	5.02	0.28	0.08	2.50		4.61	0.19	1.69	0.17	0.94	0.00	0.00	5.18
SO	M	0.46	0.00	0.70	0.00	0.28	0.00	0.00	0.00	0.36	0.00	0.00	0.00	6.26	0.00	0.61	0.25	3.76		0.15	2.46	0.00	15.83	1.09	0.00	7.30
SP	F	0.00	0.17	0.29	0.20	0.26	0.00	0.29	0.21	0.35	0.00	0.12	2.00	0.00	0.00	0.00	1.40	0.47	0.46		0.89	0.10	0.89	0.71	0.40	1.90
ST	M	1.76	0.44	0.00	0.00	0.00	0.89	0.00	0.00	0.33	0.00	0.00	0.40	6.50	0.00	9.75	4.31	1.38	2.15	1.11		0.00	3.82	0.00	0.00	8.48
SY	F	0.00	0.11	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.29	0.12	0.00	0.00	0.00		0.62	0.00	0.00	0.49
TI	M	1.13	0.00	0.26	1.13	0.00	2.15	0.00	0.50	0.12	0.00	0.20	5.05	9.30	0.00	1.33	6.97	1.18	20.00	0.44	4.36	0.44		0.00	0.00	11.74
TW	F	0.00	1.00	0.00	0.00	0.00	0.27	0.17	0.00	0.00	0.47	0.00	1.67	0.00	0.00	0.44	0.89	0.17	1.45	0.47	0.00	0.00	0.25		0.00	1.70
WA	M	0.46	0.00	0.27	0.22	0.00	0.00	0.00	0.00	0.22	0.10	0.00	1.14	0.00	0.00	0.00	0.31	0.00	0.00	0.20	0.00	0.00	0.17	0.00		0.59
REC RATE		1.00	1.55	1.17	0.94	0.69	2.95	0.23	1.00	0.85	0.56	0.31	2.59	8.32	1.36	5.23	6.34	5.05	9.05	1.40	8.12	0.56	12.56	1.37	0.39	

Table 6.2.2.e. Rate per hour at which each cat performed threat behaviour patterns towards each other cat - corrected for time pairs were available for interaction

		AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA	INIT
	SEX	M	F	M	M	M	M	F	M	F	F	F	F	M	M	F	M	M	M	F	M	F	M	F	M	RATE
AD	M		0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.05
BO	F	0.00		0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
BR	M	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.04
CE	M	0.00	0.00	0.00		0.08	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
CL	M	0.00	0.00	0.00	0.08		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.05
FA	M	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.10
FL	F	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.03
HE	M	0.00	0.00	0.00	0.00	0.00	0.00	0.09		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.17	0.00	0.00	0.00	0.00	0.08
HN	F	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.00	0.13
HT	F	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
JA	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.15	0.00	0.13	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.09
MI	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.00	0.00	0.00	0.33	0.00	0.24
OD	M	0.00	0.00	0.11	0.09	0.09	0.17	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.09	0.17	0.00	0.00	0.00	0.30	0.00	0.00	0.29
OR	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.13	0.00	0.00	0.09
PA	F	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00		0.14	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.18
RO	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.16	0.89	0.00		0.00	0.00	0.00	0.00	0.10	0.11	0.00	0.00	0.20
SM	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
SO	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.12		0.00	0.00	0.00	0.70	0.00	0.00	0.27
SP	F	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.12	0.00	0.12	0.60	0.00	0.00	0.00	0.40	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.30
ST	M	0.16	0.00	0.00	0.18	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00		0.00	0.18	0.00	0.00	0.42
SY	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.02
TI	M	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.30	0.00	0.00	0.00	0.12	1.04	0.00	0.18	0.00		0.00	0.00	0.38
TW	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.00		0.00	0.05
WA	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00		0.10
REC RATE		0.02	0.00	0.11	0.09	0.11	0.13	0.05	0.05	0.06	0.02	0.06	0.20	0.26	0.13	0.06	0.27	0.16	0.31	0.37	0.36	0.04	0.35	0.22	0.00	

Table 6.2.2.f. Rate per hour at which each cat performed defence behaviour patterns towards each other cat - corrected for time pairs were available for interaction

		AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA	INIT
	SEX	M	F	M	M	M	M	F	M	F	F	F	F	M	M	F	M	M	M	F	M	F	M	F	M	RATE
AD	M		0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.10	0.00	0.15	0.09
BO	F	0.00		0.62	0.00	0.15	0.00	0.00	0.29	0.00	0.08	0.00	0.29	0.29	0.90	0.00	0.80	0.00	0.00	0.17	0.89	0.11	0.00	0.33	0.00	1.22
BR	M	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.10	0.35	0.14	0.00	0.00	0.00	0.00	0.00	0.23
CE	M	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.72	0.08	0.11	0.20	0.36	0.00	0.21	0.00	0.00	0.43
CL	M	0.07	0.00	0.00	0.00		0.11	0.00	0.00	0.00	0.11	0.00	0.00	0.28	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24
FA	M	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.37	0.16	0.30	0.00	0.08	0.62	1.07	0.19	0.62
FL	F	0.00	0.00	0.00	0.08	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.19	0.10
HE	M	0.08	0.00	0.17	0.09	0.00	0.11	0.00		0.11	0.05	0.10	0.14	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27
HN	F	0.00	0.00	0.80	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.40	0.00	0.32	0.12	0.18	0.00	0.67	0.00	0.47	0.44	0.00	0.66
HT	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
JA	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.11	0.15	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.14
MI	F	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.57	0.00	0.00	0.00		1.00	0.00	0.00	0.20	0.32	0.35	0.40	1.20	0.00	0.21	1.67	0.57	1.22
OD	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33		0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.13
OR	M	0.00	0.13	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.13		0.26	4.89	0.69	0.00	0.22	0.57	0.29	0.13	0.00	0.00	1.28
PA	F	0.00	0.00	0.11	0.13	0.00	0.11	0.00	0.17	0.00	0.00	0.00	0.00	0.36	0.00		0.55	0.08	0.12	0.00	1.25	0.00	0.10	0.22	0.00	0.68
RO	M	0.00	0.27	0.00	0.00	0.00	0.14	0.00	0.16	0.00	0.27	0.25	0.00	0.16	0.44	0.55		0.13	0.00	0.60	0.00	0.38	0.11	0.44	0.00	0.81
SM	M	0.00	0.00	0.10	0.40	0.49	2.33	0.07	0.21	0.00	0.00	0.10	0.16	1.30	0.41	0.24	0.63		1.45	0.37	0.77	0.00	0.94	0.17	0.00	2.59
SO	M	0.11	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	2.09	0.00	0.00	0.50	1.09		0.00	0.31	0.00	2.61	0.73	0.00	1.71
SP	F	0.00	0.00	0.14	0.20	0.00	0.15	0.00	0.31	0.12	0.00	0.48	0.60	0.00	0.00	0.00	0.80	0.19	0.00		0.00	0.21	0.30	1.18	0.40	1.07
ST	M	0.16	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.40	2.00	0.00	0.00	1.23	0.62	0.00	0.00		0.00	0.91	0.00	0.00	1.73
SY	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00		0.09	0.00	0.00	0.06
TI	M	0.00	0.00	0.13	0.31	0.00	0.77	0.10	0.50	0.00	0.00	0.00	0.84	1.50	0.00	0.10	1.71	0.47	2.09	0.30	0.55	0.00		1.00	0.33	2.29
TW	F	0.00	0.33	0.00	0.00	0.00	1.07	0.00	0.00	0.22	0.00	0.62	0.00	0.19	0.00	0.44	0.89	0.00	0.00	0.47	0.00	0.00	0.50		0.00	0.99
WA	M	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00		0.15
REC RATE		0.09	0.14	0.64	0.39	0.21	1.28	0.05	0.57	0.13	0.18	0.37	0.63	2.32	0.60	0.43	2.17	1.02	1.28	0.70	1.85	0.24	1.53	1.64	0.39	

Table 6.2.2.g. Rate per hour at which cat performed play behaviour patterns towards each other cat - corrected for time pairs were available for interaction

		AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA	INIT
	SEX	M	F	M	M	M	M	F	M	F	F	F	F	M	M	F	M	M	M	F	M	F	M	F	M	RATE
AD	M		0.00	0.00	0.13	0.07	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.48	0.00	0.51	0.00	0.00	0.33
BO	F	0.00		0.00	0.00	0.00	0.00	0.00	0.14	0.22	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.44	0.11	0.00	0.00	0.00	0.28
BR	M	0.00	0.77		0.00	0.11	0.00	0.00	0.17	0.16	0.00	0.00	0.00	0.00	0.00	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60
CE	M	0.06	0.00	0.00		0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.56	0.08	0.00	0.00	0.55	0.00	0.31	0.00	0.00	0.43
CL	M	0.28	0.31	0.00	0.00		0.33	0.00	0.00	0.10	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42
FA	M	0.00	0.00	0.00	0.00	0.11		0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.46	0.29	1.77	0.00	0.59	0.00	0.00	1.38	3.73	0.00	1.80
FL	F	0.00	0.00	0.00	0.00	0.00	0.00		0.17	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.13
HE	M	0.00	1.00	0.09	0.09	0.00	0.42	0.34		0.00	0.15	0.00	0.86	0.10	0.00	0.00	0.48	0.14	0.00	0.31	0.17	0.00	0.50	0.00	0.00	1.11
HN	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.22	0.13
HT	F	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.05	0.00		0.00	0.00	0.00	0.00	0.00	0.18	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22
JA	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00		0.25	0.00	0.30	0.00	0.50	0.00	0.00	1.09	0.24	0.00	0.00	0.31	0.00	0.60
MI	F	0.00	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.63	0.67	0.00	0.49
OD	M	0.00	0.43	0.00	0.36	0.47	1.39	0.26	0.00	0.14	0.00	0.00	0.67		0.39	1.60	0.48	1.21	1.91	0.00	1.00	0.00	2.90	0.00	0.00	3.48
OR	M	0.00	1.81	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.30	0.00	0.00		0.00	0.89	0.41	0.00	0.00	0.00	0.20	0.26	0.00	0.00	1.15
PA	F	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.50	0.00	0.00	0.00	0.00	1.33	0.13		1.79	0.24	0.00	0.00	1.25	0.52	0.51	0.44	0.00	1.78
RO	M	0.00	1.33	0.00	0.08	0.00	0.57	0.00	0.16	0.32	0.09	0.13	0.00	0.00	5.33	0.69		1.13	0.25	0.60	1.23	0.29	2.86	0.00	0.00	2.61
SM	M	0.00	0.00	0.10	0.56	0.08	5.95	0.07	0.07	0.00	0.00	0.19	0.64	0.65	1.66	0.16	0.75		1.70	0.28	1.38	0.00	0.94	0.00	0.00	3.82
SO	M	0.00	0.00	0.52	0.00	0.14	0.00	0.00	0.00	0.18	0.00	0.00	0.00	1.91	0.00	0.36	0.00	0.24		0.00	0.31	0.00	4.52	0.36	0.00	1.94
SP	F	0.00	0.17	0.43	0.70	0.00	0.44	0.29	0.00	0.35	0.00	0.61	0.00	0.00	0.44	0.00	1.40	0.56	0.00		0.22	0.10	0.44	2.59	0.20	1.90
ST	M	0.48	2.22	0.00	0.00	0.00	0.44	0.00	0.17	1.33	0.00	0.00	0.80	0.75	0.57	2.50	0.92	0.46	0.92	0.00		0.00	2.73	0.50	0.00	3.76
SY	F	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.17	0.29	0.12	0.00	0.31	0.00		0.09	0.00	0.00	0.28
TI	M	0.62	0.00	0.00	0.10	0.10	1.54	0.10	0.10	0.47	0.00	0.10	0.63	2.10	0.13	0.62	1.71	0.94	4.00	0.44	1.64	0.00		0.25	0.00	3.41
TW	F	0.00	0.33	0.00	0.00	0.00	0.53	0.50	0.00	0.22	0.00	0.00	2.00	0.00	0.00	0.44	0.00	0.00	0.36	1.18	0.50	0.00	1.75		0.00	1.86
WA	M	0.15	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.17	0.00		0.29
REC RATE		0.35	2.12	0.30	0.60	0.29	3.38	0.38	0.54	0.79	0.13	0.34	1.22	2.03	1.74	1.75	2.41	1.99	2.14	1.23	2.93	0.30	4.35	1.86	0.10	

Table 6.2.2.h. Rate per hour at which each cat performed affiliative behaviour patterns towards each other cat - corrected for time pairs were available for interaction

CAT	SEX	AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA	INIT RATE
AD	M		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.02
BO	F	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BR	M	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CE	M	0.00	0.11	0.00		0.00	0.51	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.43	0.00	3.12	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	1.11
CL	M	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FA	M	0.17	0.00	0.00	0.00	0.00		0.00	0.21	0.00	0.15	0.00	0.00	1.39	0.38	1.26	0.00	1.86	0.16	0.00	0.22	0.08	1.54	0.00	0.00	1.97
FL	F	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HE	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HN	F	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.06
HT	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
JA	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MI	F	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.29	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.16	0.35	0.00	0.00	0.00	0.63	0.00	0.00	0.44
OD	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OR	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PA	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00		0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.12
RO	M	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.13	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.10
SM	M	0.00	0.00	0.00	0.40	0.08	13.49	0.41	0.00	0.00	0.00	0.00	0.48	0.37	2.48	0.08	1.75		4.00	0.00	0.92	0.35	2.12	0.00	0.00	6.80
SO	M	0.00	0.00	0.00	0.11	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	1.21		0.00	0.31	0.00	0.17	0.00	0.00	0.62
SP	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00		0.00	0.00	0.00	0.24	0.00	0.07
ST	M	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.17	0.14	0.00	0.00	0.00	0.00	1.00	0.62	1.23	0.92	0.00		0.42	0.36	1.00	0.00	1.61
SY	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00		0.09	0.00	0.00	0.04
TI	M	0.00	0.00	0.00	0.31	0.00	1.23	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.57	0.00	0.52	0.00	0.55	0.09		0.50	0.00	0.88
TW	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.25		0.00	0.11
WA	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00
REC RATE		0.05	0.05	0.04	0.24	0.11	5.18	0.20	0.14	0.06	0.05	0.00	0.15	0.61	0.98	0.52	2.14	1.05	1.63	0.03	0.78	0.24	1.12	0.27	0.00	

Table 6.2.2.i. Rate per hour at which each cat performed approach/sit behaviour patterns towards each other cat - corrected for time pairs were available for interaction

		AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA	INIT
	SEX	M	F	M	M	M	M	F	M	F	F	F	F	M	M	F	M	M	M	F	M	F	M	F	M	RATE
AD	M		0.00	0.10	0.19	0.28	0.26	0.24	0.00	0.24	0.00	0.00	0.00	0.09	0.00	0.00	0.57	0.20	0.57	0.00	0.16	0.00	1.44	0.00	0.15	1.07
BO	F	0.35		0.62	1.26	0.15	0.00	0.00	0.00	0.67	0.24	1.04	0.00	0.43	0.00	0.50	0.27	0.32	0.89	0.67	0.00	0.65	0.46	0.00	0.00	2.78
BR	M	0.20	0.77		0.21	0.00	0.65	0.00	0.35	0.48	0.00	0.00	0.00	0.23	0.31	0.23	0.19	0.39	0.35	1.14	0.00	0.55	0.26	0.00	0.00	1.96
CE	M	0.32	0.57	0.72		0.33	0.92	0.08	0.37	0.29	0.37	0.10	0.92	0.18	0.00	0.26	2.72	0.64	0.00	0.30	0.73	0.47	1.33	0.21	0.00	2.87
CL	M	2.76	1.08	0.00	0.57		0.56	0.30	0.19	0.10	0.32	0.34	0.00	0.19	0.14	0.10	0.24	1.39	0.97	0.65	0.00	0.07	0.76	0.00	0.00	3.15
FA	M	0.43	0.00	0.13	0.31	0.44		0.00	0.11	0.00	0.00	0.00	0.00	2.09	0.19	0.91	0.00	3.91	0.32	0.89	0.67	0.83	1.85	1.33	0.00	3.77
FL	F	0.00	0.00	0.00	0.00	0.00	0.00		0.77	0.00	0.21	0.00	0.00	0.17	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.50
HE	M	0.00	0.00	0.09	0.09	0.00	0.32	0.68		0.34	0.21	0.00	0.57	0.29	0.00	0.42	0.48	0.07	0.00	0.62	0.17	0.06	1.30	0.19	0.00	1.57
HN	F	0.00	0.22	0.48	0.00	0.00	0.00	0.00	0.11		0.00	0.00	0.00	0.14	0.00	0.48	0.00	0.35	0.55	0.00	0.00	0.09	0.12	0.00	0.00	0.57
HT	F	0.00	0.16	0.00	0.26	0.22	0.59	0.00	0.21	0.00		0.00	0.00	0.06	0.00	0.00	0.18	0.19	0.00	0.00	0.14	0.45	0.00	0.24	0.00	0.81
JA	F	0.63	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00		0.25	0.00	0.00	0.00	0.50	0.00	0.00	0.12	0.00	0.00	0.29	0.00	0.16	0.54
MI	F	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.14	0.00	0.00	0.25		1.00	0.00	0.00	0.60	0.48	0.35	1.00	0.00	0.00	5.47	0.00	0.00	2.20
OD	M	0.09	0.14	0.34	0.44	0.28	1.22	0.17	0.19	0.14	0.06	0.11	0.33		0.00	2.76	0.96	2.60	3.13	0.00	4.25	0.24	4.00	0.00	0.00	5.52
OR	M	0.00	1.29	0.15	0.57	0.00	0.76	0.33	0.00	0.00	0.00	0.15	0.00	0.00		0.00	2.22	1.79	0.00	0.00	0.00	0.88	0.13	0.00	0.00	2.17
PA	F	0.00	0.00	0.00	0.26	0.29	0.23	0.00	0.50	0.24	0.00	0.00	0.00	0.71	0.00		0.41	0.00	0.61	0.00	0.75	0.26	0.21	0.44	0.17	1.32
RO	M	0.23	1.60	0.38	2.64	0.73	0.57	0.71	0.96	0.00	0.36	1.38	0.40	1.28	6.67	2.34		1.63	3.00	4.80	2.15	0.95	7.43	0.00	2.46	8.95
SM	M	0.00	0.00	0.29	1.36	0.24	8.28	0.27	0.00	0.00	0.00	0.67	0.64	0.65	1.38	0.16	1.13		1.58	0.09	1.38	0.23	1.76	0.00	0.00	5.20
SO	M	0.23	0.89	0.87	0.22	1.10	0.16	0.00	0.00	1.27	0.30	0.00	0.00	2.26	0.00	2.55	1.25	3.39		0.31	2.77	0.11	17.74	2.18	0.00	8.50
SP	F	0.00	0.67	0.57	0.30	0.52	1.04	0.10	0.31	0.35	0.00	0.36	0.00	0.00	0.00	0.00	1.40	0.09	0.00		1.56	0.31	0.15	0.71	0.60	1.97
ST	M	1.60	1.78	0.00	0.00	0.00	1.11	0.83	1.04	0.00	0.29	0.00	2.00	1.75	0.29	2.00	1.85	2.92	3.38	0.44		1.47	3.64	0.50	0.00	7.28
SY	F	0.00	0.65	0.00	0.21	0.43	0.25	0.00	0.46	0.09	0.16	0.00	0.00	0.00	0.68	1.30	0.67	0.23	0.32	0.10	0.84		0.09	0.00	0.00	1.58
TI	M	2.36	0.15	0.00	2.05	0.29	3.69	1.56	0.30	0.24	0.73	0.39	1.05	2.10	0.77	1.74	2.17	2.00	5.22	0.89	2.73	0.44		0.25	1.33	7.56
TW	F	0.00	0.67	1.20	0.42	0.00	1.60	0.50	0.57	0.00	0.24	0.00	1.00	0.57	0.00	1.33	1.78	0.00	2.55	0.24	0.50	0.00	0.75		0.00	2.74
WA	M	0.31	0.00	1.07	0.44	0.00	0.19	0.38	0.00	0.22	0.30	0.16	0.00	0.00	0.00	0.33	0.92	0.00	0.00	1.40	0.00	0.00	0.17	0.00		1.41
REC RATE		2.35	2.73	1.66	2.80	1.46	6.10	1.43	1.70	1.01	0.95	1.16	1.56	3.19	1.91	4.55	4.47	5.52	4.85	2.73	4.96	2.07	10.32	1.42	1.07	

Table 6.2.2.j. Rate per hour at which each cat performed investigative behaviour patterns towards each other cat - corrected for time pairs were available for interaction

		AD	BO	BR	CE	CL	FA	FL	HE	HN	HT	JA	MI	OD	OR	PA	RO	SM	SO	SP	ST	SY	TI	TW	WA	INIT
	SEX	M	F	M	M	M	M	F	M	F	F	F	F	M	M	F	M	M	M	F	M	F	M	F	M	RATE
AD	M		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.46	0.00	0.00	0.00	0.10	0.00	0.00	0.16
BO	F	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
BR	M	0.00	0.15		0.00	0.00	0.00	0.00	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30
CE	M	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.31	0.00	0.00	0.00	0.72	0.00	0.00	0.00	0.00	0.00	0.31	0.21	0.00	0.36
CL	M	0.07	0.00	0.00	0.00		0.00	0.00	0.09	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
FA	M	0.00	0.00	0.00	0.00	0.11		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.27	0.00	0.10
FL	F	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HE	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
HN	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HT	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
JA	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
MI	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.05
OD	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.14	0.00	0.00	0.00		0.00	0.09	0.00	0.28	1.22	0.00	0.50	0.00	0.00	0.00	0.00	0.48
OR	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PA	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RO	M	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.16	1.78	0.00		0.75	0.25	1.20	0.00	0.00	0.91	0.00	0.00	1.02
SM	M	0.00	0.00	0.00	0.08	0.00	0.28	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.12	0.00	0.15	0.00	0.00	0.00	0.00	0.18
SO	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.12	0.25	0.85		0.00	0.00	0.00	1.91	0.00	0.00	0.82
SP	F	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.22	0.00	0.00	0.00	0.00	0.10
ST	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.29	0.50	0.92	0.15	0.92	0.00		0.00	0.18	0.00	0.00	0.72
SY	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00		0.09	0.00	0.00	0.06
TI	M	0.10	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.10	0.00	0.12	0.35	0.15	0.00	0.09		0.00	0.00	0.35
TW	F	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.50	0.00	0.00		0.00	0.22
WA	M	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00		0.10
REC RATE		0.05	0.05	0.08	0.11	0.03	0.10	0.03	0.08	0.28	0.04	0.03	0.10	0.10	0.21	0.25	0.51	0.47	0.70	0.30	0.30	0.02	0.79	0.11	0.00	

Table 6.2.2.k. - Number of behaviour patterns performed and received by each cat in each category as a proportion of the colony total.

Behaviours performed

Cat	Sex	Defence	Aggr	App/Sit	Affil	Play	Threat	Invest
AD	M	0.01	0.02	0.02	0.00	0.01	0.02	0.05
BO	F	0.05	0.01	0.03	0.00	0.01	0.02	0.01
BR	M	0.01	0.01	0.02	0.00	0.02	0.01	0.05
CE	M	0.04	0.02	0.06	0.11	0.02	0.04	0.11
CL	M	0.02	0.01	0.05	0.00	0.02	0.02	0.02
FA	M	0.04	0.04	0.05	0.13	0.06	0.04	0.02
FL	F	0.01	0.00	0.01	0.00	0.01	0.01	0.00
HE	M	0.02	0.02	0.02	0.00	0.04	0.02	0.01
HN	F	0.04	0.01	0.01	0.00	0.00	0.04	0.00
HT	F	0.00	0.02	0.02	0.00	0.01	0.01	0.01
JA	F	0.01	0.01	0.01	0.00	0.02	0.02	0.01
MI	F	0.05	0.02	0.02	0.02	0.01	0.04	0.01
OD	M	0.01	0.13	0.08	0.00	0.11	0.09	0.10
OR	M	0.06	0.01	0.02	0.00	0.03	0.02	0.00
PA	F	0.04	0.07	0.02	0.01	0.06	0.07	0.00
RO	M	0.04	0.12	0.12	0.01	0.08	0.07	0.20
SM	M	0.18	0.09	0.09	0.55	0.15	0.01	0.05
SO	M	0.08	0.09	0.10	0.03	0.05	0.09	0.14
SP	F	0.06	0.03	0.03	0.01	0.06	0.05	0.02
ST	M	0.05	0.07	0.05	0.06	0.06	0.09	0.08
SY	F	0.01	0.01	0.03	0.00	0.01	0.01	0.02
TI	M	0.15	0.18	0.11	0.07	0.12	0.15	0.08
TW	F	0.03	0.01	0.02	0.00	0.03	0.01	0.03
WA	M	0.01	0.01	0.01	0.00	0.01	0.02	0.01

Behaviours received

	Sex	Defence	Aggr	App/Sit	Affil	Play	Threat	Invest
AD	M	0.01	0.02	0.05	0.00	0.02	0.01	0.01
BO	F	0.01	0.02	0.03	0.00	0.05	0.00	0.01
BR	M	0.03	0.01	0.02	0.00	0.01	0.04	0.01
CE	M	0.03	0.02	0.05	0.02	0.03	0.04	0.03
CL	M	0.01	0.01	0.02	0.01	0.01	0.05	0.01
FA	M	0.07	0.04	0.08	0.34	0.11	0.05	0.02
FL	F	0.00	0.00	0.03	0.02	0.02	0.02	0.01
HE	M	0.04	0.02	0.03	0.01	0.02	0.01	0.02
HN	F	0.01	0.01	0.01	0.00	0.03	0.01	0.06
HT	F	0.02	0.01	0.02	0.01	0.01	0.01	0.01
JA	F	0.02	0.01	0.02	0.00	0.01	0.01	0.01
MI	F	0.02	0.02	0.01	0.01	0.03	0.02	0.01
OD	M	0.13	0.12	0.05	0.04	0.07	0.07	0.02
OR	M	0.03	0.01	0.02	0.05	0.04	0.04	0.03
PA	F	0.03	0.08	0.07	0.04	0.06	0.02	0.06
RO	M	0.12	0.09	0.05	0.13	0.07	0.09	0.10
SM	M	0.07	0.09	0.09	0.08	0.08	0.07	0.13
SO	M	0.06	0.11	0.05	0.09	0.06	0.09	0.13
SP	F	0.04	0.02	0.04	0.00	0.04	0.07	0.06
ST	M	0.06	0.06	0.04	0.03	0.05	0.07	0.03
SY	F	0.02	0.01	0.04	0.02	0.01	0.02	0.01
TI	M	0.10	0.20	0.16	0.08	0.15	0.13	0.19
TW	F	0.06	0.01	0.01	0.01	0.04	0.05	0.01
WA	M	0.01	0.00	0.01	0.00	0.00	0.00	0.00

However, when the oldest male FA was scruffed, and he yowled as did many of the others, a large-scale fight broke out instantly amongst all the other colony members. It appeared that each cat literally turned to its nearest neighbour at that moment and began to fight. The fighting calmed down after approximately five minutes and a very tense, cautious atmosphere remained amongst the cats for the rest of the day. This phenomenon was repeated on two other occasions when FA had to be scruffed. It was noted, although only subjectively, that the male OD was the first to respond to the distress noise of FA by becoming extremely aggressive. He tried to direct this aggression towards FA himself but was prevented from so doing by human intervention.

ii) Threat (Table 6.2.2.e)

Occurring at a very low rate throughout the colony, this was probably a precursor for aggression, as illustrated by its relatively high rate between TI and SO. Such low rates make interpretation much more speculative, so this will not be attempted.

iii) Defence (Table 6.2.2.f)

This gives some insight into which partner in the aggressive pairs of cats showed the most defensive behaviours and was therefore possibly at a disadvantage, even if aggression was also displayed. The highest rate of defence was shown towards OD and, to a slightly lesser extent, towards RO. Neither of these showed unusually high rates of defence. TI, the highest aggressor, showed a much higher rate of defence towards both OD and RO than vice versa, and slightly less defence towards SO than vice versa. The male OR showed a high rate of defence against RO, and SM was relatively highly defensive towards FA.

iv) Play (Table 6.2.2.g)

A generally widespread but low rate behaviour category, performed at the highest rate by the males SM, ST, OD and TI. The highest dyadic rate was between SO and TI, a roughly reciprocal relationship. Two strongly asymmetrical relationships were SM towards FA and RO towards OR, both male pairs. High rates of play also occurred within the male pairs TI/OD, TI/RO, and TI/ST. Some of the female-female relationships (e.g., SP/TW, MI/TW), had an above average play

component, as did some of the female-male pairs (e.g., BO/ST, PA/ST, TW/FA).

v) Affiliative (Table 6.2.2.h)

Affiliative behaviour occurred at a very low rate in the colony, never featuring at all in 160 of the 218 pairs of cats that actually interacted, i.e., 73 % of dyads that interacted never used any affiliative behaviour towards one another. Probably the most notable feature of this category is its intense use by one particular male cat, SM, with 55 % of all affiliative behaviour observed within the colony performed by him (Table 6.2.2.k). 33 % of all affiliative behaviour was received by the male FA (Table 6.2.2.k) and as Table 6.2.2.h shows, most of this came from SM with a strongly asymmetric 13.5 affiliative behaviours/hour present from SM to FA compared with 1.86/hr in reverse. SM did not restrict his affiliative behaviour to FA, showing what were, in comparison with the rest of the colony, relatively high rates to others including SO, OR, TI and RO, notably all males and all involved in high rates of aggressive behaviour. None of them reciprocated SM's affiliative behaviour at such a high level, and, in the case of OR and TI, not at all. The only other notably high incidence of affiliative behaviour was between the two males CE and RO (3.12 reciprocated by 0.08 affiliative behaviours per hour present respectively).

vi) Approach/Sit (Table 6.2.2.i)

The highest rate of this category occurred between the two males SO and TI with SO performing such behaviours at over three times the rate at which TI reciprocated. This probably reflects the high rate of sequence initiation by SO to TI, beginning with a tail lowered approach. Such initiations probably then led on to aggression (see section 3.2, Chapter 3).

With a much larger spread throughout the colony, strong flows between particular pairs are less apparent. The females seem to have performed these behaviours at a higher rate than other categories, indicating a tendency towards sitting and grooming behaviours.

vii) Investigative behaviour (Table 6.2.2.j)

Occurring at a generally low rate throughout the colony, where this did occur at a higher rate, it seemed to be strongly asymmetrical, indicating a strong investigative interest by one interaction partner in the other. Such relationships were shown by SO

towards TI, by RO towards OR, OD towards SO, and, a previously unmentioned pair, RO towards the female SP.

4. Summary of individual and dyadic characteristics

Examination of the rate at which individuals initiated interactions towards each other revealed four males, SM, OD, ST and RO, who initiated interactions at a substantially higher rate than others. The male TI received interactions at a higher rate than any other and, to a lesser extent, so did FA. The proportion of initiated to received interactions showed a significant positive correlation with the proportions initiated to received of Aggressive, Approach/Sit, Investigatory and Play categories of behaviour. There was a significant negative association with Defensive behaviours and no association at all with Threat and Affiliative behaviours. This was notably different to the Knowle and Chilworth colonies where some affiliative elements e.g. Head Rubbing correlated positively with sequences initiated to received and aggressive elements such as Cuff correlated negatively.

Interactions within the colony involved mainly the high initiating and receiving male cats mentioned above, TI, FA, SM, OD, ST, and RO, and also the males SO and OR and the female PA. Amongst themselves, these nine cats accounted for 42% of the colony's interactions.

Within this group aggressive behaviour dominated the interactions. The highest concentration of aggression was between the three young males TI, OD, and SO. Aggression was high between the older males RO and OR, between RO and the younger male TI and between RO and the younger female PA. Interestingly aggression did not occur at a high rate between RO and the two aggressive young males OD and SO, or between OR and any other cat. The young male ST was also quite highly aggressive, particularly towards the young female PA.

Aggression at a fairly high level occurred on an equal basis between the older males SM and FA. This relationship was dominated, however, by the high rate of affiliative behaviour shown by SM towards FA, reflected in the high frequency of close proximity observed between these two cats (Figure 6.2.2.). SM also displayed affiliative behaviour at an above average level towards SO, OR, TI, and RO - four of the aggressive cats. These reciprocated at a much reduced level, if at all. OD, the other young, highly aggressive male received little affiliative behaviour from SM and showed a higher level of aggression towards him than did other cats.

Defensive behaviour was concentrated amongst the same group of aggressive cats with the young male OD and older male RO receiving most defence.

5. Discussion of individual and dyadic characteristics

A colony of this size (26), composed of approximately equal numbers of males and females of roughly the same age and living in a confined environment, is evidently quite far removed from the free-living farm cat situation described by previous authors (e.g. Kerby 1987). There, societies are centred around groups of interrelated breeding females, one or two older males dominate the breeding and other younger males either disperse or maintain a low profile until old and strong enough to challenge the breeder(s).

The situation for the females of the University colony, apart from the obvious missing component of communal rearing and nursing of kittens, is not that different to the farm situation in terms of mutual co-operation and sharing of limited space and resources. It is interesting, however, to see what occurs in a situation where the males are all of approximately the same age and breeding status (i.e., neutered). The most obvious representation of this is the fact that of the colony's interactions 57% occurred between males, 37% between males and females and only 6% between females, suggesting a much more intense form of interaction between males. Looking at the interactions and their behavioural content as a whole in relation to the personal details of the cats involved suggests a possible structure within the colony. This is only really possible amongst the most intensely interacting members of the group of cats mentioned above, i.e., TI, OD, SO, RO, OR, FA, and SM.

The male FA, as shown in Table 6.2.B, was approximately four months older than the rest of the original male members of the colony and was therefore one year old when neutered. His head, as a result, had a much larger, rounder shape, characteristic of intact tom cats, than the other males. This combined with the complete upheaval that occurred amongst the others when he was scruffed by a human, as described in section 6.2.2.(i), suggests that he might well have been the dominant male cat of the colony. This was certainly the subjective impression gained from spending many hours with the group. Although much less aggressive than some of the other males, he nevertheless appeared to have a special status within the group, highlighted by the attentions of his persistent companion, SM.

For a period of about one month, approximately one year before the

observation began, FA appeared to lose his status within the group and this role was taken over by the male OR. This cat, previously spending most of his time sleeping in a box, became far more outgoing, was approached more and yet received little aggression. FA regained his former status after this one month period. Although purely a subjective impression, this observation may help explain the aggression shown by the male RO towards OR during the study period if RO regarded OR as possible competition for dominance.

A possible hypothesis to explain the interactions is that during the study period, FA was the dominant male, his status established and, at that particular time, unchallenged by any of the others. Around FA the remaining six males mentioned may have been competing for superiority amongst themselves. Three of these, TI, SO and OD, were from the younger group of cats, introduced at a later stage to the colony. This may have been a disadvantage to them and made them more competitive and aggressive in order to gain status.

Of the older males, RO was strongly aggressive towards OR (who he may have regarded as a threat previously) and also towards the young male TI. This suggests that, of the three young aggressors, TI may have been the most important for RO to defeat in that RO was not involved in fights with the other two.

Apart from SM who had a unique relationship with FA, TI and OD were the only two cats to have above average levels of aggression with FA. TI/FA was roughly symmetrical, with FA slightly more aggressive. OD, however, was more aggressive towards FA than vice versa, suggesting that he might have been the most likely challenge to FA's dominance. This is supported by the fact that, when FA was scruffed by a person, OD took the opportunity to attempt an attack on FA in his defenceless state (see section 6.2.2.i).

OD was also the highest recipient of defence behaviour and this was asymmetrical in his favour with all possible partners, again highlighting his very aggressive and competitive nature. RO also received high levels of defence behaviour, mainly from OR who he seemed to pursue relentlessly, but also from TI who he challenged frequently and from whom he also received more aggression than he gave. TI and RO therefore were possibly quite evenly matched in terms of status. SO, although a very persistent interactor and aggressor towards TI, received more aggression and less defence in response, and was therefore probably challenging TI rather than vice versa.

If, as suggested, OR had become dominant some time earlier in the history of the colony, the three younger males, TI, OD, and SO may have been less aware or affected by it - this would explain the lack of contact or animosity shown by them towards OR during this study, in contrast to RO.

The competitive part of the colony's structure may therefore have comprised FA as the most dominant male, followed by OD then RO and TI and then SO. OR, as a previously dominant male, may have presented a threat to some of the older members of the group, e.g., RO and SM. SM, apparently the only strongly affiliative member of the colony, may have been a very subordinate cat, and directed his affiliative, possibly appeasement behaviour towards key cats within the colony, i.e., mainly FA, but also TI, RO, SO and OR. His notable lack of affiliation and high aggression with OD probably reflects the reluctance of OD to develop amicable relations with any male.

The rest of the colony exhibited some special relationships based, for example, on play e.g., the female pairs SP/TW and MI/TW, or on aggression e.g, the male-female pair ST/PA. No clear order or competitiveness was evident suggesting that, apart from the males competing for dominance, the rest of the colony had an established and accepted, but unfortunately undetectable, social structure.

6.2.3. Analysis of sex/class characteristics

Having identified some of the more distinctive individuals and relationships within this colony, it is possible to move on and look at some of the more general features of the group as a whole with which to compare it with the other colonies studied.

1. Proximity to others

Proximity scores were calculated for each cat by dividing the number of scans in which it was recorded less than one metre away from one or more cats by the total number of scans it was recorded as present. A one-way ANOVA was then performed on these proximity scores by sex. Although not highly significant ($P=0.0717$), there was a suggestion that there may have been a difference between the sexes, with males spending more time in close proximity to others than females (see Table 6.2.3.a).

Looking at the data in more detail, proximity scores were calculated for each

Table 6.2.3.a. *Arithmetic means of variables analysed by one-way ANOVA on sex. For each variable means followed by the same letter are not significantly different at P=0.05 using transformed data*

	MALES		FEMALES
PROXIMITY (proportion of scans present)	0.16 a		0.11 a
INTERACTION RATE (sequences/hr)	3.67 b		1.73 a
INITIATION RATE (sequences/hr)	2.01 b		0.65 a
PROPORTION OF SEQUENCES INITIATED	0.55 b		0.35 a

Table 6.2.3.b. *Arithmetic means of variables analysed by ANOVA on sex of partner. For each variable means followed by the same letter are not significantly different at P=0.05 using transformed data*

	F-F		M-M		F-M or M-F
PROXIMITY (scans < 1m as proportion of total possible)	0.02 a		0.04 b		0.02 a
INTERACTION RATE (sequences/hr)	0.25 a		0.89 c		0.38 b

	F-F		M-M		F-M		M-F
INITIATION RATE (sequences/hr)	0.13 a		0.44 b		0.12 a		0.26 b

possible pair of cats by dividing the number of scans they were observed less than one metre apart by the number of scans they were both visible on camera. This information is shown in section 6.2.2., Table 6.2.2.b. Each dyad was then classified as a male-male, male-female (or female-male, since no directional component is involved with proximity data) or female-female association. A one-way ANOVA was then carried out on proximity by this sex class categorisation. This showed there to be a significant difference between categories (P=0.0017) with male-male associations occurring significantly more often than male-female and female-female associations between which there was no significant difference (see Table 6.2.3.b).

The higher degree of proximity between males than between females or males and females is illustrated in the dendrogram drawn from the cluster analysis of these associations (Figure 6.2.2, section 6.2.2.). Male clusters are concentrated at the top of the figure with the lines joining further to the left (lower RMS distance) than the clusters involving females further down.

A Spearman rank correlation was run on proximity versus relatedness scores for each dyad. There was no significant correlation (r=0.04, p=0.5), i.e., proximity between individuals was independent of their overall degree of relatedness. To test for the effects of being raised in the same litter, each dyad was classified as coming from the same or different litter. One-way ANOVAs were then performed on the proximity scores for male-male, male-female and female-female dyads separately (as these had already been shown to differ). This showed there to be a suggestion of an effect, although not a significant one in (P=0.0750), in the female-female dyads, with littermates spending more time in close proximity to one another. With a sample size of only two pairs of females coming from the same litters, this effect may be an artefact. There was no effect of coming from the same litter in male-male (P=0.6502) or male-female dyads (P=0.3875) (Table 6.2.3.c).

2. Interactions

The rate at which each cat initiated interactions plus its overall interaction rate (i.e., based on the number of sequences the cat was involved in regardless of initiator or recipient status) were calculated for each cat. These rates were calculated according to the time present in the field of view as described earlier, and therefore eliminated any trends due to different amounts of time spent by cats in the field of view of the camera.

Table 6.2.3.c. *Arithmetic means of variables analysed by one-way ANOVAs on whether pairs came from the same or different litter, for male-male (M-M), male-female (M-F), and female-female (F-F) dyads separately. For each variable means followed by the same letter are not significantly different at P=0.05 using transformed data. For both the proximity and interaction rate variables, the F-F dyads showed significant differences between categories at P=0.01.*

	DYAD TYPE	SAME LITTER	DIFFERENT LITTER
PROXIMITY BETWEEN CATS (proportion of scans present)	M - M	0.04 a	0.04 a
	M - F	0.03 a	0.02 a
	F - F	0.06 a	0.02 a
INTERACTION RATE BETWEEN CATS (sequences/hr)	M - M	0.93 a	0.89 a
	M - F	0.60 a	0.37 a
	F - F	1.30 a	0.20 a

Analysis of overall interaction rate by one-way ANOVA on sex showed that females interacted at a significantly lower rate than males (P=0.0114) (Table 6.2.3.a). Initiation rates showed an even stronger difference (P=0.001), with females initiating at a much lower rate (Table 6.2.3.a). Interaction rate was also compared between the 20 original members of the colony and the six younger cats. One-way ANOVA showed that the younger cats interacted at a significantly higher rate than the older ones (P=0.0386).

Looking at interaction rates in more detail, interactivity rates were calculated for each possible pair of cats by dividing the number of interactions performed between the two cats (regardless of initiator or recipient status) by the time they were present on camera together. This was analysed by one-way ANOVA on the male-male, male-female, female-female classification as with the proximity data. A significant difference was found (P=0.000), with male-male interactions occurring at a higher rate than male-female, which in turn occurred at a higher rate than female-female interactions (Table 6.2.3.b).

To examine this effect further, the rate at which cats *initiated* interactions to all possible partners was calculated. This introduced a directional component to the dyads, creating a division between male-female and female-male initiations in addition to the female-female and male-male categories. This was analysed by one-way ANOVA on these categories. There was a significant difference between the four possible categories of partner (P=0.000). There was no significant difference between female-female and female-male initiation rates but these were significantly lower than the male-female and male-male initiation rates, between which there was no difference (Table 6.2.3.b).

Looking at the effect of relatedness on interaction between cats, a Spearman rank correlation showed there to be no relationship between overall relatedness and rate of interaction between pairs of cats (r=0.02, p=0.75). One-way ANOVAs were then carried out on the effect of coming from the same or a different litter in male-male, male-female and female-female dyads separately (as these had already been shown to differ). There was an effect in female-female dyads, although not highly significant (P=0.0658), with littermates interacting at a higher rate with each other than with non-littermates. As with the proximity results, this may have been due to a sample size of only two female dyads coming from the same litters. This effect did not occur in male-male dyads (P=0.3110) or male-female dyads (P=0.4499) (Table

6.2.3.c).

One-way ANOVA on the proportion of interactions initiated to received by individuals showed a significant difference between the sexes (P=0.0032), with males having a higher ratio, i.e. initiating more than they received, than females who received more than they initiated (Table 6.2.3.a). Comparing the 20 older with the six younger cats on proportions of sequences initiated to received, one-way ANOVA showed there to be no difference between the two categories (P=0.708).

3. The behaviour

With attendance data being less meaningful for this colony than for the Chilworth group since the area sampled was an arbitrary part of the colony's space, there was little point in identifying behaviours characteristic of frequent attenders as was done for the Chilworth data. However the use of behaviours by the different sexes could be compared and the family tree data could be utilised to explore any tendencies for related cats to utilise certain behaviours.

Behaviour patterns were combined into seven categories (Aggressive, Threat, Defence, Play, Affiliative, Approach/Sit, Investigative) according to the cluster analysis of interactions (Figure 3.1.3.). The rate at which each cat performed and received each category was then calculated and a discriminant analysis run comparing the rates between males and females. There was no significant difference for either behaviours performed (P=0.1402) or behaviours received (P=0.1410), indicating no difference between the sexes in their use of behaviour.

Rates of each behaviour category were then calculated for each possible pair of cats (regardless of initiator or recipient status). Canonical correlation analysis was run comparing these rates with the overall relatedness score for each dyad. This showed no significant correlation (P=0.4658), indicating that overall relatedness between individuals had no effect on the quality of behaviour used between them.

Looking at parental influences in more detail, each dyad was classified in three ways as with the proximity and overall interaction rate data as having the same or different father, the same or different mother and as coming from the same or different litter. Discriminant analyses were then run on the seven behaviour categories, using each of these classifications. These revealed no difference between pairs with the same or different mother (P=0.2726) or between pairs with the same or different father (P=0.4264). There was, however, a significant difference (P=0.0154)

between pairs coming from the same and different litters. Pairs from the same litter showed 1.3 times more Approach/Sit, 1.3 times more Aggression, 1.5 times more Defence, 2.3 times more Threat and 2.3 times more Play than non-littermates. However, they also showed 2.3 times *less* Affiliative and 1.3 times less Investigative behaviours. Figure 6.2.3. illustrates these differences.

4. Summary and discussion of colony characteristics

As with the Chilworth colony, a number of significant characteristics were discovered in this colony, mostly concerning differences between the sexes. Following the same pattern as at Chilworth, females spent less time in close proximity to others (although not significantly so), and interacted at a significantly lower overall rate than did the males. They initiated interactions at a significantly lower rate than males, and consequently received proportionally more interactions than they initiated compared to the males. As at Chilworth, when involved in interactions, females interacted significantly more often with males than with other females, presumably due to the higher initiation rate by males. Unlike at Chilworth, initiating females showed no preference for male or female partners. This was reflected in the proximity data where females showed no preference for sitting with either sex.

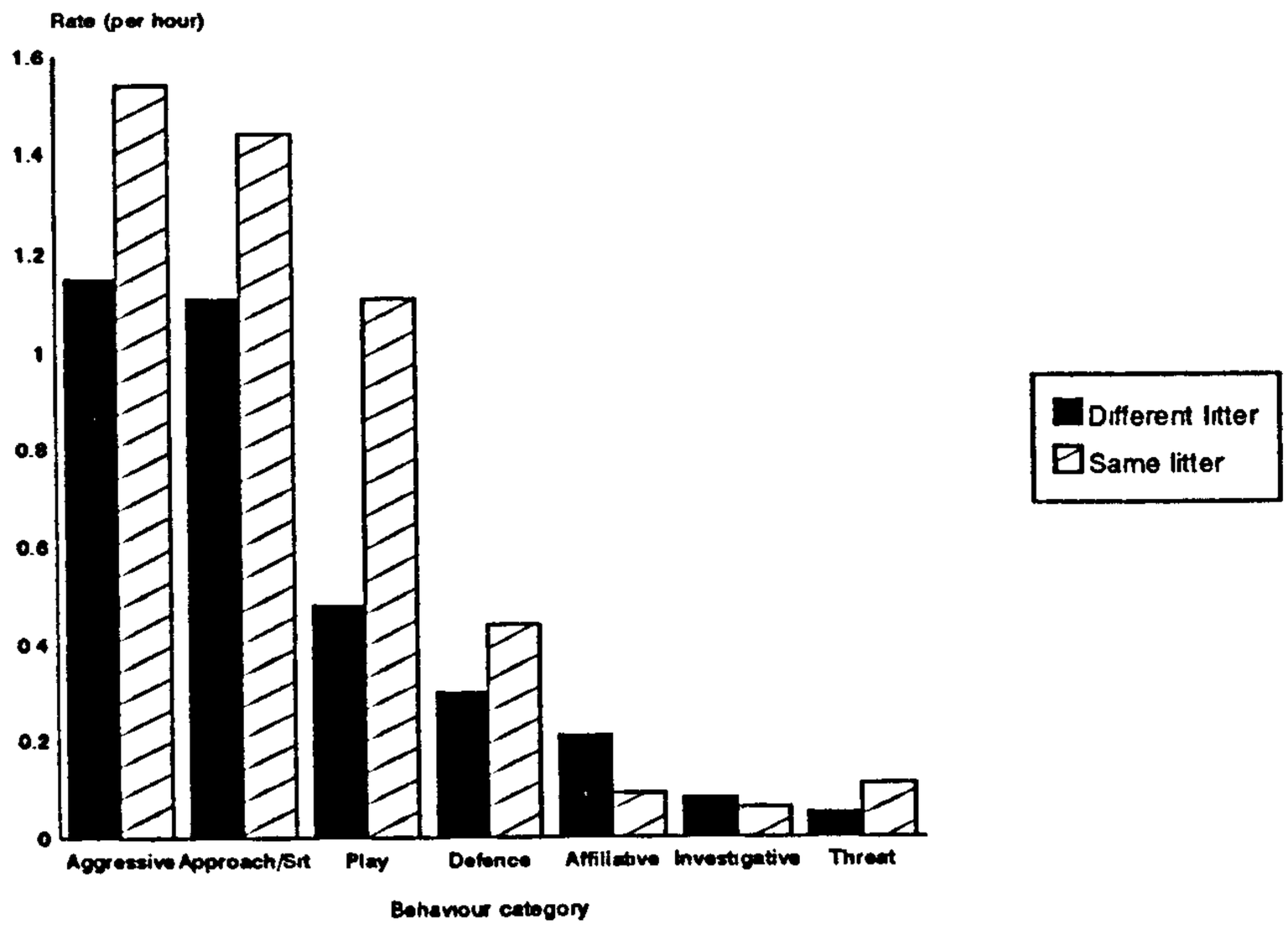
When interacting or associating with other females, female cats preferred littermates to non-littermates. Although based on a small sample size, this may be a representation in neutered cats of the matrilineal ties between females observed in intact colonies (e.g.,Kerby, 1987)

Males, although showing higher proximity and interaction rates than females as at Chilworth, behaved rather differently regarding partners. They both interacted at a higher rate with and spent proportionally more time in close proximity to other males rather than females. However, when initiating interactions, they chose male and female partners equally. This effect is probably due to the significantly higher initiation rate of males compared to females - males initiating more interactions and dividing them equally between males and females will result in male-male interactions occurring more frequently than male-female interactions.

Despite clear differences between males and females in their interaction rates and proximity preferences, there was no difference between the sexes in the quality of behaviours performed or received.

Looking at interactions between individuals, the type of behaviour used showed

Figure 6.2.3. *Rates of each behaviour category performed between littermates and non-littermates.*



no relationship to their overall relatedness, or indeed to any maternal or paternal connections. The most important factor was whether they originated from the same or different litter.

Most interesting is *how* the quality of behaviour was affected, with, for example, non-littermates showing much more of the affiliative category of behaviours compared to littermates. It is possible that this result is driven by the strong domination of affiliative behaviours by the male SM (section 6.2.2.v). Nevertheless it does follow logically from the discussion of the sequence analyses described in Chapter 3. It was mentioned that the tail-raised display appeared to be a safe, unambiguous signal which rarely resulted in an aggressive response from a recipient cat. As such, it was most often used preceding rubbing displays to announce the cat's friendly intentions. Within a long-established colony consisting of littermates and non- littermates, the cats will all be very familiar with one another. Littermates, however, together from a much earlier stage, will have established much firmer relationships, whether friendly or not. This may mean they have less need for the tail-raised appeasement displays when interacting with each other. Approaches can occur confidently with the tail lowered and be followed by the companionable Sit With and mutual grooming displays.

An alternative for littermates in this colony was an abundance of fighting and play behaviours, notably reduced between non-littermates (Figure 6.2.3.). This may have been a legacy of kittenhood for these cats - having been neutered young (six months old) and being raised in confined, very sheltered conditions, such kittenish behaviours would be much more likely to be retained than in a feral or free-living population. High frequency play and fighting behaviours would be less likely to develop amongst non-littermates later in life, especially in a confined environment.

The different relationships between individuals in this colony highlights an important feature of early development, namely the recognition of littermates. Research has revealed many species capable of recognising siblings, e.g., Hepper (1986) showed that the domestic dog had this ability. Relationships between littermates develop at an early stage, and, in the case of these cats at least, the sibling-specific relationships appear to have been maintained into adulthood. This seems surprising considering that the colony had been established for over four years at the time of the study and serves to emphasise the strength of these early bonds.

6.2.4. Discussion

Whilst there was quite evidently a social structure within the University colony, social interactions recorded during the study period were strongly dominated by the males. This is evident from examining the dyadic relationships visually and is confirmed by the analysis of the whole colony showing that males were more interactive than females. Examination of the interaction data and the behavioural categories involved revealed that a group of seven cats, all male, were particularly interactive with one another. A closer look at the data suggested a possible social order within this group, with the oldest male FA at the top. The fact that he was neutered at an older age than the other males may or may not have been the reason for his high status - it does, however, seem a likely explanation in view of his more developed physical appearance and the effect on the rest of the colony when he was scruffed (section 6.2.2.i). If this is the reason, the fact that this cat was only four months older than the rest of the males when neutered raises an important point regarding the age of neutering in males.

Hart & Barrett (1973) reported an immediate or gradual decline in fighting, roaming and urine spraying occurs following neutering in the majority of cats castrated after reaching sexual maturity. FA showed few of these behaviours despite having been one year old at the time of neutering, supporting Hart & Barrett's results. However, his maintenance of a high social position typical of an older more mature intact male within the colony suggests that neutering does not necessarily affect the social status of a cat within a group of similarly neutered individuals.

The original 10 male members of the colony had been neutered for almost a year and had time to establish a social organisation before the six new cats were introduced, four of them male and recently neutered. Although the study was not carried out until two years after this introduction, these males may still have been struggling to fit into the social structure which would explain the high rate of interaction and, in particular, aggression between these younger males.

The females of the group, though interacting less frequently than the males interestingly showed no differences to males in their behavioural repertoires suggesting that rather than having a different method of social communication to males it was simply reduced to a lower intensity. It is interesting to see that, with the removal of the reproductive and, in the case of the females, the mother-kitten elements of the behavioural repertoires, that the behaviour of these male and female

neutered cats was qualitatively the same.

This may be an important area for future study - many potential cat owners regard females as much less aggressive and more "friendly" than males, probably an accurate prediction in the unneutered individual. However, if the social tendency of the cat in the cat-cat situation is comparable to that of the human-cat situation, then the choice between male and female cats as pets may simply be a choice of how interactive the owner wants the cat to be rather than its behavioural tendencies. These are much more likely to be predicted by the personality of the cat than by its sex if it is neutered.

More important, in this cat society at least, seemed to be the recognition of littermates with respect to the type of behaviour used. As mentioned earlier it is possible that one or more individual personalities were driving this effect but interestingly the overall rate of interaction tended to be higher between littermates. Of the nine cats which amongst themselves accounted for 42 % of the colony's interactions (see section 6.2.2. Summary) only two pairs came from the same litters, out of a total possible 13 littermate pairs within the whole colony; so the higher littermate interaction rate was not an artefact due to this group.

One of the most surprising aspects of the behavioural repertoire of this colony was the marked absence of affiliative behaviours such as the Tail-raised Approaches and Head Rubbing seen in the other two study groups. Possibly the confined environment in which the cats lived was responsible for this. If so, it suggests another possible feature of affiliative behaviour -that it is shown most often between cats that have not been aware of each others presence for some time. Thus cats interacting in view of the camera in the University colony may not have utilised such "greeting" behaviour as they could monitor each other's presence for much of the time whatever part of the colony's ranging area they were in. Only when one or other of them had been elsewhere in an indoor area of the range might they feel the need to greet one another.

Macdonald et al. (1987) reported a marked asymmetry of head rubbing in their study colony, with, in particular, younger animals initiating rubs on older ones. The absence of a natural age structure amongst the University cats, with most of them being of similar age, might therefore help account for the lack of rubbing and other affiliative behaviours exhibited amongst them.

The high rate of aggression and large number of aggressive behaviour patterns

observed within this colony may similarly have been caused by the confined conditions creating competition for space. Alternatively, the large number of males of roughly equal age and sexual status was a feature rarely seen in entire colonies. In such colonies there is usually a spread of different aged males with, as a result, different breeding statuses (Liberg, 1980). Such males accept that they are unevenly matched and aggression is reduced. In this neutered group, with many of the males equally matched, aggression between them would inevitably increase.

The high aggressive component of the interactions is shown in the correlation of the proportion of aggressive behaviours initiated to received compared with overall interactions received (i.e., cats receiving most interactions also received most aggression). Aggression seems therefore to have an important role in maintaining the structure of the colony, in contrast to the rubbing/sniffing patterns observed in the Knowle and Chilworth colonies.

Although raised and studied in rather artificial surroundings, this, the largest colony of cats studied, provided useful information on the social behaviour of neutered groups. Most feral populations of cats are neutered after reaching sexual maturity and therefore have developed a social system on which to base future relations. Probably the most important finding from this study is therefore that, despite never having had the opportunity to develop a social structure as intact adults, they nevertheless developed one following neutering. The development of social structure within the group was not dependent on their being able to breed.

CHAPTER 7

The Use of Tail-raised and Rubbing Behaviour Patterns during Cat-Human Encounters

SI and HO head rubbing with their tails raised (Chilworth colony).

CHAPTER 7

THE USE OF TAIL-RAISED AND RUBBING BEHAVIOUR PATTERNS DURING CAT-HUMAN ENCOUNTERS

Rubbing is one of the cat's most characteristic and endearing social behaviours. There are diffuse clumps of sebaceous glands along the tail (caudal glands), forehead (temporal gland), lips (perioral gland), and chin (Fox, 1975). These areas of the body may be rubbed on an inanimate object, on another cat or, in the domestic situation, on a human. The fact that sebaceous glands are involved suggests some olfactory purpose to rubbing. Verberne & DeBoer (1976) confirmed this by demonstrating different reactions (olfactory inspection and/or rubbing) by cats to objects rubbed by other cats.

Macdonald et al (1987) observed marked asymmetries of conspecific scent marking between individuals in their study colony, whereby some cats tended to rub on others. This suggested a possible role in the maintenance of social structure and dominance hierarchies within the group. Similar asymmetric patterns have been described for the neutered groups described in earlier chapters of this thesis.

It seems likely that rubbing involves the transfer of social odours, but during mutual cheek rubbing the transfer of odour from the cheek glands could be in either direction, making it unclear which cat is marking the other.

Even less clear is the function of rubbing by a cat on a human, and a cat rubbing on an inanimate object. A study by Mertens and Turner (1988) investigated interactions between colony cats and persons unknown to them. In staged encounters the person deliberately ignored the cat for the first five minutes and then interacted freely with them for the second five minutes. Significantly more head rubbing and less vocalisation was displayed by the cat towards the person after the person had signalled friendly intentions, i.e, after the first five minutes. The frequency of flank rubbing did not change.

Looking at cats interacting with *familiar* humans (their owners) in the home setting, Mertens (1991) found that cats that are allowed out of doors rub on their owners more frequently than cats confined indoors, and cats in multi-cat households tend to rub less on their owners than do single cats. This supports one of the suggestions made for the lack of rubbing observed within the University colony (Chapter 6), i.e., that rubbing, along with other affiliative patterns, is most often used

as a greeting behaviour pattern after a cat has been absent from its social group for some time. It also highlights the possibility that the cat regards the human owner as part of its social group and therefore uses cat-cat behaviour patterns in the same way in the cat-human situation.

There do not appear to have been any studies published on the use of the tail-raised signal in either the cat-cat or the human-cat situation. Considering the close association of this and rubbing behaviour in all the colonies studied (Chapter 3), it seems logical to study the use of both patterns together. A series of experiments were therefore carried out to investigate the use of rubbing and the tail-raised posture in the human-cat situation.

Methods

The experiments used cats from the University colony described in Chapter 6. Individuals were selected on the basis of being both approachable and affectionate to the observer (i.e., as a pet cat might be to its owner). All tests were carried out in a room familiar to the cats and information recorded on video camera, the cats having been familiarised with this apparatus beforehand. Analysis was mainly by multifactor analysis of variance (ANOVA), transforming the data by log(x+1) for count data, by square root for time data, and by arcsine where proportions were used. Cat to cat variation was taken into account when examining the results of these tests, by using the mean square of the cat interaction calculation as the error term for the variable being tested. Chi-squared tests were used where appropriate.

7.1. Experiment 1

Six cats were tested under each of three different treatments. Treatment 1 involved the cat being released into a familiar room containing four different objects with no human present. Treatment 2 contained the same layout as Treatment 1 and a familiar person was also present in the room standing in the middle of these objects. This person was not allowed to interact with the cat in any way. Treatment 3 was the same as Treatment 2 only the person was allowed to interact with the cat freely. Treatments were allocated by a 3X3 Latin square design, and the whole experiment was replicated once. The objects used were as follows : 1 cardboard box; 1 wooden box; 1 cardboard cylinder; 1 bucket.

Each cat was left in the room for ten minutes and its behaviour recorded on video. The video tapes were then examined thoroughly to record the total number of each type of rub (cheek, ear, flank, tail). The cat often rubs the whole of one side of its head and body along a person or object, incorporating several or all of the different rub types into one movement. Another measure was therefore recorded of the total number of rubbing sequences, plus the number of sequences performed on each object by each cat for each of the 3 treatments. When present, the human was not always visible on the video recording so only rubbing on objects was examined. Tail position was not recorded during this experiment.

Results

One individual performed no rubbing throughout the experiment and was therefore omitted from the analysis. Tables 7.1.1. and 7.1.2 summarise the combined results from the other 5 cats. Figure 7.5.1. illustrates the number of object rubs in comparison to the results from the other experiments.

The total numbers of rub sequences were examined by multifactor ANOVA on the log transformed numbers of rub sequences on each object for each treatment and each replicate. There was a significant difference in the amount of rubbing in the three treatments ($P<0.005$), with virtually no rubbing at all in Treatment 1 (only one observation)

There was also a significant difference in the number of sequences performed on the different objects ($P<0.025$) and a significant preference for the two objects with corners over the two cylindrical objects when data from the two types was combined. When the experiment was replicated, the cats showed a significant increase in the overall amount of rubbing on the objects ($P<0.025$), however the distribution of these on the different objects and the effect of the different treatments did not change. Looking at the relative use of different parts of the body when rubbing on objects, chi-squared analysis revealed that parts of the head (cheek and ear) were used for rubbing on objects significantly more than other parts of the body (flank and tail) ($P<0.005$, Table 7.1.2.).

Conclusion

Apart from a preference for rubbing on objects with corners, and a tendency to use only the head regions for this rubbing, this experiment revealed a marked effect

Table 7.1.1. *Arithmetic means of number of rub sequences on each object and under each treatment. ANOVA performed on log transformed data - for each comparison, figures followed by the same letter are not significantly different at P<0.05.*

		Mean no. rub sequences in ten minutes
Treatment	1 - no person	0.03 a
	2 - person, no contact	2.83 b
	3 - person + contact	10.40 c
Object	Cardboard cylinder	2.6 a
	Bucket	3.8 ab
	Wooden box	5.5 bc
	Cardboard box	5.8 c

Table 7.1.2. *Mean number of each type of rub (independent of number of sequences) recorded on the objects.*

Part of body	Mean number of rubs
Cheek	15.5
Ear	14.5
Flank	2.2
Tail	0.1

of both the presence of and contact from a human on the amount of rubbing that occurred on objects. The next experiment examined the effect of human contact further, by standardising the level of contact from the person and exploring its effect on object rubbing, rubbing on the person, and the amount of time the tail was held in a raised position during the test.

7.2. Experiment 2

Only 2 different conditions were examined in this experiment. In Treatment 1 the person was not permitted to interact with the cat in any way (the "no contact" treatment). In Treatment 2 the person petted the cat in a consistent way for the five minutes of the test, stroking it for 20 seconds every minute and talking to the animal as often as desired (the "contact" treatment). Six cats were tested, two of them the same as in Experiment 1. Each test lasted five minutes and each cat received both treatments. The treatments were ordered by latin square design, and one replication was made. Since this experiment focussed more on the effect of the human than on the objects rubbed, only the wooden box, the most consistent object as regards number of rubs on it in the previous experiment, was made available for the cat to rub on in the room. A familiar person was present in each treatment. Hence the cat was given a choice between rubbing on the person or rubbing on the single object in the room.

Each test was recorded on video and later analysed in detail to determine the number of sequences and types of rub directed at the object and at the person in the two different conditions. The amount of time the cat spent on screen and the proportion of that time that its tail was held vertical were also recorded.

Results

One of the cats became ill during the experiment and was omitted from the analysis. Tables 7.2.1. and 7.2.2. summarise the results from the remaining 5 cats. Figures 7.5.1 - 7.5.5 show these results in comparison with those of the other experiments.

Table 7.2.1. *Arithmetic means of number of rub sequences recorded on object and person, and the mean proportion of time the tail was held raised under the two treatments. For each variable, figures followed by the same letter are not significantly different at P=0.05 by ANOVA on transformed variables*

	Treatment	
	1 - no contact	2 - contact
Object rubs	9.0 a	23.8 b
Person rubs	5.3 a	6.9 a
Average time on screen (secs)	181.3 a	251.7 b
Average time tail raised (secs)	137.0 a	230.7 b
Proportion of time tail raised	0.78 a	0.92 b

Table 7.2.2. *Mean number of each type of rub (independent of number of sequences) recorded on person and the object. Cheek and ear rubs were categorised for analysis as "head rubs", whilst flank and tail rubs were classifed as "body rubs".*

Part of body	Rubs on object	Rubs on person
Cheek	14.5	3.0
Ear	9.5	5.4
Flank	0.6	4.8
Tail	0.0	3.6

a) Rubbing

ANOVA on the results supports suggestions from the first experiment. There was a significant increase in rubbing on the object when contact is provided by the person ($P<0.025$). This did not, however, apply to rubbing on the person which stayed at approximately the same level whether or not contact was given. Unlike in the first experiment, there was no change in frequency of rubbing between replicates for either object or person rubbing. Chi-squared analysis of the different elements of the rubbing sequences showed that, as in the first experiment, objects received almost exclusively head rubs (maximum 2% flank rubs) ($P<0.0001$, Table 7.2.2.). The person, however, received an equal number of head and body rubs ($P>0.05$). This was the case in both the contact and no contact treatments.

b) Tail raised response

Recording of the amount of time the cats had their tails raised was complicated in this and subsequent experiments by there being a limited field of view of the camera - the cats as a result spending different amounts of time in view. An area of approximately half a metre was visible around both the person and object. Rubbing on the object and person was always within the field of view but the cats occasionally wandered in and out of camera shot with their tails still raised, although they tended to lower their tails on leaving the vicinity of the person as they lost interest in them.

Obviously only the "on camera" activity could be recorded from the video so some information was lost if the cat went off screen. With individuals spending different amounts of the possible 5 minutes on camera, it would be inaccurate to compare total amounts of time recorded with the tail raised, as this may have occurred off screen.

The only reliable method of comparing tail up was therefore to compare the proportion of time on screen that the tail was raised. This in itself may be a rather misleading measure if, as appeared to be the case, the tail was generally held vertical whenever the cat was close to the person. To help interpretation, therefore, all three measures: time on screen, time tail held vertical and proportion of time tail held vertical were analysed (Table 7.2.1., Figures 7.5.3 - 7.5.5).

ANOVA on the proportion of time visible that the cat had its tail raised, showed that the cats had their tails raised for a significantly higher proportion of the time in the contact treatment compared with the no contact treatment ($P<0.05$). They also

spent significantly more time on screen ($P<0.005$) and therefore in the vicinity of the person in the contact treatment.

Conclusion

The experiment shows a differential effect of human contact on rubbing on objects and a person, with contact producing no significant effect on person rubbing but an increase in object rubbing. Whilst the cats used both head and body rubs on the person, object rubbing was restricted almost entirely to the head region. In addition, human contact increased the amount of time the cats spent close to the person and exhibited the affiliative tail-raised posture. Experiment 3 explored this effect further by introducing the effect of the presence of another cat on rubbing and tail-raised behaviours.

7.3. Experiment 3

The contact and no contact treatments as described for experiment 2 were used again using the same familiar person and a box. Five cats were tested, only one of which featured in the first two experiments. The cats were tested, under the two treatments, both singly (twice) and with every combination of partner (once) using a chain block design. From the video, measures of the number of rubs and rub sequences on the object, the person and, where present, the other cat were recorded, along with the amount of time the cat was visible on the screen and the proportion of that time that its tail was held vertical.

Results

Tables 7.3.1. and 7.3.2. summarise the results. Figures 7.5.1 - 7.5.5. show the results in Table 7.3.1 in comparison to the results of the other three experiments.

a) Rubbing

The cats never rubbed on each other during the experimental periods. ANOVA on the number of rub sequences on the object showed there to be significantly more under the contact compared to the no contact treatment ($P<0.025$). The presence of another cat decreased the amount of object rubbing, but this effect was not significant. ANOVA on the number of sequences observed on the person showed a

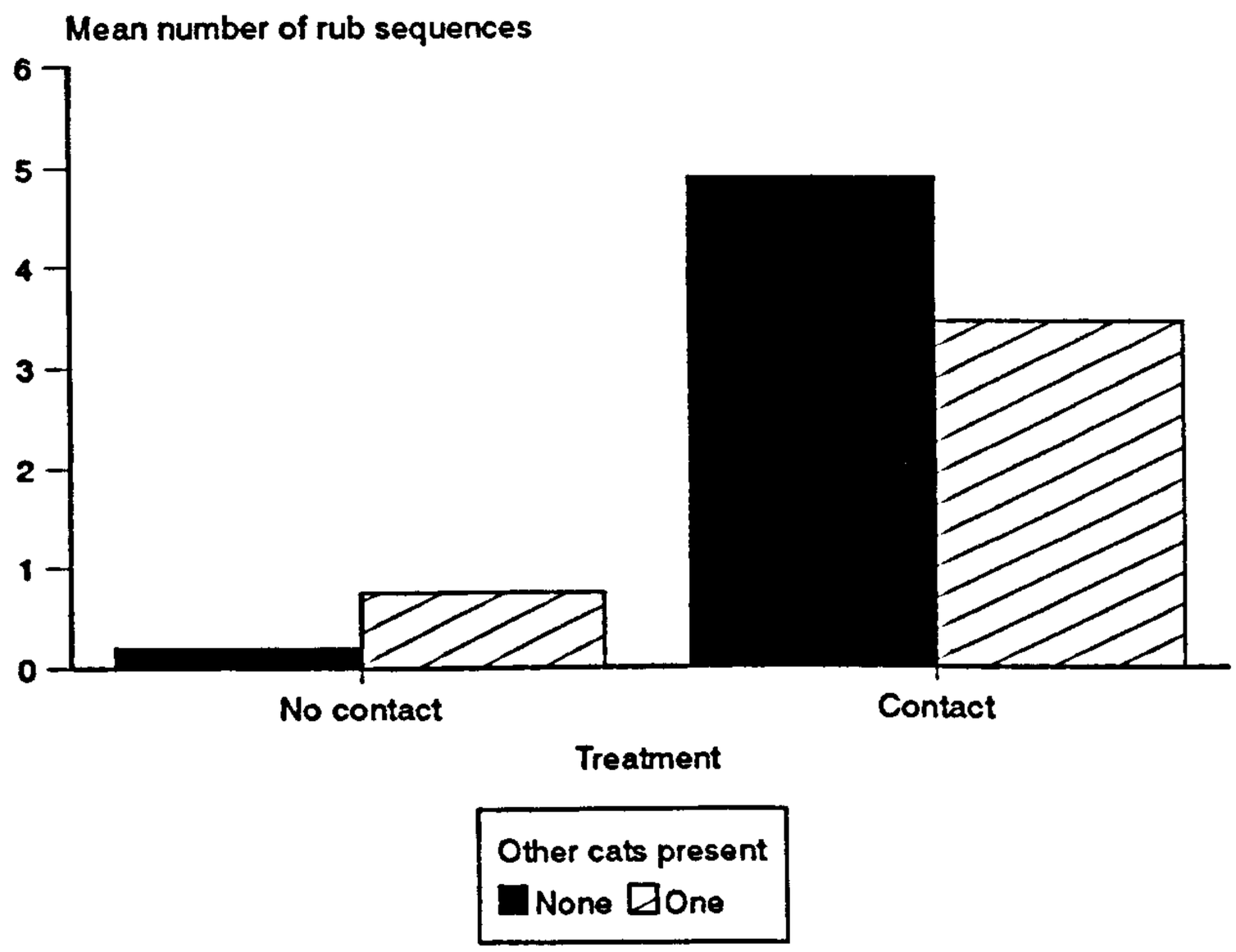
Table 7.3.1. *Arithmetic means of rubbing, attendance and tail raised measures for the two treatments and for single and 2-cat tests. For each variable, figures followed by the same letter are not significantly different at P=0.05 by ANOVA on transformed variables.*

	Treatment		Other cats present	
	1 No contact	2 Contact	None	One
Object rubs	1.9 a	9.4 b	7.1 a	4.9 a
Person rubs	0.6 a	3.9 a	2.6 a	2.1 a
Average time on screen (secs)	94.8 a	152.5 a	125.7 a	122.7 a
Average time tail raised (secs)	31.4 a	127.3 b	93.5 a	72.3 b
Proportion of time tail raised	0.44 a	0.87 b	0.73 a	0.62 a

Table 7.3.2. *Arithmetic means of rubbing, attendance and tail raised measures recorded in single and 2-cat tests under each treatment.*

Treatment	1 No contact		2 Contact	
Other cats present	None	One	None	One
Object rubs	2.8	1.4	11.4	8.4
Person rubs	0.2	0.8	4.9	3.5
Average time on screen (secs)	77.4	103.5	173.9	141.8
Average time tail raised (secs)	33.6	30.3	153.4	114.2
Proportion of time tail raised	0.55	0.38	0.91	0.85

Figure 7.3.1. *Effect of presence or absence of another cat on rubbing on the person under the no contact and contact treatments.*



non-significant increase with contact and no effect at all due to the presence or absence of a partner. There was, however, a significant interaction between treatment and the effect of a partner being present ($P<0.05$). In the no contact treatment the frequency of person rubbing was higher when another cat was present. In the contact treatment it was lower when another cat was present. Figure 7.3.1. illustrates these results.

Chi-squared analysis of the types of rub used showed, as before, that overall the object received almost exclusively head rubs (0.01 % body rubs) whilst the person received head and body rubs in exactly equal proportions (50:50). This was the case for both treatments, and there was no effect of the presence of another cat on the types of rubs used.

b) Tail raised response

The cats spent more time (although not significantly so) on screen and close to the person when contact was given and a significantly larger proportion of that time with their tails raised ($P<0.005$, Table 7.3.1., Figures 7.5.3 - 7.5.5). The presence of another cat had no effect on the amount of time spent close to the person but the tail was raised for a slightly lower (though not significantly) proportion of the time compared to when cats were tested singly.

Conclusion

Contact from the person produced the same effects as before, increasing object rubbing and proportion of time with the tail raised, but having a smaller non-significant effect on person rubbing. Rubbing on the object was restricted to head rubbing whilst the person received head and body rubs equally, regardless of treatment.

The presence of another cat slightly reduced object rubbing and the proportion of time the tail was raised. The only *significant* effect of the presence of another cat detected was a reduced amount of person rubbing when contact was given in comparison to the no contact treatment where the presence of another cat increased person rubbing. Experiment 4 explored this element of competition further by testing cats alone and in a group of four.

7.4. Experiment 4

This trial used the same treatments as in the previous two experiments. Four cats were tested, all different from those in Experiment 3, to avoid any possible learning effects across experiments. Each cat was tested, under the two treatments, both singly and in a group containing all four cats. This was performed twice. As in Experiment 3, from the video measures of the number of rubs and rub sequences on the object, the person and, where present, the other cats were recorded, along with the amount of time the cat was visible on the screen and the proportion of that time that its tail was held vertical.

Results

Tables 7.4.1 and 7.4.2 summarise the results. Figures 7.5.1 -7.5.5 illustrate the results in Table 7.4.1 in comparison with the results of the other three experiments.

a) Rubbing

As in Experiment 3, no inter-cat rubbing was observed. ANOVA on the number of rub sequences on the object showed that, although as before contact produced an increase, this was not significant. The presence of the other three cats reduced object rubbing, but as in the previous experiment, this was not significant.

ANOVA on the rub sequences on the person showed a significantly higher frequency of rubbing when contact from the person was received ((P<0.05). There was also a significant effect of the presence or absence of the other three cats (P<0.05) with less rubbing on the person when others were present. Chi-squared analysis of the types of rub used showed that the object received exclusively head rubs with no body rubbing elements recorded at all, whilst the person received head and body rubs in roughly equal proportions (53:47 overall). This was the case for both treatments, and there was no effect of the presence of another cat on the types of rubs used.

b) Tail raised response

The cats spent more time in the vicinity of the person (although not significantly so) and spent significantly more time with their tail raised (P<0.01) when contact was given. The proportion of time with the tail raised was also higher but not significantly so. When other cats were present the cats spent significantly less time in the vicinity

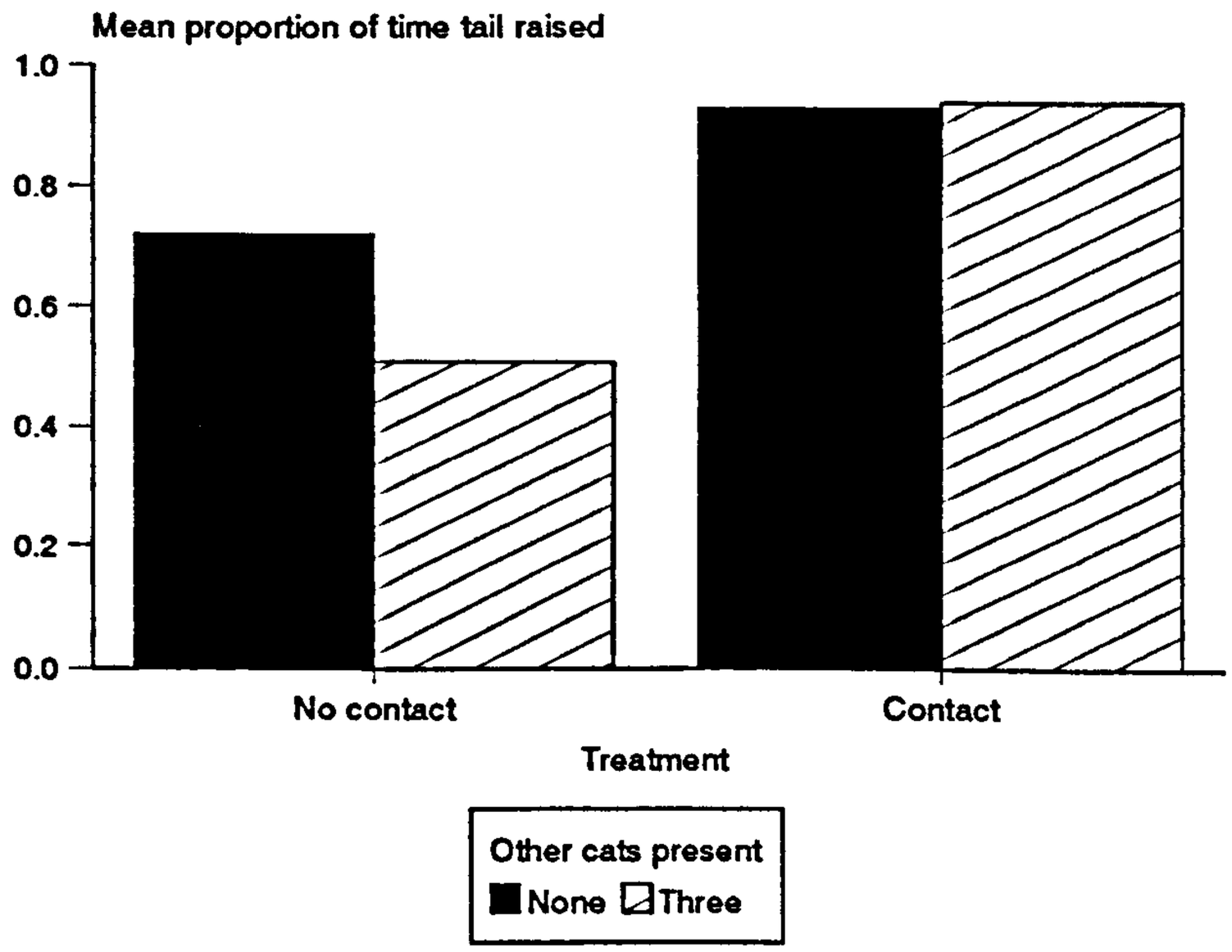
Table 7.4.1. *Arithmetic means of rubbing, attendance and tail-raised measures recorded under the two treatments and for single and 4-cat tests. For each variable, figures followed by the same letter are not significantly different at P=0.05 by ANOVA on transformed variables.*

	Treatment		Other cats present	
	1 No contact	2 Contact	None	Three
Object rubs	8.6 a	16.2 a	14.6 a	10.3 a
Person rubs	1.7 a	6.3 b	5.8 a	2.3 b
Average time on screen (secs)	97.0 a	217.3 a	184.1 a	130.1 b
Average time tail raised (secs)	52.8 a	201.4 b	156.5 a	97.6 b
Proportion of time tail raised	0.62 a	0.93 a	0.83 a	0.73 a

Table 7.4.2. *Arithmetic means of rubbing, attendance and tail raised measures recorded in single and 4-cat tests under each treatment.*

Treatment	1 No contact		2 Contact	
Other cats present	None	Three	None	Three
Object rubs	9.4	7.9	19.8	12.6
Person rubs	2.4	1.0	9.1	3.5
Average time on screen (secs)	110.5	83.5	257.8	176.8
Average time tail raised (secs)	72.5	33.0	240.5	162.3
Proportion of time tail raised	0.72	0.51	0.93	0.94

Figure 7.4.1. *Effect of presence of three or no other cats on proportion of time on screen that the tail was held vertical, under the no contact and contact treatments.*



of the person ($P<0.05$) and significantly less of the time visible with their tails raised ($P<0.01$). The proportion of time visible that the tail was raised was lower when other cats were present, but this effect was not significant.

There was also a significant interactive effect between contact and the presence of the other cats ($P<0.01$) with, in the no contact treatment, a lower proportion of time spent with tail raised when the other cats were present than when cats were tested singly. When contact was given the tail raised response was equal in both single and multiple cat conditions. Figure 7.4.1. illustrates this differential effect.

Conclusions

This experiment showed more significant effects with respect to rubbing on the person with contact from the human than the previous ones, with less significant effects apparent in the object rubbing. This aside, the overall pattern seems similar, with contact from the person increasing object and person rubbing and the amount of time spent close to the person with the tail raised. Object rubbing consisted only of head rubs, whilst the person received head and body rubs equally, regardless of treatment.

The presence of more than one other cat significantly reduced both the time spent by the cats close to the person and the amount of rubbing on the person. This was also apparent with the object rubbing, although the reduction was not significant. The effect of other cats on the tail raised response was more complicated. In the no contact treatment when other cats were present the cats spent proportionally less time with their tails raised but in the contact treatment the tail was held vertical for almost all the time the cat was visible, regardless of the presence or absence of other cats.

7.5. Summary

Figures 7.5.1 - 7.5.5 summarise the comparable results from the four experiments.

The importance of rubbing as a display behaviour in human-cat relationships is illustrated by experiment 1, where the presence of a familiar yet uncommunicative person in a room significantly increased the amount of object rubbing by the cat. Contact, in the form of talking and petting, significantly increased the amount of object rubbing even further, an effect repeated in experiments two three, and four,

Figure 7.5.1. *Mean number of rub sequences observed on objects under no contact and contact treatments in Experiments 1-4. Where bars within each experiment carry the same letter, treatments were not significantly different at P=0.05.*

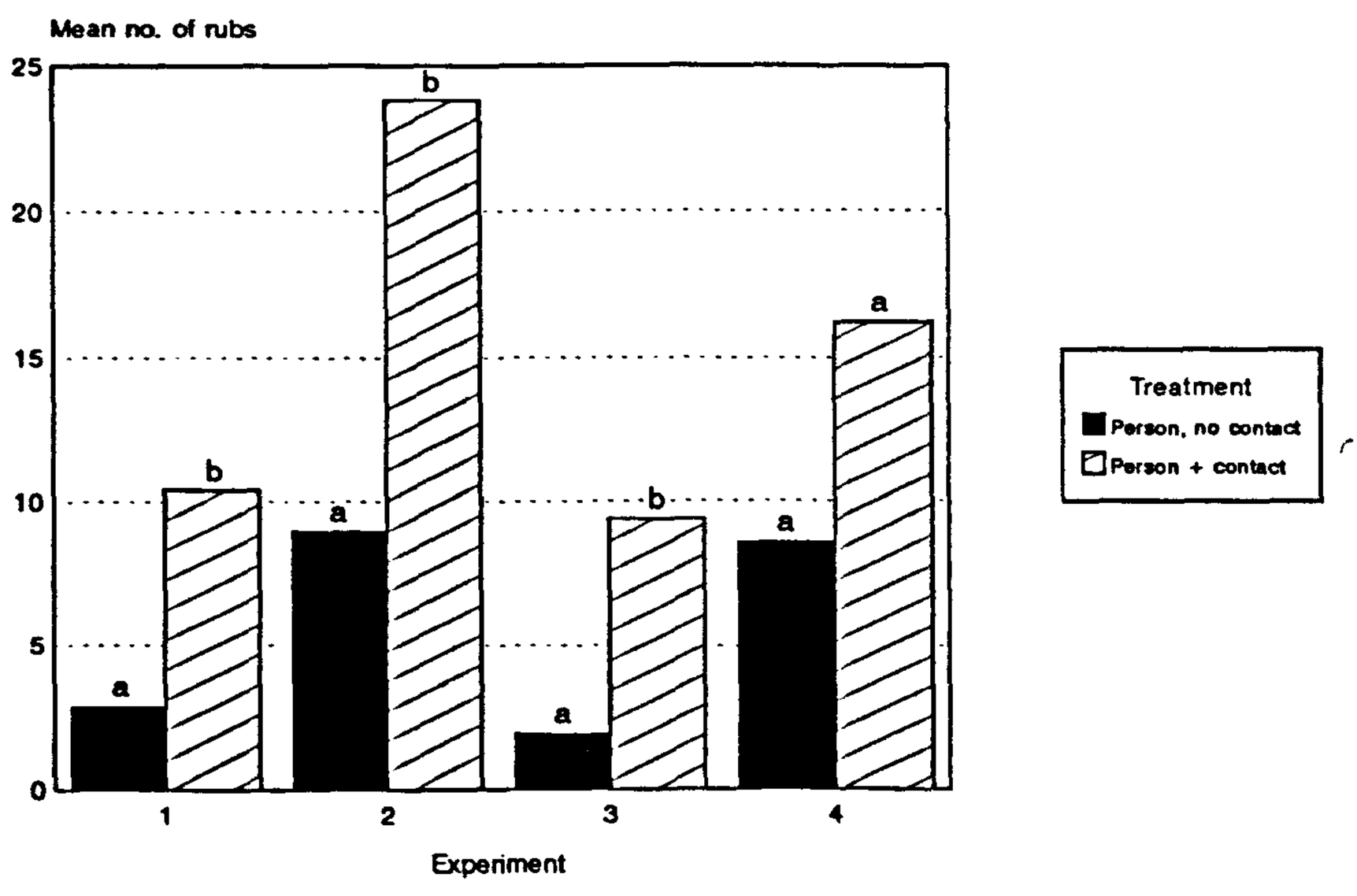


Figure 7.5.2. *Mean number of rub sequences observed on person under no contact and contact treatments in Experiments 2-4. Where bars within each experiment carry the same letter, treatments were not significantly different at P=0.05.*

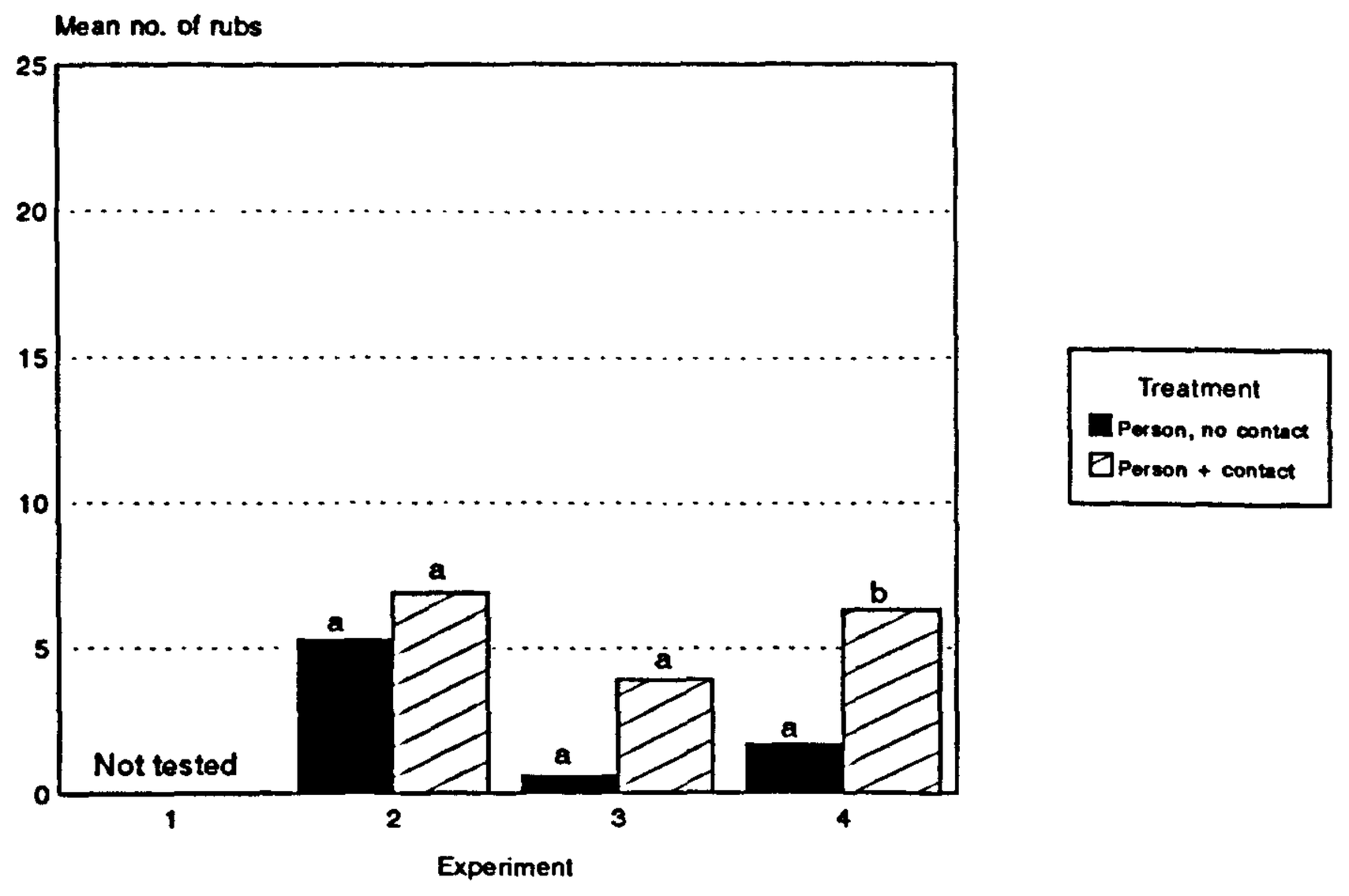


Figure 7.5.3. *Mean amount of time on screen (maximum 5 minutes) under contact and no contact treatments in Experiments 2-4. Where bars within each experiment carry the same letter, treatments were not significantly different at P=0.05.*

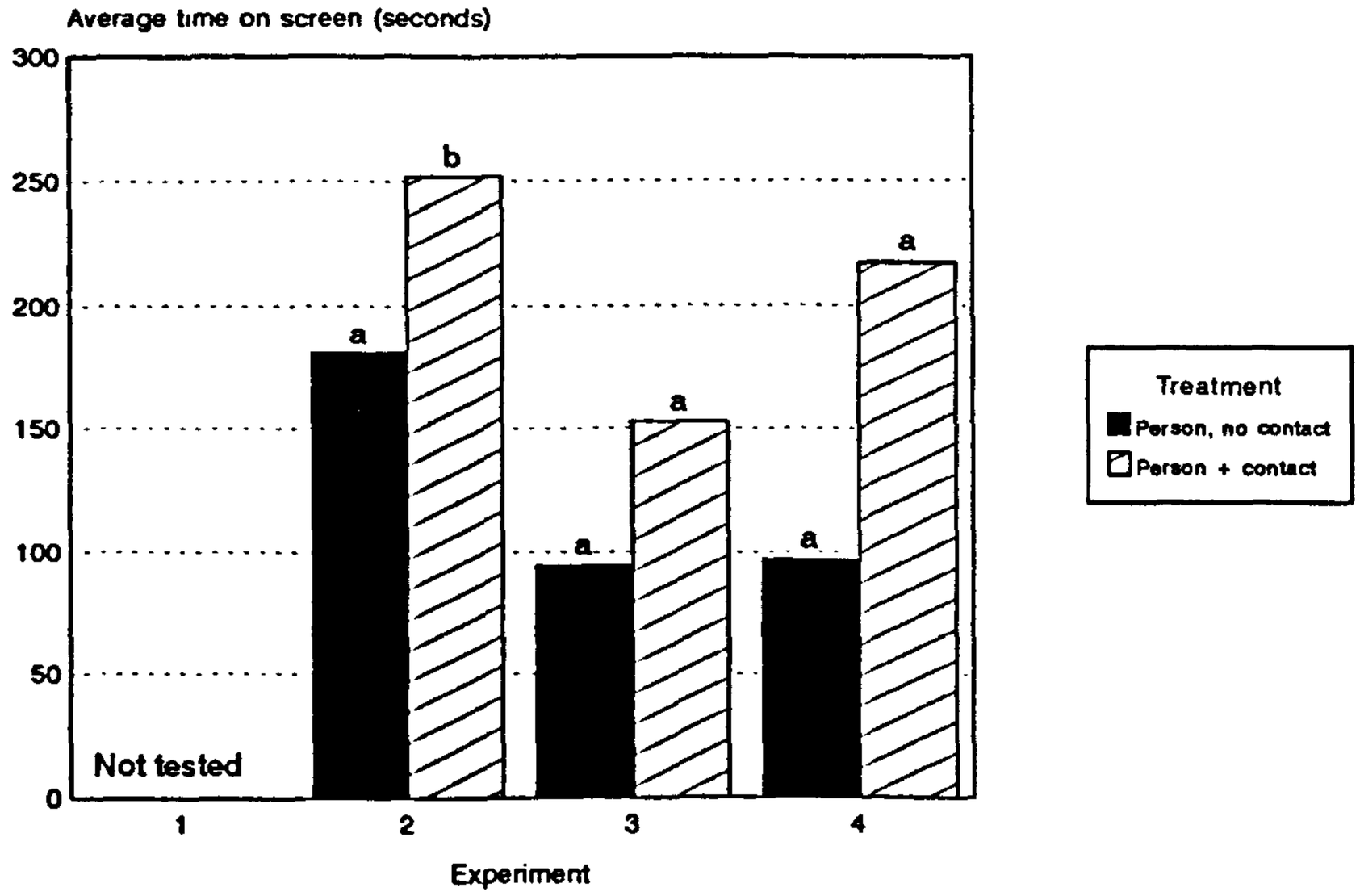


Figure 7.5.4. *Mean amount of time with tail held in vertical position on screen under contact and no contact treatments in Experiments 2-4. Where bars within each experiment carry the same letter, treatments were not significantly different at P=0.05*

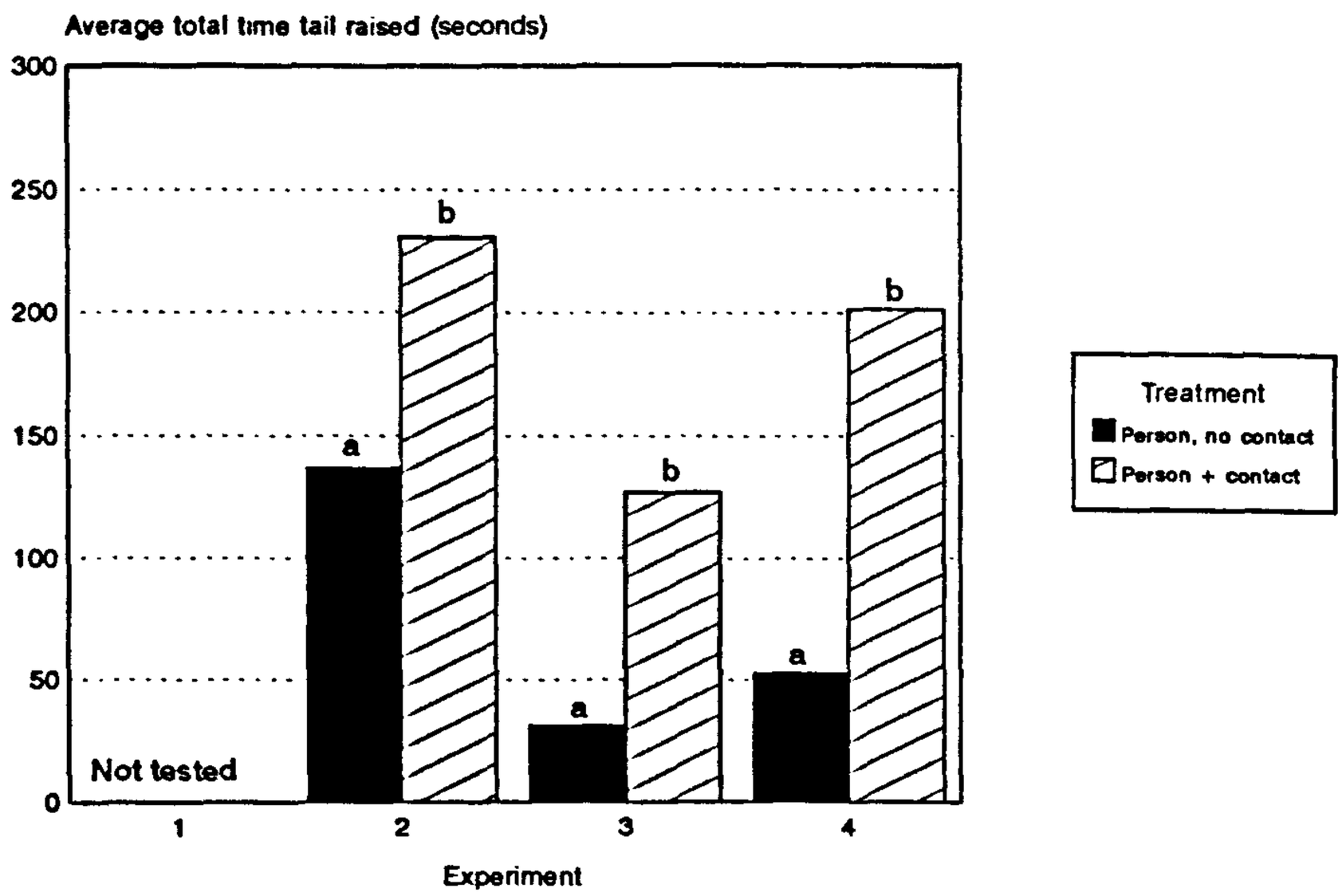
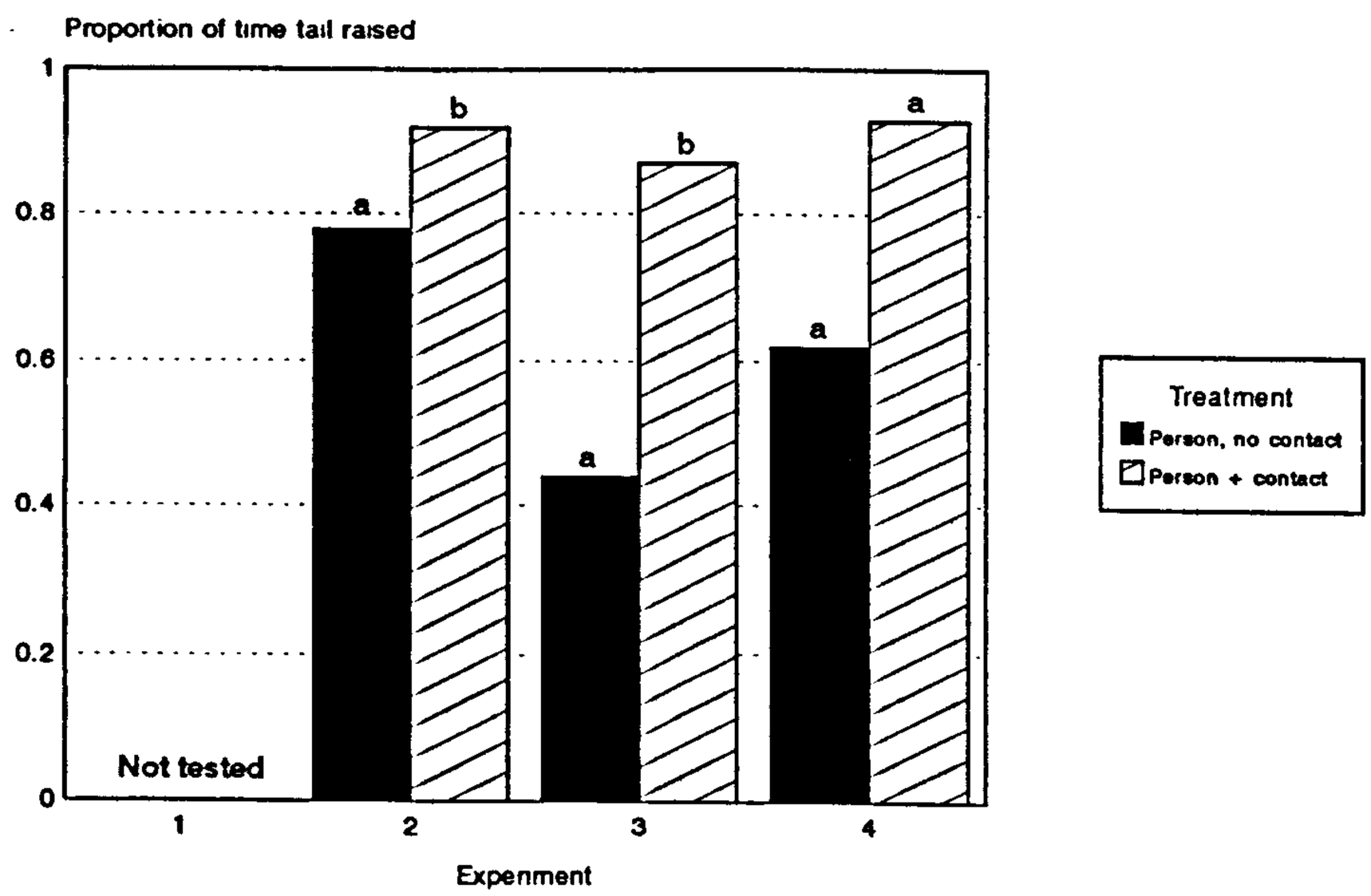


Figure 7.5.5. *Mean proportion of time tail held vertical when on screen under contact and no contact treatments in Experiments 2-4. Where bars within each experiment carry the same letter, treatments were not significantly different at P=0.05.*



although not significantly so in the latter case (Figure 7.5.1).

Rubbing on the person increased in all cases, significantly in experiment 4 but not in experiments 2 and 3 (Figure 7.5.2).

The cats spent more time on screen and therefore in close proximity to the person when contact was given (Figure 7.5.3), and more time was recorded with their tails raised (Figure 7.5.4). A combination of these measures showed that the proportion of time visible that the tail was held vertical increased with contact from the person in all cases, although significantly only in experiments 2 and 3 (Figure 7.5.5).

These effects became more complicated when other cats were introduced in experiments 3 and 4. In experiment 3 where only one other cat was present, this reduced object rubbing slightly but not significantly and had no overall effect on the total amount of person rubbing. However, the presence of another cat had a different effect on time spent close to the person and on person rubbing according to whether contact was given or not (Figure 7.3.1.). Attendance was higher and more person rubbing occurred when another cat was present under the no contact treatment and less compared to the single cat test under the contact treatment.

A possible explanation for this is that the presence of another cat increased the amount of attention-seeking behaviour by both cats in the no contact treatment. When attention was given, rubbing on the person increased (although not significantly) but competition for the rubbing target (i.e. the persons' leg) reduced the number of rubs each cat could possibly perform compared to a cat tested alone. The cat might therefore spend more time walking on and off the screen in between rubs, hence the lower attendance score for the contact treatment. Although not significant, the proportion of time spent with the tail raised was less when another cat was present, under both treatments, so any increase in attention-seeking rubbing under the no contact treatment was not reflected in increased use of the tail raised signal (Table 7.3.2).

Experiment 4 looked at the effects of the presence of other cats in more detail by comparing three with no other cats present (Table 7.4.2.). The presence of three other cats significantly reduced the amount of time spent close to the person under both treatments and, probably partly as a result of this, the amount of rubbing on the person. Object rubbing was also reduced, although not significantly so. The proportion of time spent with the tail raised was less when others were present under

the no contact treatment but the same as for single cat tests when contact was given (Figure 7.4.1).

Experiment 3 showed a similar effect though not significant, with the tail being raised for a very high proportion of the time under the contact treatment, both with and without the presence of another cat (Table 7.3.2.).

Looking at rubbing in Experiment 4, even in the no contact treatment where rubbing was relatively rare anyway, the presence of the other three cats reduced the mean number of person rubs from 2.4 to 1.0 and object rubs from 9.4 to 7.9. The effect described in experiment three where rubbing increased where competition was present in the no contact treatment was reversed here.

7.6. Discussion

As shown by Mertens & Turner (1988) in response to a stranger, the amount of rubbing performed by these cats on a familiar person increased following contact from that person. It also increased on an inanimate nearby object, presumably functioning as a display behaviour pattern. Similarly, the proportion of time that the cat displayed the tail-raised posture increased with interaction from the human.

The introduction of one more cat to the encounter produced different effects to the introduction of three other cats. There are several possible explanations for the different effects caused. Firstly, and hopefully not the sole reason, there is the possibility that experimental conditions produced the effects. The complication with camera view has already been mentioned. Also, different animals were used for each experiment and, although cat to cat variation was accounted for in the analysis the overall group tendencies may have differed.

On a more behavioural basis perhaps what was recorded was a representation of the strong link between the use of the rubbing and tail-raised behaviours. Earlier chapters have emphasised the link between these two types of behaviour patterns which is why they were singled out for these experiments. Looking at the rubbing response on the person it seems quite plausible that simple competition for attention would produce the result described above in Experiment 3 with increased rubbing on the person to gain attention and less rubbing possible by two cats compared to one once attention was given. It is interesting that this effect was not reflected in the object rubbing suggesting that the cats were competing for the person specifically, not

just for rubbing surfaces.

Along the same lines it may be that in Experiment 4 there were just too many cats in the vicinity of the person to rub satisfactorily even to gain attention in the no contact treatment. The cats might be expected to compensate for this, seeking attention by increasing the level of tail-raised displays. However, they did the complete opposite, spending proportionally more time with the tail lowered.

The fact that the tail-raised display was inhibited in a situation where it was the one of the few non-competitive unambiguous signals that the human would understand (being familiar), suggests that the cats had some strong reason for not using it. It may be that the increased use of the tail-raised posture in situations where rubbing could not ensue is inappropriate in cat society. The human-cat relationship may not have evolved to the extent that cats exhibit different relationships between behaviour patterns used in cat-human situation compared to the cat-cat situation.

Alternatively, the cats may have been avoiding the possible misinterpretation of the tail-raised response by the other cats as a cat-cat signal rather than a cat-human signal - this would be most likely when the human was not responding and the cats were more aware of each other in the no contact situation. Contact from the person restored the level of use of the tail-raised display to that of a cat tested singly in Experiment 4 and just below this in Experiment 3. Possibly with attention focussed more strongly on the person giving contact, the cats were less aware of signals given by each other which, if misinterpreted as being towards each other, may have been inappropriate to the relationship or situation.

The reduction in rubbing and tail-raised gestures towards the person in the presence of other cats has an important implication for the owners of more than one cats. If these results are applicable to the domestic situation, then owners of more than one cat may suffer a reduction in the amount of interaction-seeking behaviours received from each cat and less response from each individual when giving them attention (although the net effect, from more than one individual, will be more). The results of Experiment 3 suggest that owners of just two cats may benefit from competition between them in receiving raised levels of attention-seeking head rubbing.

With such small numbers of cats involved, it is difficult to judge the applicability of these results to the domestic situation. Much larger scale experiments, using more individuals and more replicates should help to confirm some of the complexities of

the use of tail-raised and rubbing displays by cats towards familiar humans, especially if performed in the cat's home environment.

Nevertheless these experiments have, in addition to examining the human-cat relationship, stressed the close association between the use of head rubbing and raising the tail even in the cat-human context.

CHAPTER 8

General Discussion

The young male, SI, shortly after being released at Chilworth following neutering.

SI one year after neutering.

CHAPTER 8 - GENERAL DISCUSSION

8.1. The existence, origins and functions of sociality in neutered cat colonies

The three neutered colonies of cats investigated in this thesis all showed a complex network of social relationships between the group members. In each case there was large variation both in the behavioural styles of individuals and in the relationships between pairs of cats. Cats directed certain behaviour patterns towards, and received certain patterns from particular partners. This indicated that they recognised individuals, or at least individual status, and were therefore reacting in a socially based manner.

Sociality was thus observable in a group of cats neutered before reaching sexual maturity (the University colony) and in two groups whose members were neutered after reaching sexual maturity (the Knowle and Chilworth colonies). This applied in the year following neutering, 2-3 years later, and 4-5 years later in the Chilworth, University and Knowle cats respectively. In addition, the colonies were all of different size, age/sex structure and experienced very different ecological surroundings to one another. The existence of sociality in such different groups of neutered cats suggests that it is a feature likely to be associated with most neutered groups.

Whether an inherited inclination towards sociality in the cat is responsible for the formation of groups, or whether sociality arises secondarily as a result of grouping around a food source, has received little attention in the literature. It is, however, an important question when considering the origins and functions of sociality in both entire and neutered groups of cats.

The basis of sociality studied in breeding groups appears to be centred around the females, with matrilineal affiliations dictating the success of raising kittens (Kerby, 1987). Even when colonies have not been studied in such detail, authors generally regard the females and their offspring as the core social units in cat society e.g., Laundre (1977). Breeding males appear loosely linked to the groups in order to attain maximum mating success, e.g., Dards (1979). By inhibiting sexual behaviour and preventing maternal behaviour, neutering therefore removes the apparent main function of sociality for both males and females.

The question therefore arises as to why group-living cats continue to display social behaviour following neutering. Neutering removes, or at least reduces, the

proximate (internal) stimuli of hormone levels. It might therefore reduce sociality if this was controlled by the same hormone balances. Evidence from the colonies studied shows that this is not the case, implying that the proximate causes of non-sexual, non-maternal social behaviour are not (primarily) sex hormones.

Although possibly serving a role in *promoting* social behaviour, the expression of maternal and sexual behaviour is not apparently necessary for its development, as illustrated by the University colony where the cats were not able to express these behaviours before neutering. The group nevertheless developed a social structure.

That sociality continues and, in some cases, develops with no consequent reproductive advantage suggests that cats must have a strong proximate reason for behaving socially that is unaffected by reproductive activity. In all three colonies studied, food provided by humans was ample to feed all the colony members. There was therefore no need for competition or aggression with respect to food, sexual partners, or nesting sites. It is possible that competition for space was a factor in the University colony but this was unlikely in the other groups. The preference for particular resting sites by the different individuals at Knowle may have reflected either personal preferences or possibly resulted from competition for the better sites.

Benefits of sociality for the Knowle and Chilworth groups may have included increased retention of body warmth through close association with others during the winter months, and reduced parasite load through mutual grooming. The availability of warm indoor quarters in the University colony suggests that the maintenance of body warmth was not a problem for them, whilst, as an isolated population, no external parasites were present. Though possibly of importance to the Knowle and Chilworth groups, these benefits, nevertheless, do not seem strong enough to account for the development of sociality. Also, a low level of allogrooming was observed in both the Knowle and Chilworth groups (at least during daylight), suggesting that removal of parasites was not a major driver of social interaction. The lack of any obvious strong advantage to sociality in these colonies may provide some evidence that group-living cats behave socially through an innate tendency to be social rather than from any secondary benefits of sociality accompanying group-living.

Whether sociality is inherent in all cats is another matter and is discussed by Bradshaw (1992) in relation to the flexibility of cat social behaviour. One theory suggested is that all cats have the ability and behavioural repertoire necessary to adapt to living at any density and with or without conspecifics, according to their

ecological circumstances. This accounts for those individual cats who, during their lives switch between a solitary non-social and a group-living social state, as documented by Corbett (1979).

8.2. The social behaviour of males and females in neutered groups

In the University and Chilworth colonies, sufficient numbers of cats existed to make generalisations about the different sexes. In both colonies the males were more interactive and showed a higher level of proximity to other cats than did the females. An interesting effect in the University colony (unfortunately untestable in the other two groups) was that the behaviour of the male and female cats, although different in quantity, was qualitatively the same. Thus neutering, by removing the reproductive and, in the case of the females, the mother-kitten elements of the behavioural repertoire, has left a basic set of behaviour patterns available equally to both males and female cats.

Females

As mentioned earlier, the low interaction rate by and among females might be due to the reduction in female bonding behaviour observed in breeding colonies in connection with the sexual and maternal behaviour of females.

Evidence from studies of other mammals suggests that females in non-breeding condition display very different social characteristics from when they are in oestrus, pregnant or raising young. Fallow deer, for example, are seasonal breeders, with the rut occurring during October and most births during June and July (Putman, 1988). As females prepare for the birth of their fawns they become more solitary and the number of large groups correspondingly decreases. By August, group sizes increase again as does and fawns join with other family groups. They then rise again during September and October as females collect at the rutting stands (Putman, 1988).

Looking more specifically at social *behaviour,* many species exhibit the phenomenon of socially induced reproductive suppression in females, e.g., wolves (Schotte & Ginsburg, 1987; Zimen, 1975; Rabb et al, 1967) and many primate species (Heistermann et al, 1989). Such females, often reduced to an anoestrus state, have been shown to display different social behaviour to the individual(s) exhibiting

reproductive behaviour, often assisting the latter in raising young. Altmann (1987) comments that in his wolf packs the most central role appeared to be that of the alpha female. However, he points out that the social functions associated with other, seemingly peripheral, pack members may be essential to the integrity of group organisation and that removal of these individuals might result in abnormal social behaviour.

Neutered female cats in a colony may therefore assume a similar pattern of behaviour to reproductively suppressed females in other species. The different social system (e.g., lack of co-operative hunting) and absence of any dominant reproductively active female in the cat, however, makes any analogies between cats and wolves rather tenuous. A more likely possibility is that the removal of the reproductive hormones in neutered female cats may reduce their social behaviour to a level similar to that of females in anoestrus condition. Unfortunately, studies of intact colonies of cats have concentrated on the reproductive success of breeding females and have not distinguished their behaviour outside the breeding condition.

Tobach (1988) points out that studies of social behaviour are primarily devoted to aspects of reproduction. In addition to the obvious processes of sexual reproduction, incubation, and parenting, the patterns of aggression and utilisation of space are often studied in regard to reproduction. Tobach therefore highlights the need for a consideration of aspects of social behaviour that are not related to reproductive behaviour. If included in future studies of unneutered cat colonies, this would certainly aid interpretation of behavioural studies on neutered groups.

Males

In the University colony the male population appeared to have two sections; one group of males were highly aggressive and were fighting amongst themselves, presumably for status; the other males were characterised by much lower interaction rates and less aggression. At Chilworth, again the population was divided. Two of the males appeared hostile towards each other - these were the two older males. The two younger males appeared to have had their aggressive development halted at neutering and, rather than becoming increasingly aggressive towards one another as would occur in entire tom cats, they formed an affiliative relationship instead.

Neutering therefore reduced aggression in some of the males by halting male development at an early stage. Chipman (1990) made a similar observation regarding

male home-ranges in urban areas, those males neutered younger having reduced ranges compared to those neutered later.

Neutering did not, however, prevent males from being aggressive where opportunity for conflict was high (in the University colony) or where hostile relationships had evidently been formed prior to neutering (as shown by GI and GH at Chilworth).

8.3. The structure of sociality in neutered colonies

The feature of sociality common to all three of the colonies studied was that pairs of cats present in the core area for less time interacted at a higher rate than those pairs present for a greater amount of time. This suggests that social interaction occurred in its most intense form when one or both of a pair had been absent from the core area for some time (i.e., on returning to the rest of the group). In this way, social behaviour, by reinforcing the social order when cats returned to the group, serves as a mechanism for maintaining the group as a social unit.

Within each colony, certain individuals appeared (subjectively) to be dominant. In each case, this was the cat that received the highest proportion of interactions in relation to the number it performed (i.e., it was the net recipient of the overall flow of interactions).

In both the Knowle and the Chilworth colonies, head rubbing was the behaviour pattern that showed the highest correlation to the overall flow of interactions. This was also found by Macdonald et al. (1987) in their small farm cat population. As in their study, the net direction of flow of rubbing and overall interactions did not yield a linear hierarchy. No obvious advantage accrued to the cats in net receipt of head rubs but these were the individuals that subjectively appeared to be socially dominant. Interactions and, in particular, head rubbing therefore appears to flow from socially subordinate to dominant animals. A similar observation was made by Rowell (cited in Lockwood, 1979) studying baboon groups, with low ranking animals initiating much of the behaviour.

In the University colony, head rubbing (and the Affiliative behaviour category in general) was a relatively rare behaviour and was only regularly performed by one male. The strongest correlate to the overall flow of interactions in this group was the aggressive category of behaviours.

The difference between the colonies in the type of behaviour most closely reflecting pattern of social interactions is probably due to the different surroundings of the groups. It seems logical that, in established free-roaming groups of cats such as the Knowle and Chilworth colonies, social status of individuals will have been established at an early stage and group members will attempt to maintain that structure peacefully where possible. Colony members may reduce intra-group aggression and reinforce their social status via head rubbing. Head rubbing, occurring at a level commensurate with a cat's status in the colony is directed at those individuals with which the cat feels the most need to ingratiate itself, (i.e., towards dominant cats).

Most cats in a free-roaming group are not permanently present in the core area. When one returns, social status is reinforced within the group through interaction, cats interacting with both the returning cat and/or amongst themselves. Interaction and, in particular, head rubbing, may be initiated by the returning cat or by other group members, according to the returning cat's status.

In a group unable to range freely such as the University colony, apart from movements to other areas of their restricted range, the cats have no opportunity to leave the group for any time. The result is a reduction in the rubbing (and, in the case of the University colony, affiliative behaviours in general) performed to maintain social cohesion. Instead the crowded conditions, and the inability to escape from the group, continually forces confrontation between individuals of similar age and social status who, under natural conditions, would probably disperse. This type of enforced confrontation results in aggression. In the University colony, the large number of cats, and particularly male cats, of similar age and physical development, further increased the levels of aggression.

Thus in neutered groups where the social order has been established to the satisfaction of all its members, the social structure will be maintained through affiliative head rubbing from subordinate to dominant individuals. In groups where, due to circumstances such as overcrowding or restricted ranging, social confrontation is difficult to avoid aggression will be common.

8.4. The use of specific behaviour patterns by neutered cats and the significance of the tail-raised posture

The classification of behaviour patterns used by the three groups of neutered cats, and the analysis of behavioural sequencing within interactions, both emphasise the importance of the tail-raised posture when used by one cat approaching another. The position of the tail seems to be crucial in determining which patterns both the Initiator and Recipient cat perform during the ensuing interaction. The tail-raised approach appears to be a form of appeasement, indicating an initiating cat's intention to head rub on the Recipient. The Recipient, as a result, is unlikely to react with an aggressive response. The association of the tail-raised approach with head rubbing suggests that they may occur from a more submissive to a more dominant individual, i.e., when the relationship between two cats is more one-sided.

In the University colony, littermates used the Affiliative behaviour category less often than non-littermates, suggesting a reduced need for affiliative appeasement interactions between neutered cats born and raised in the same litter.

In all three colonies there was a separate category of behaviours, not involving the tail-raised posture, but still apparently amicable in nature. This category (described as Approach/Sit) encompasses those interactions when an Initiator approaches with the tail lowered and sits with the Recipient. They may stay like this for some time, occasionally grooming or sniffing one another.

De Waal (1991) observed that in captive groups of rhesus monkeys, animals with positions close to one another in the rank order tended to associate more frequently, feed and drink together more frequently and also engaged in more aggression than individuals far apart in the rank order. He suggests that the relatively high frequency of aggression among close ranking monkeys did not remove the beneficial components of such relationships, as reconciliation behaviour allows primates fully to integrate aggressive tendencies into their social relationships.

From the analysis in Chapter 3 of this thesis, the Approach/Sit category of amicable behaviour is more closely linked to the Aggressive category than is the Affiliative group of behaviours. Approach/Sit behaviours may therefore occur between individuals more evenly matched in terms of social status, making it unnecessary for the Initiator to appease the Recipient by raising the tail on approaching and then head rubbing, whilst at the same time making an aggressive

confrontation more likely.

The existence of group to group variations in the organisation of behaviour patterns was another feature of the three colonies studied. This raised the possibility of genetically based "dialects" of behaviour occurring in different groups. If the development of such dialects is a reflection of the flexibility of cat social behaviour, this may help explain why certain behaviours, less open to misinterpretation by a strange cat, appear to serve many purposes in cat society. Two of these core behaviours, the tail-raised approach and head rubbing have already been shown to feature strongly in cat to cat interactions, and as shown by the experimental work carried out subsequently, also feature strongly in cat-human interactions.

8.5. The behaviour of the neutered cat towards humans.

The importance of the tail-raised posture and head-rubbing as methods of communication in the neutered cat-human relationship is emphasised in the experiments described in Chapter 7. Head-rubbing on objects appears to be an attention-seeking display behaviour, illustrated by its increased use by each cat when a familiar but uncommunicative person was in the same room, compared to when the cat was alone. Head rubbing, both on objects and on the person, plus the amount of time spent with the tail-raised increased further with attention in the form of talking and stroking from the person.

Pet cats often head rub on their owners when returning to the house after a period away. The use of head rubbing by pet cats in this socially interactive way is reflective of its use in the group-living cats described earlier. This suggests that the cat may regard its owner as a dominant individual in its "core group". Possibly the human response of stroking the cat may serve as a substitute form of rubbing from the cat's point of view, producing a more even flow of "rubbing" between cat and owner.

The rubbing response of cats towards humans appears to be far more intense than that used in the cat-cat situation. The cats used in the experimental studies outlined in Chapter 7 were all members of the colony studied in Chapter 6. Very little cat-cat head rubbing was observed within this colony yet all the individuals tested showed a high response towards humans. The cause is unclear. Possibly, the cat has fewer avenues of communication available to it when interacting with a

human compared to another cat (e.g., many facial expressions may be misread or not even noticed by a human). This might cause the cat to concentrate on the performance of obvious and established forms of communication such as head rubbing.

That cat-human and cat-cat communication and relationships are not entirely separate is suggested by the effect of the presence of a human observer on the cat-cat interaction in the University colony cats. Similarly, the experiments described in Chapter 7 support findings from Mertens (1991) that the presence of more than one cat in a human-cat encounter results in a reduced degree of interaction from each cat towards the human, in comparison with single-cat situations. This may have an inhibitory effect on cat-human communication, suggesting that owning several cats may create competition among the cats for attention from the human. In contrast to this, the presence of just two cats may raise the level of competition between the cats to a level that benefits the owner in terms of amount of head-rubbing received. This latter possibility requires further work.

In the neutered pet cat, head-rubbing, in addition to being used as a general means of social communication, is often used as a food-soliciting behaviour towards humans (Bradshaw and Lowe, personal communication). In studies of reproductively intact cat colonies, Macdonald et al. (1987) and Passanisi (unpublished) have reported that most rubbing occurred from kittens to adult females. In Macdonald et al.'s group there was a close relationship between the number of times that each kitten rubbed on a certain female, and the number of nursing bouts it received from that female. For the pet cat, dependent on its owner for food, it seems logical that it would use the same behaviour which when used on humans, as with the mother cat, seems to be particularly effective at eliciting the provision of food.

As one of the most distinctive forms of cat communication, head-rubbing provides an example of a behaviour developed as a kitten and maintained into adulthood. This occurs in both neutered group-living cats and neutered pet cats in single-or multi-cat households.

8.6. The future of neutered cat social behaviour

Head rubbing was closely associated with the tail-raised approach in the free-living groups and in the cat-human interactions studied in this thesis. This suggests that, with respect to certain behaviour patterns at least, the cat-human relationship may not have evolved to the extent that cats exhibit different relationships between behaviour patterns used in cat-human situations compared to the cat-cat situation. In order to retain the ability to move from an existence close to and dependent on humans to a free-living feral state if necessary, it makes sense to maintain a single system of communication.

From an evolutionary point of view, and in comparison with the amount of time that cats have been living alongside humans (since at least 1600 BC), the widespread introduction of neutering is a very recent phenomenon. The fact that nowadays most pet cats are neutered might be expected potentially to have great significance for future pet cat behaviour. Any aspect of a neutered pet cat's personality that results in the expression of new variations in the use of behaviour patterns will not be passed on to future generations unless the cat is allowed to reproduce before neutering occurs. However, considering the number of centuries that pet cats have been allowed to breed and perpetuate any advantageous alterations in their behaviour towards other cats and towards humans, it is notable that cat-human behaviour still differs relatively little from cat-cat behaviour.

Cat-to-cat variation in behaviour towards conspecifics and towards people does not therefore seem to have produced characteristics that are strongly selected for or against through successive generations. Instead cats appear to inherit certain broad personality types which different cats and people find attractive. So long as all personality types remain equally popular then all of them will remain in the population.

While natural selection is not favouring certain personality types, then neutering is unlikely to make any impact on subsequent generations. Neutering may produce a gradual effect, however, if, as is often the case nowadays, many kittens are sired by the same father. Some owners still allow their female cats to raise one or more litters before having them neutered. There is usually little or no control over the choice of father for these kittens and this role is usually assumed by a local tom cat. As few owners allow their male pet cats to remain sexually intact after reaching sexual maturity, entire males are usually feral or semi-feral in temperament. Thus

many kittens born to pet female cats will be sired by fathers with fairly wild temperaments towards humans. Most kittens if properly socialised when young will develop sociable characteristics towards humans, but the paternal wild disposition still seems to surface in many cases. This gradual increase in feral type pet cats may have a far reaching impact for pet cats in the long term if, as is usually the case, people prefer more a more equable affectionate personality type in their cat.

Future projections aside, the welfare implications of neutering, particularly in feral group-living cats seem to favour the practice. As shown by these studies, sociality remains in such groups following neutering and many of the competitive pressures associated with breeding are removed. Provided food is available on a regular basis, the physical condition of the animals improves and the resulting lack of competition seems to give the animals a much more relaxed and peaceful existence.

APPENDIX 1

LETTER CODES AND DEFINITIONS OF INTERACTIVE BEHAVIOUR PATTERNS.

Behaviour patterns could be performed by the initiator (I) of the interaction or the recipient (R) or both simultaneously (B). The two-letter behaviour code was suffixed with an I, R or B accordingly. Patterns are not listed in any particular order, although locomotory patterns which tend to occur at the start and finish of interactions are listed first.

AP	APPROACH	One cat moves towards another cat whilst looking directly at it. The tail of the approaching animal is not raised vertically.
AR	APPROACH RUNNING	As AP but cat moves at speed.
TA	TAIL-RAISED APPROACH	As AP but with the tail held in a vertical position.
TR	TAIL-RAISED APPROACH RUNNING	As TA but cat moves at speed.
FO	FOLLOW	One cat follows another. The tail of the following animal is not raised vertically.
TF	TAIL-RAISED FOLLOW	As FO but with tail held in vertical position.
MA	MOVE AWAY	Cat moves away from another cat without the tail raised.

TM	TAIL-RAISED MOVE AWAY	As MA but with the tail held in a vertical position.
RE	RETREAT	One cat backs away from another, maintaining eye contact and without raising the tail.
WP	WALK PAST	One cat walks past another, within 1 metre.
TP	TAIL-RAISED WALK PAST	As WP but with the tail held in a vertical position.
CH	CHASE	One cat races in pursuit of another cat.
FL	FLEE	One cat runs away from another cat.
SK	STALK	Cat attempts to approach another cat without alerting it. The belly is pressed to the ground and the ears flattened. The animal moves slowly forward when the other individual is not watching. This often precedes a pounce (PO).
PO	POUNCE	Cat leaps upon another individual.
AT	ATTACK	Cat leaps upon another cat and immediately engages in physical combat.
SI	SKITTISH	Cat races round at high speed playing with objects or with other cats in short, sharp bursts. The behaviour is characterised by extremely rapid and seemingly undirected movements.
CR	CROUCH	Cat crouches on the ground, with all four legs tucked underneath it.

CT	CROUCH TAIL SWISHING	Cat crouches on ground, swishes its tail from side to side and treads with its hind legs.
TU	TAIL UP	Cat raises its tail to a vertical position.
SN	SNIFF CAT	One cat investigates another cat by "sniffing" with its nose.
SR	SNIFF REAR	One cat sniffs the peri-anal area of another.
TN	TOUCH NOSES	Two cats touch/sniff each other on the nose whilst they both stand facing each other. (This pattern can only be performed simultaneously, otherwise it is recorded as a sniff by each cat).
SW	SIT WITH CAT	One cat sits less than one cat's width away from another.
GC	GROOM CAT	One cat licks another cat.
RH	RUB HEAD CAT	Cat rubs its cheek and/or ear against another cat. It begins to rub from the corner of the mouth and continues back along the side of the head.
HF	RUB FOREHEAD CAT	Cat rubs forehead region against another cat.
RF	RUB FLANK CAT	Cat rubs the side of its body against another cat. This often follows on from a head rub (RH).

RT	RUB TAIL CAT	Cat rubs its tail against another cat. when performed simultaneously between two individuals tails may become entwined.
OH	RUB HEAD OBJECT	Cat rubs its cheek and/or ear against an object as with RH. This is often used as a display behaviour during interactions.
OF	RUB FLANK OBJECT	Cat rubs the side of its body against an object. This often follows on from a head rub (OH) and may be used as a display behaviour.
RO	ROLL	Cat rolls on the ground - often used as display behaviour during interactions.
CU	CUFF	One cat strikes another with its forepaw, usually with claws extended.
RP	RAISE PAW	One cat raises its forepaw at another, as if to cuff it (CU) but no contact is made.
PA	PAW/PAT	Cat hits another individual with forepaw but with claws retracted.
WC	WRESTLE WITH CAT	Cat struggles with another individual, raking with its hind legs and pulling it towards the body with its forelegs.
RE	REAR	Cat stands up on hind legs and paws at another individual, frequently twisting its body round or leaping in the air.

BA	BODY ARCH	Cat arches its back upwards and stands rigidly on four legs. Tail is usually curved upwards, ears turned inwards and the fur is fluffed out, maximising the apparent size of the animal.
BI	BITE	One cat bites another.
FI	FIGHT	Two cats engage in physical combat, often wrestling with one another, scratching and biting as they roll over and over.
FR	FREEZE	Cat becomes immobile in response to the behaviour of another cat.
EF	EARS FLAT	Cat flattens its ears to its head so that they lie flush with the top of the head.
EB	EARS BACK	Cat lays ears back, not flat against the head but pointing backwards and inwards.
CE	CROUCH EARS FLATTENED	Cat crouches (CR), flattening its ears (EF) at the same moment.
ST	STARE	Cat stares fixedly at another cat and is not easily distracted by other activity around it.
TS	TAIL SWISHING	Cat moves its tail from side to side rapidly.
TJ	TAIL JERKING	Cat twitches its tail from side to side, up and down, in very jerky movements.
HS	SHAKE HEAD	Cat shakes head from side to side rapidly.

HI	HISS	Cat hisses through its teeth at another cat.
SQ	SQUEAL	Cat shrieks loudly, usually in pain during fighting or playing.
MI	MIAOW	Cat makes a distinct miaow vocalisation when it appears to be trying to obtain something from another cat.
GR	GROWL	Cat makes low throaty growling noise at another cat.
YO	YOWL	Cat makes deep whining noise at another cat.
TL	TRILL	Cat makes high-toned chirruping noise at another cat.
WA	WATCH	One cat watches another cat. This can be distinguished by the way in which the cats eye and head movements track what it is watching.
AV	AVOID INTERACTION	One cat responds to the behaviour of another by deliberately not approaching.
MT	MOUNT ATTEMPT	One cat attempts, but does not achieve intromission. This behaviour is often accompanied by treading movements of the hind legs along the flanks of the recipient cat and holding the recipient firmly at the nape of the neck.
WW	WALK WITH	Two cats walk a short distance side by side parallel to each other and less than one metre apart.

APPENDIX 2

Table 3.2.1. *Transitions significantly (P<0.001) likely to occur between behaviour patterns during interactions in the Knowle, Chilworth and University colonies (behaviour codes are explained in Appendix 1).*

Preceding Behaviour	Behaviours significantly likely to follow (P < 0.001)		
	University	Chilworth	Knowle
API	SNI SRI TUI TNB POI GCI SWI	SNI SRI TUI CUI	SNI SRI SWI
ARI	CHI CUI POI TUI TUB CRR TUR		
BII	WCB ROR SQR WCR		
CHI	FLR	FLR CUI	
CTI	ARI WAI		
CUI	MAR CRR FLR RER	MAR CRR FLR CER	MAR
EBI	CUI FLI TSI		
FLI	CHR		

Preceding Behaviour	Behaviours significantly likely to follow ($P < 0.001$)		
	University	Chilworth	Knowle
FOI	API CTI POI	API	API TAI
GCI	BII MAI SWI GCI HSR		
MAI	API HSI APR HSR WAR	WAR	
OHI	OHI		
PAI	GCR POR RER		
POI	BII FIB WCB SQR		
REI	STB APR		
RHI	RHI ROI SWI TPI SRR	RFI RHR	RFI
RFI		SRR	
ROI	PAI BIR		
RPI	RPR		
SKI	ARI CTI		

Preceding Behaviour	Behaviours significantly likely to follow ($P < 0.001$)		
	University	Chilworth	Knowle
SNI	MAI SWI TNB SNR	WPI	
SRI	MAR TJR		
SWI	GCI MAI MAR	MAR SNR	
STI		STR	
TAI	RHI SNI WPR	RHI TAR TUR	RHI
TFI		TAI TPI	TAI
TMI	HSI TJI		
TPI		SRR TJI WAR	
TRI	TUR		
TUI	RHI TUR WAR	TMI	
WAI	API ARI CTI SKI TRI TSI WAR	TJI	

Preceding Behaviour	Behaviours significantly likely to follow (P < 0.001)		
	University	Chilworth	Knowle
WPI	CUR SNR	WAR WAI TUI STI	TUR CUR
EBB	TSI STB TSB		
FIB	STB		
HFB		RFB	
RFB		TMI	
RHB		RFB	
STB	TSI EBB TSB TSR		
TNB	MAI WPI		MAI RHB
TSB	POI POR		
WCB	REI EBB FIB STB CHR		
APR	RPI	HFB SNR	
ARR	FLI RPI CHR		
BIR	WCB		
CHR	FLI		

Preceding Behaviour	Behaviours significantly likely to follow (P < 0.001)		
	University	Chilworth	Knowle
CRR		EFR	
CER		HIR	
CUR	EBI FLI REI STB BIR EBR	MAI	MAI
EBR	CUR FLR STR TSR	HIR	
FLR	CHI FOI WAI	CHI	
GCR	TMI BIR SRR		
MAR	API FOI TAI TJR	API FOI TAI TFI	TAI TFI
PAR	ROI TSI		
POR	FIB WCB BIR		
RHR		RHI	
ROR	WCB EBR CUR PAR	WAI	

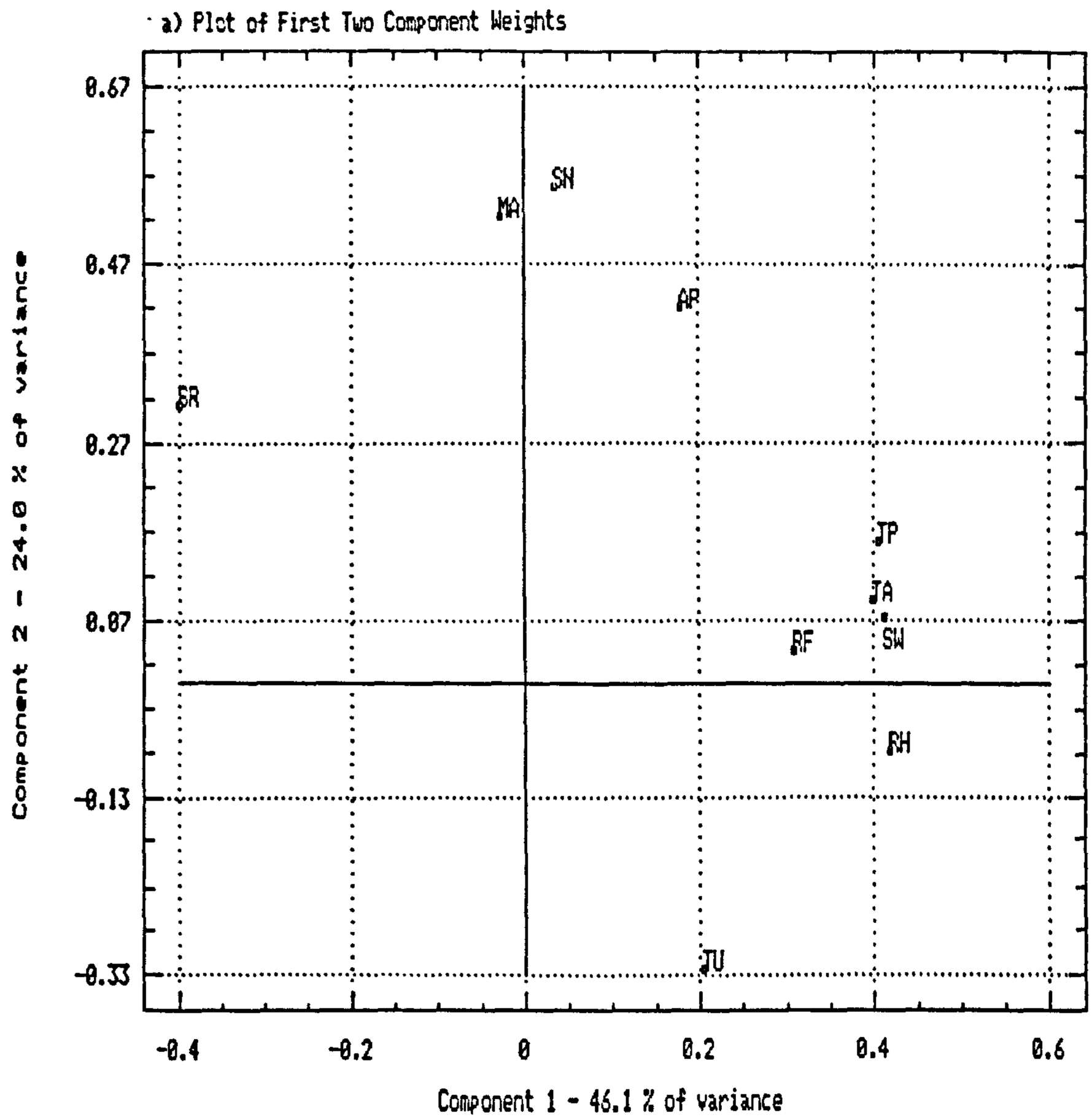
Preceding Behaviour	Behaviours significantly likely to follow (P < 0.001)		
	University	Chilworth	Knowle
RPR	EBI REI STB		
SNR	MAI GCR		
SQR	WCB CUR ROR WCR		
SRR	TJI TUI	SWI	
STR	REI EBR TSR	STI	
TAR		HFB SNR	
TJR	MAR		
TMR	ARI FOI TFI TJR	TFI TAI	
TSR	WAI WAR		
TUR	FLR TMR	SRI RHB	
WAR	ARR TSR	TMR	
STARTING BEHAVIOURS	API TAI CTI SKI ARI WPI	API TAI CHI TPI WPI	API TAI TPI FOI

Preceding Behaviour	Behaviours significantly likely to follow ($P < 0.001$)		
	University	Chilworth	Knowle
ENDING BEHAVIOURS	MAI MAR TMI TMR FLI FLR	MAI MAR TMI TMR TPI	MAI SWI MAR

APPENDIX 3

Figure 5.3.1. a-x. *Principal Components Analyses of behaviour patterns performed and received by each cat in each period and in all three periods combined at Chilworth.*

Figure 5.3.1. a & b. *PCA on behaviour patterns performed by cats during Period 1 at Chilworth. Components 1 and 2.*



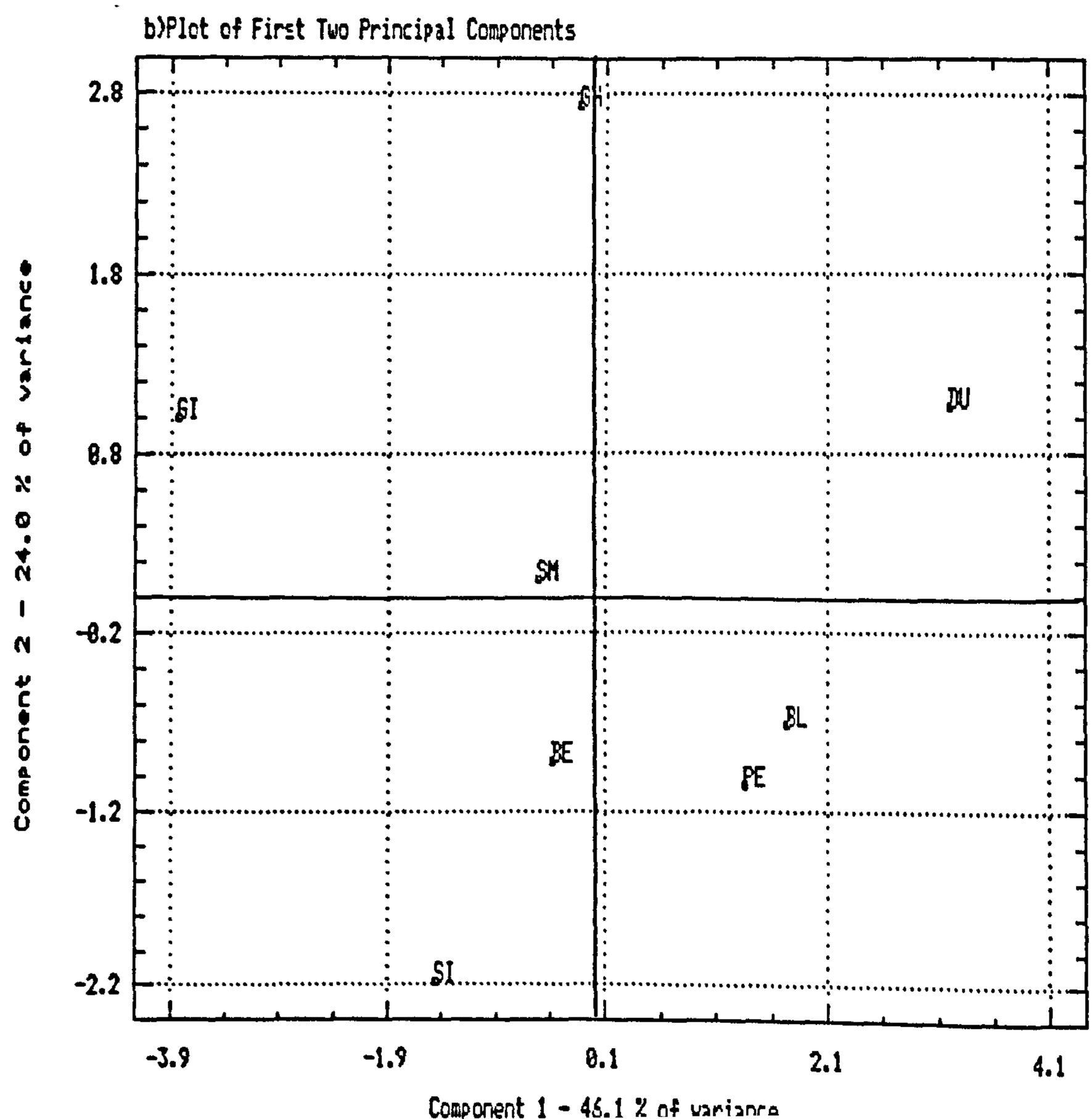
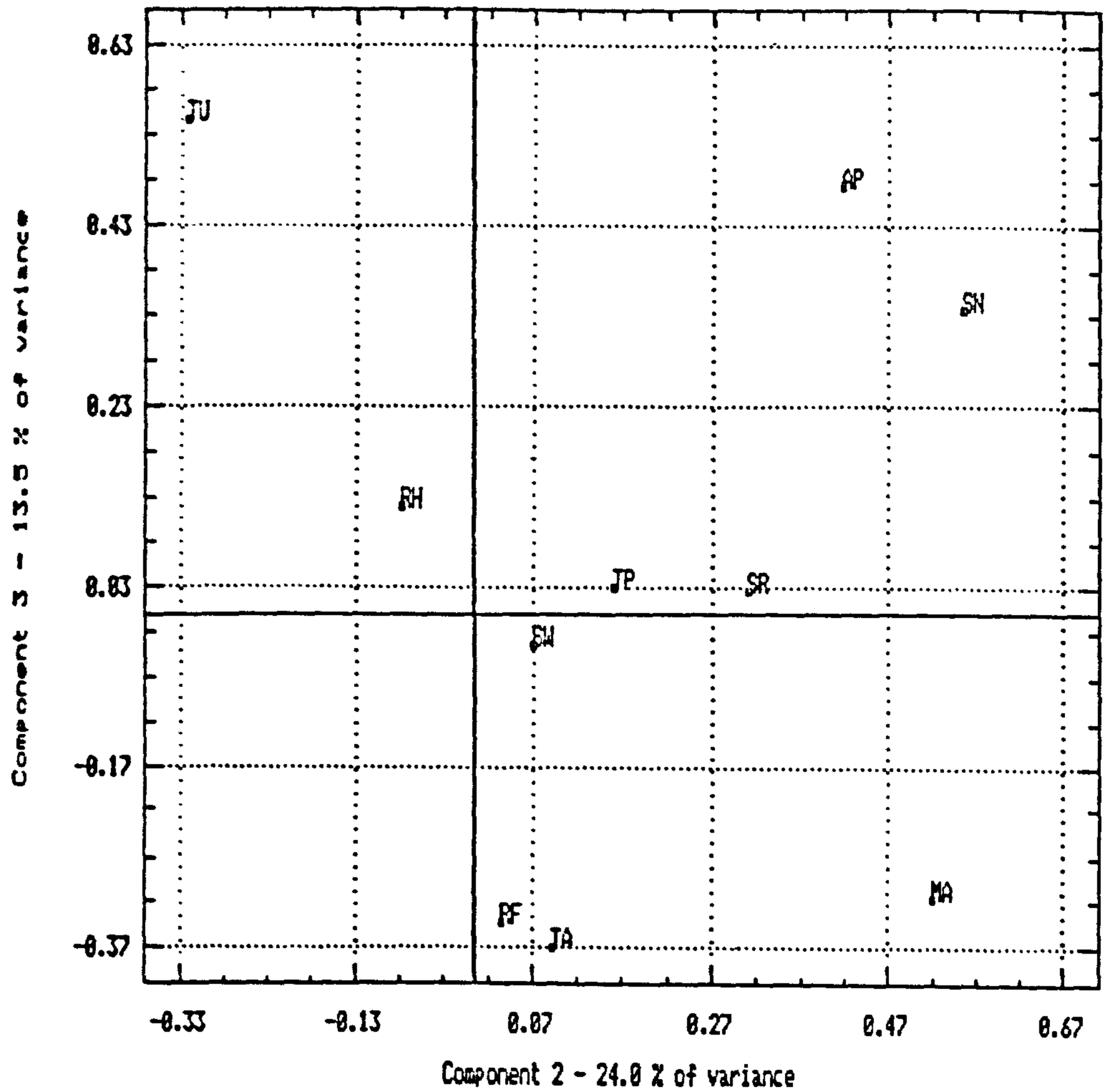


Figure 5.3.1. c & d. *PCA on behaviour patterns performed by cats during Period 1 at Chilworth. Components 2 and 3.*

c) Plot of Component Weights 2 and 3



d) Plot of Principal Components 2 and 3

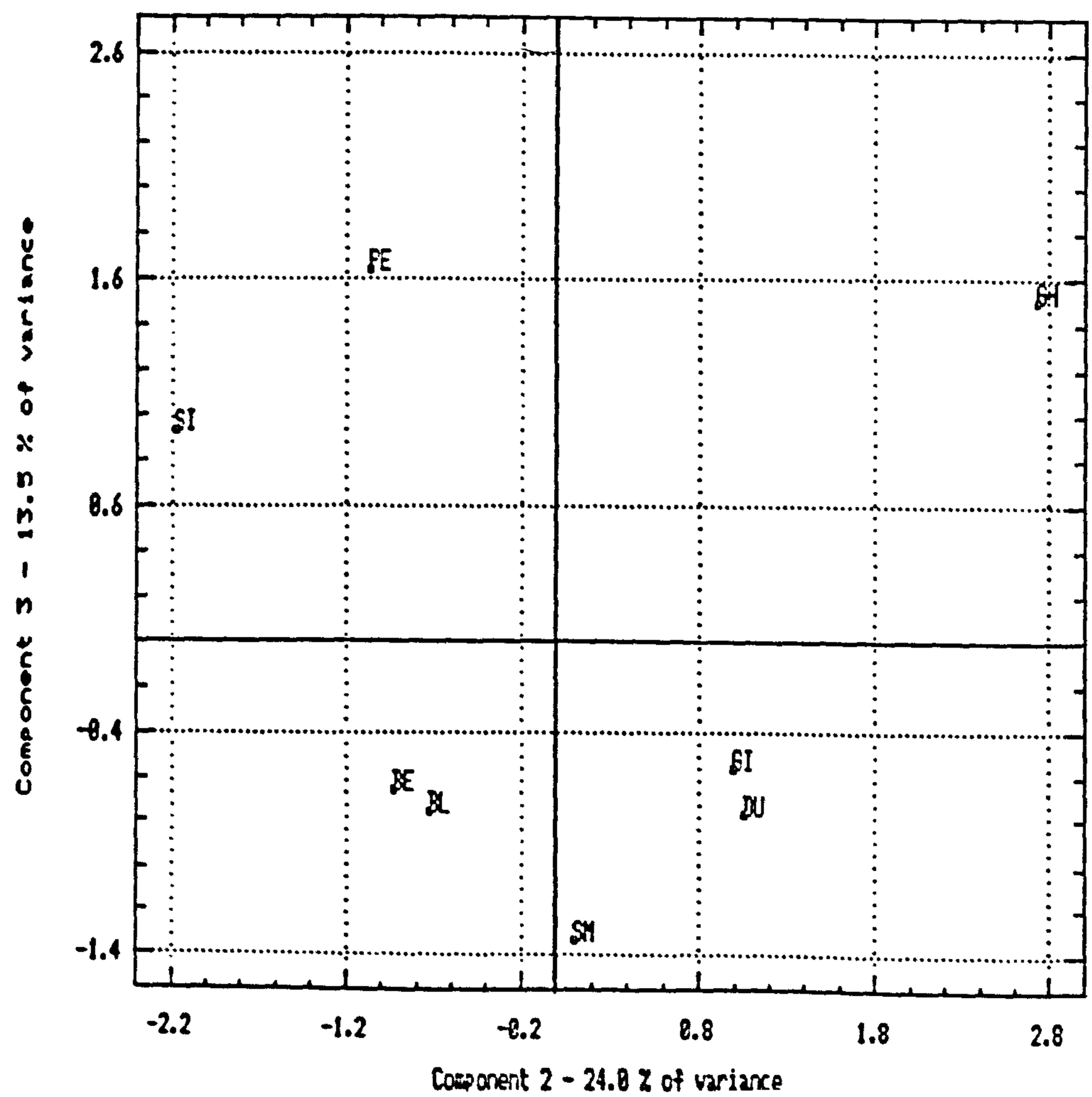
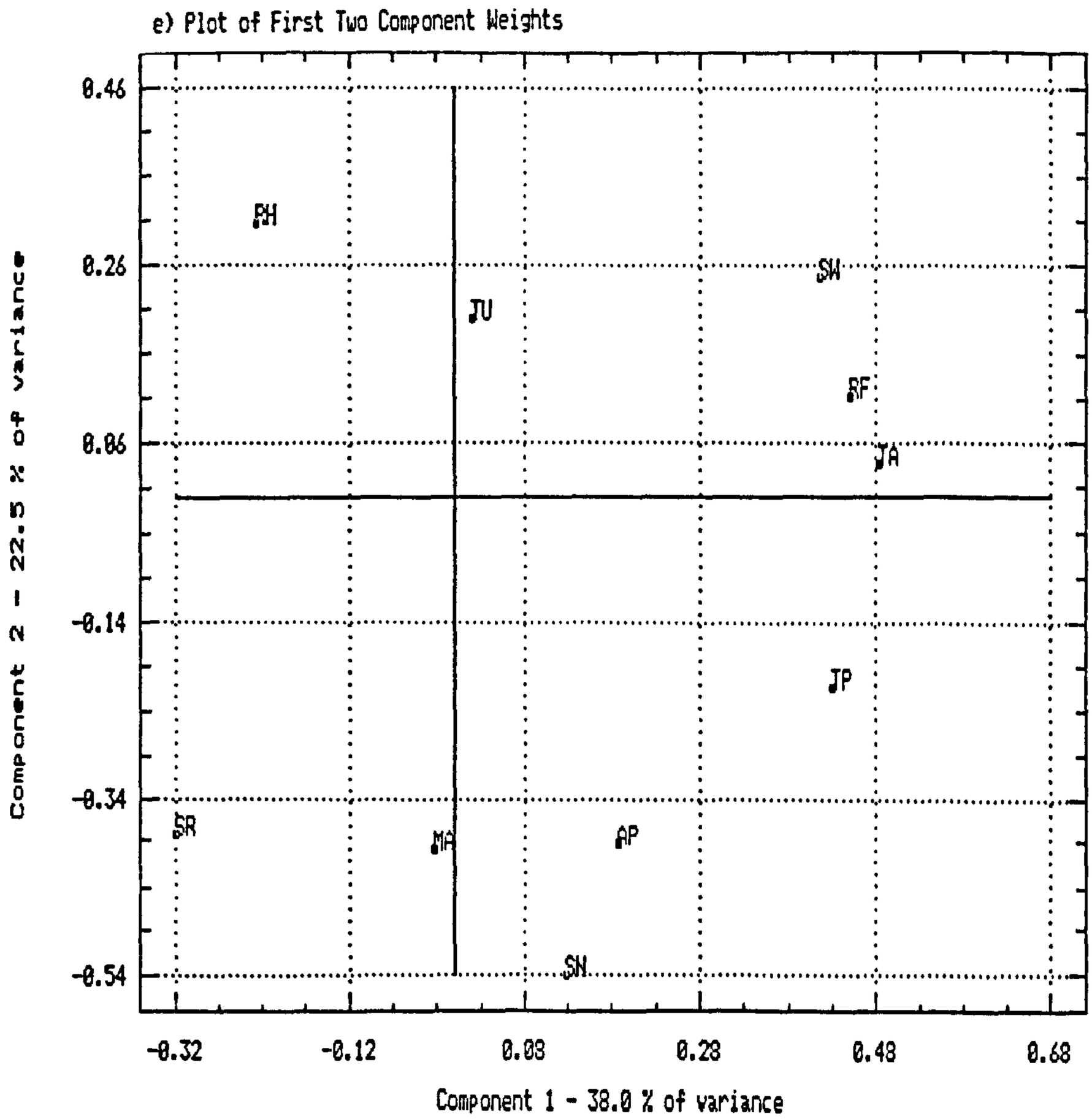


Figure 5.3.1. e & f. *PCA on behaviour patterns received by cats during Period 1 at Chilworth. Components 1 and 2.*



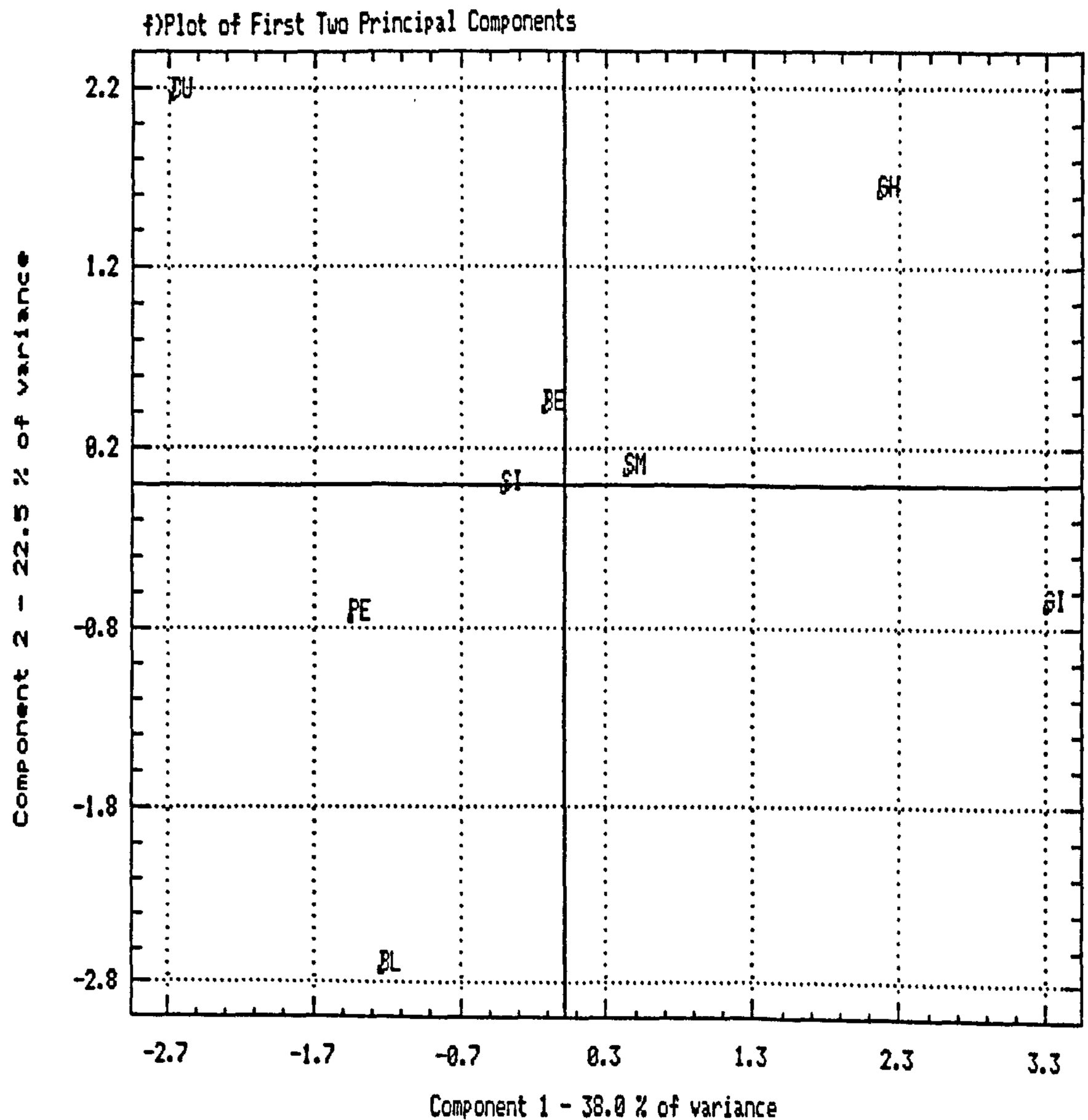
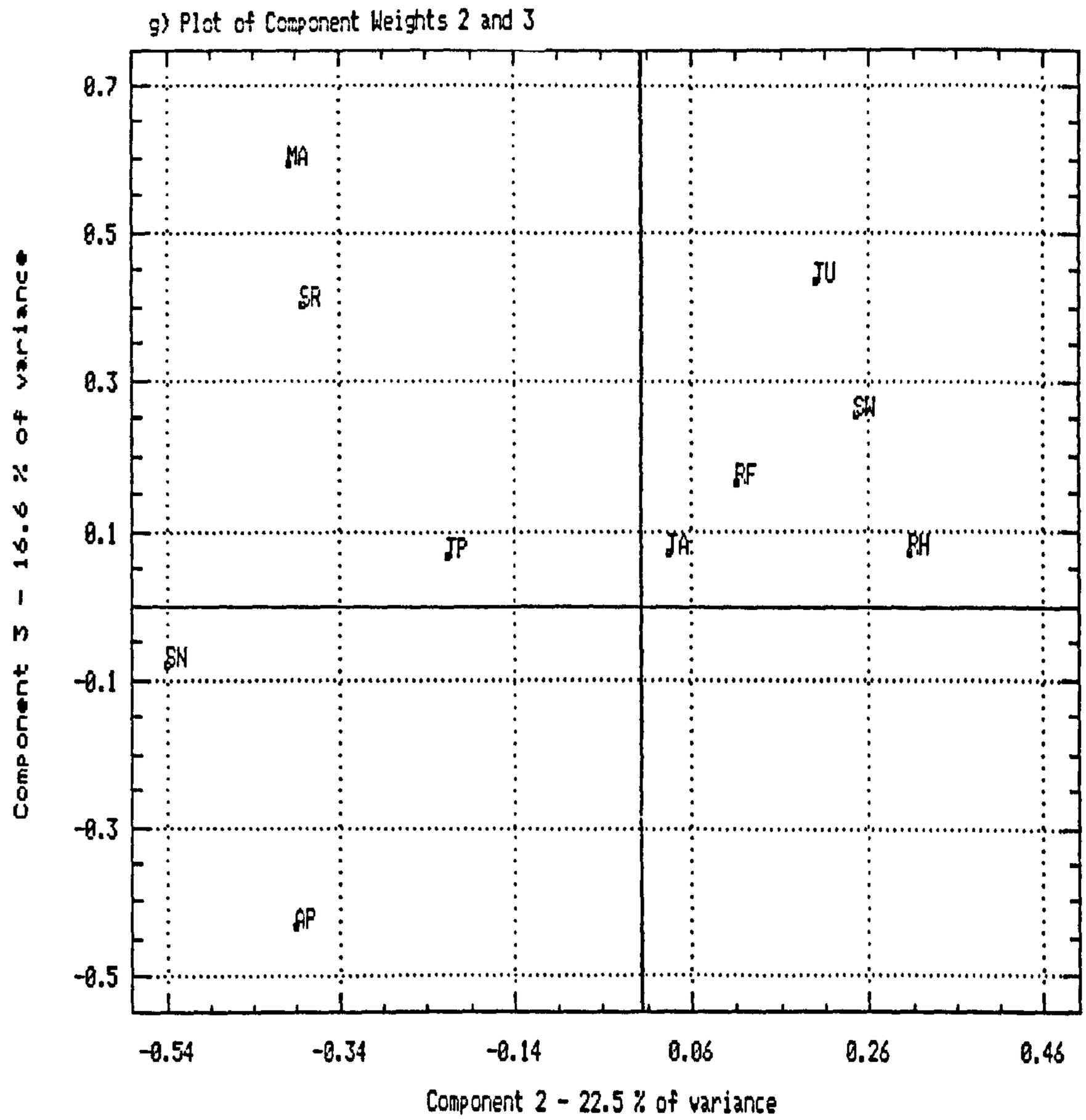


Figure 5.3.1. g & h. *PCA on behaviour patterns received by cats during Period 1 at Chilworth. Components 2 and 3.*



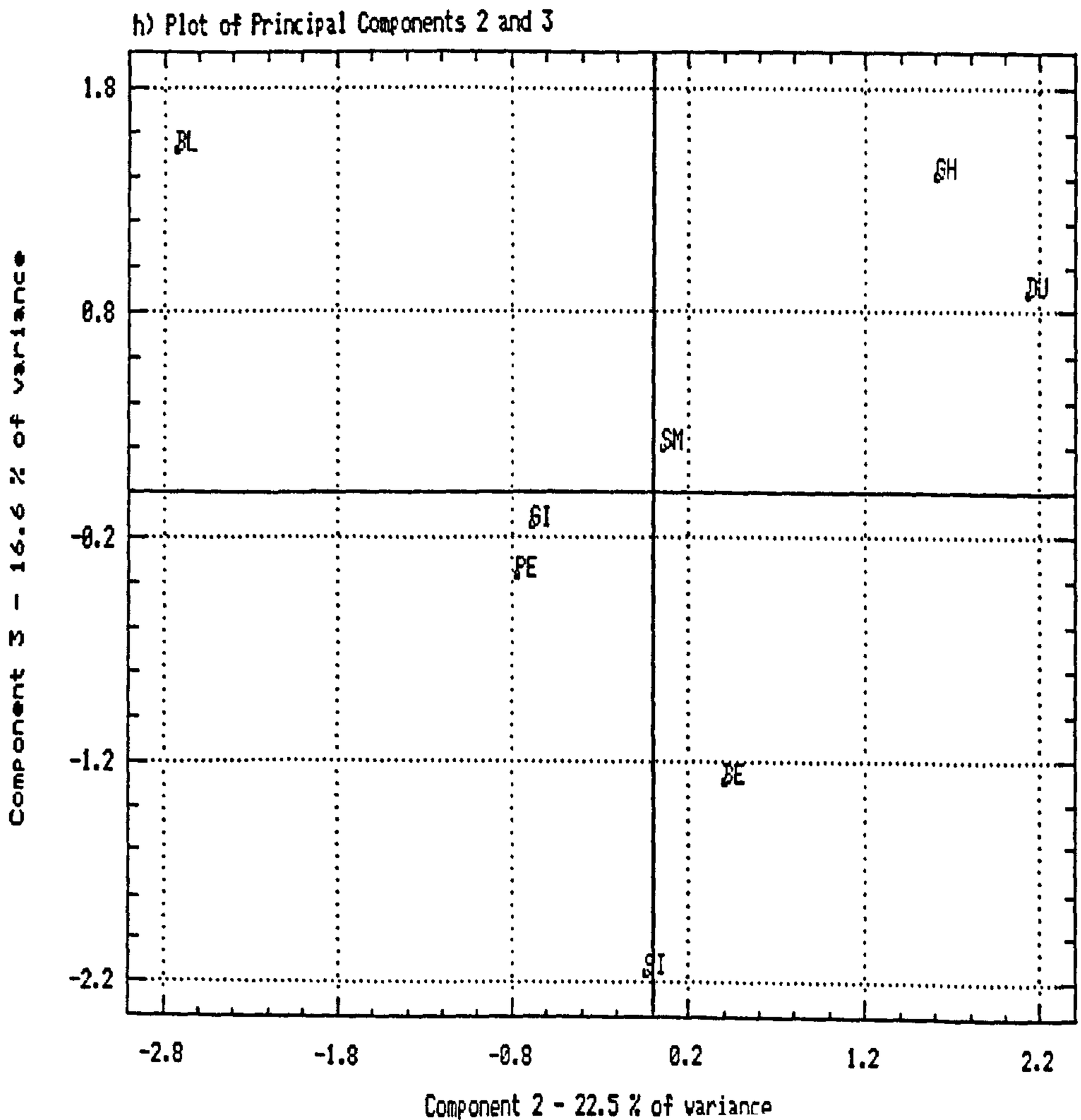
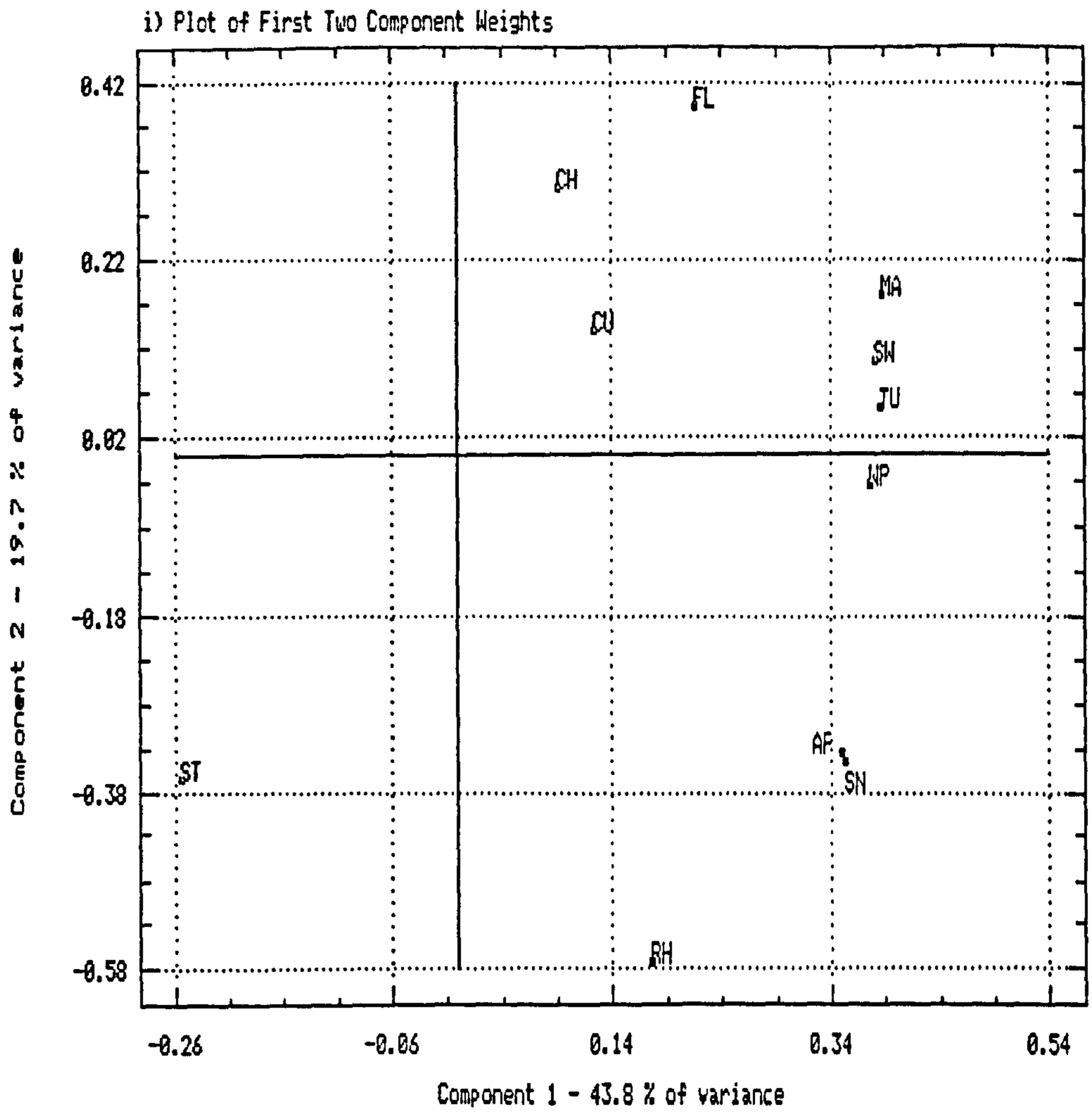


Figure 5.3.1. i & j. *PCA on behaviour patterns performed by cats during Period 2 at Chilworth. Components 1 and 2.*



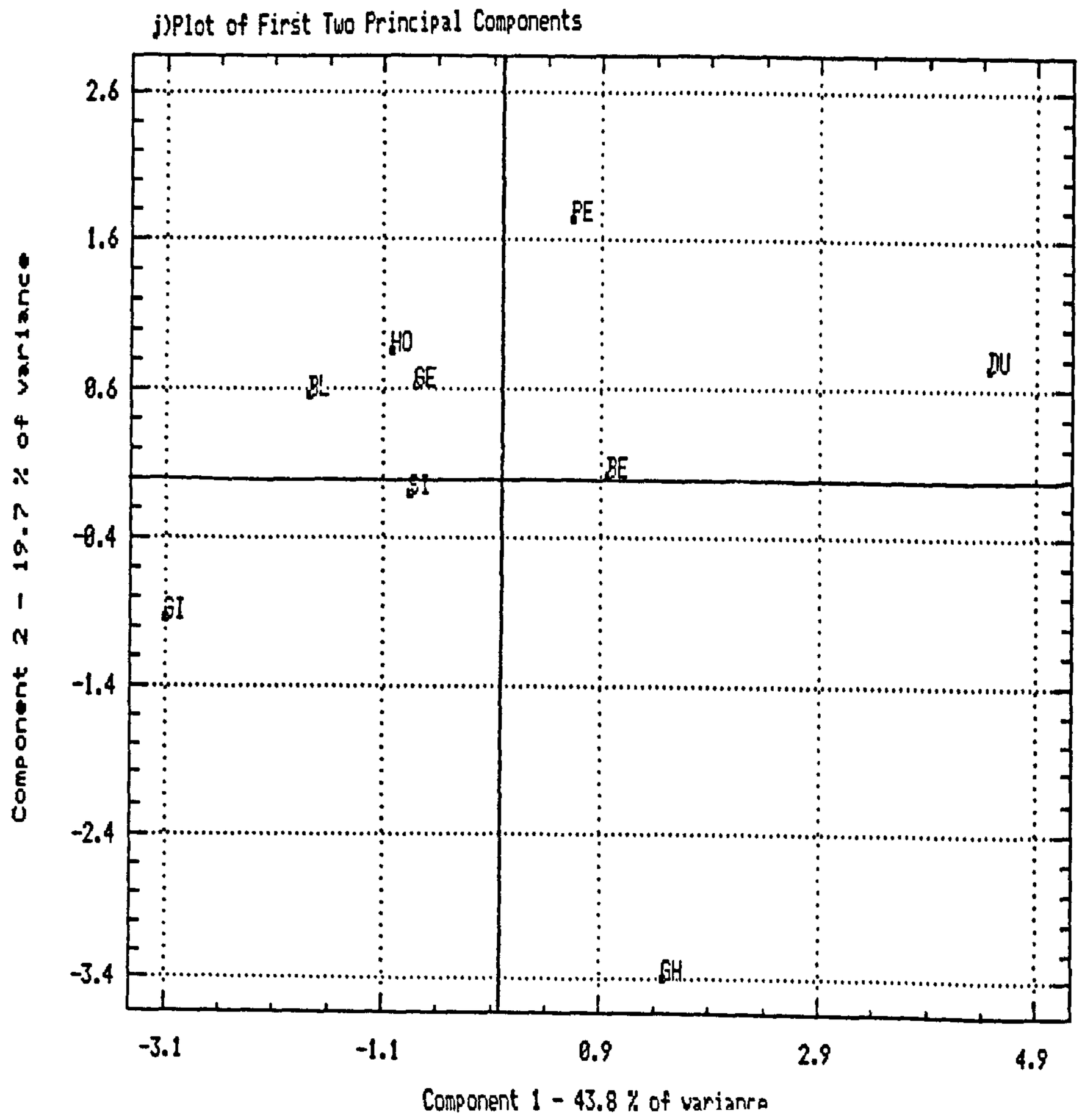
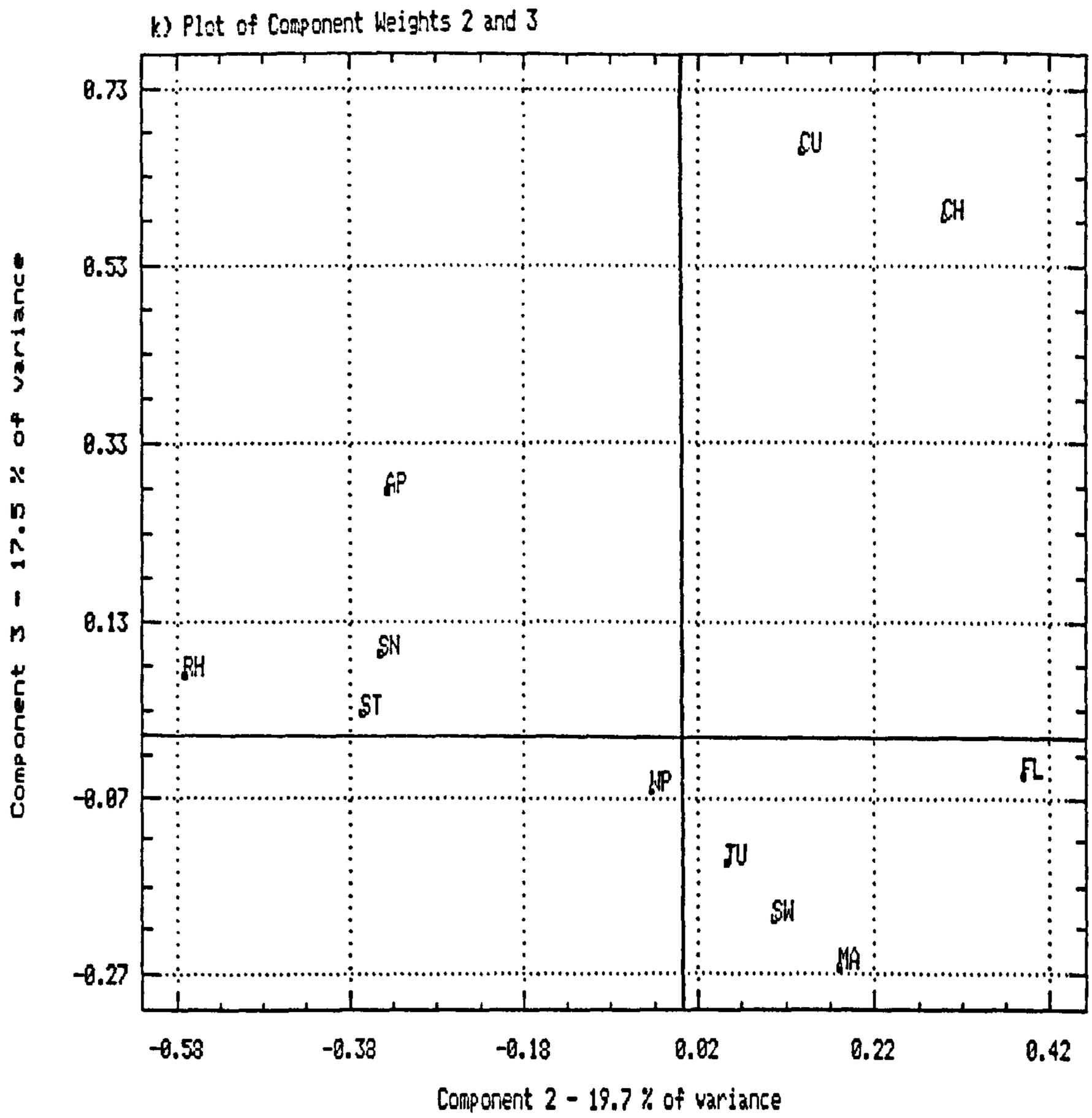


Figure 5.3.1. k & l. *PCA on behaviour patterns performed by cats during Period 2 at Chilworth. Components 2 and 3.*



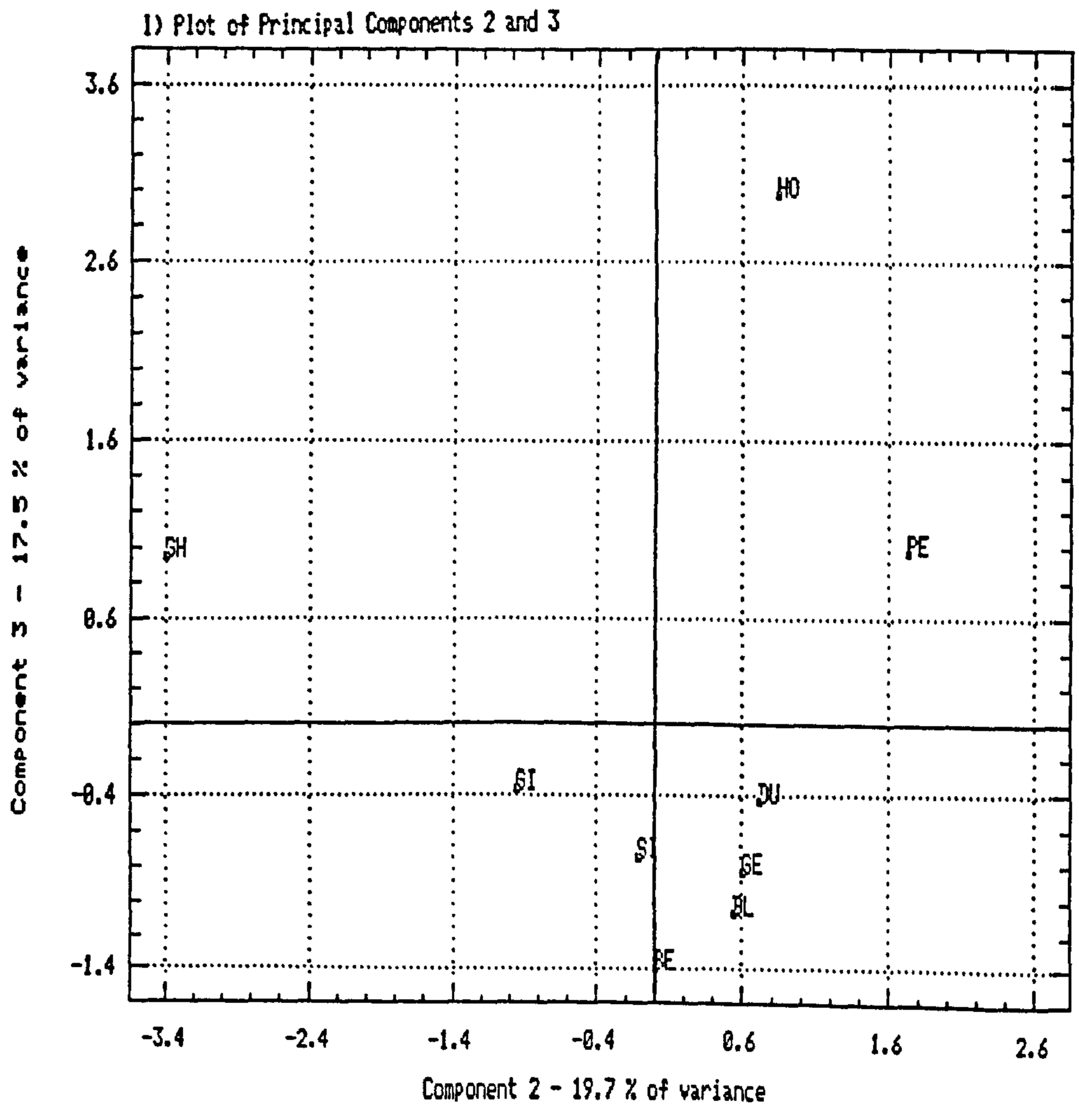
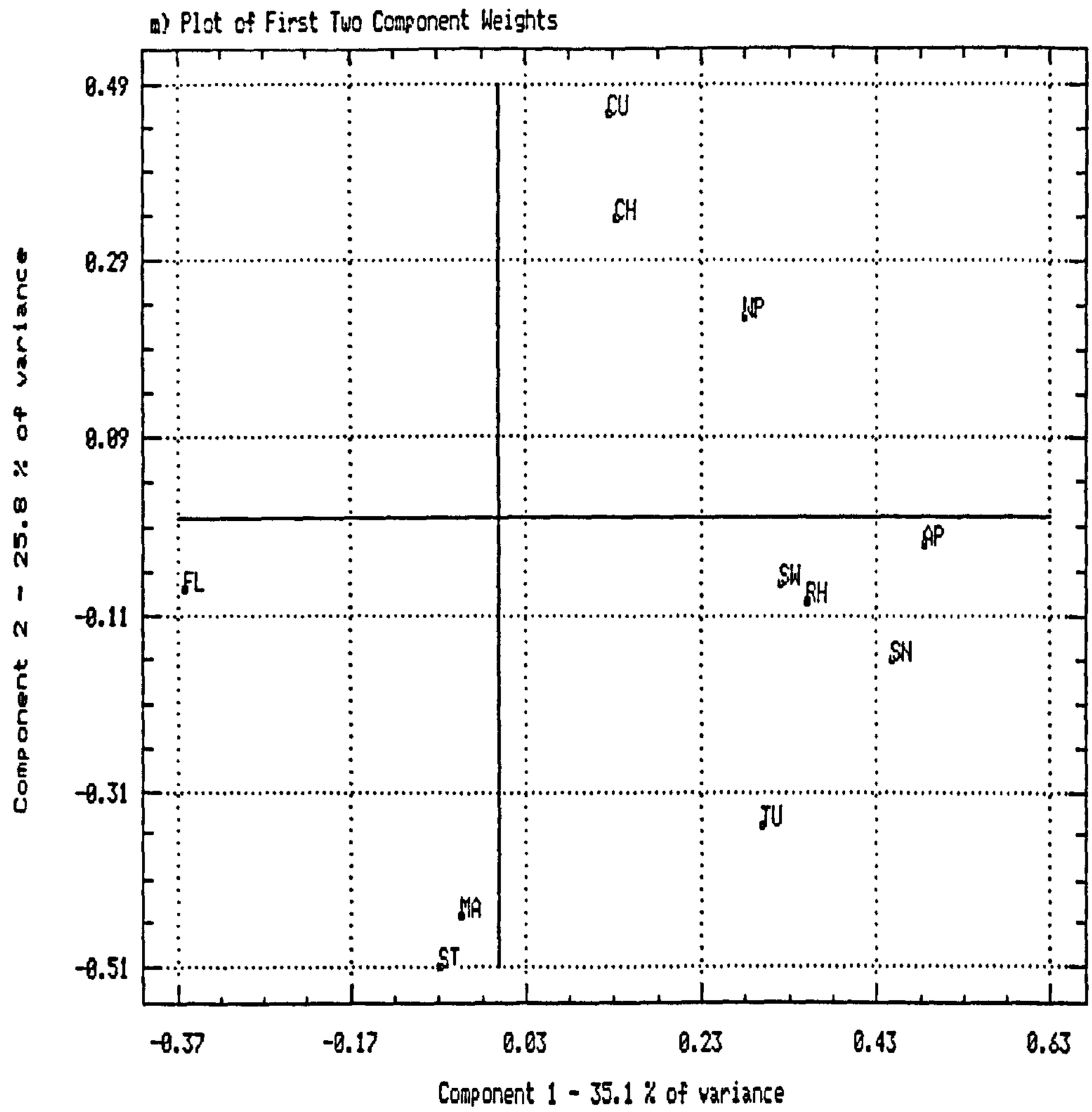


Figure 5.3.1. m & n. *PCA on behaviour patterns received by cats during Period 2 at Chilworth. Components 1 and 2.*



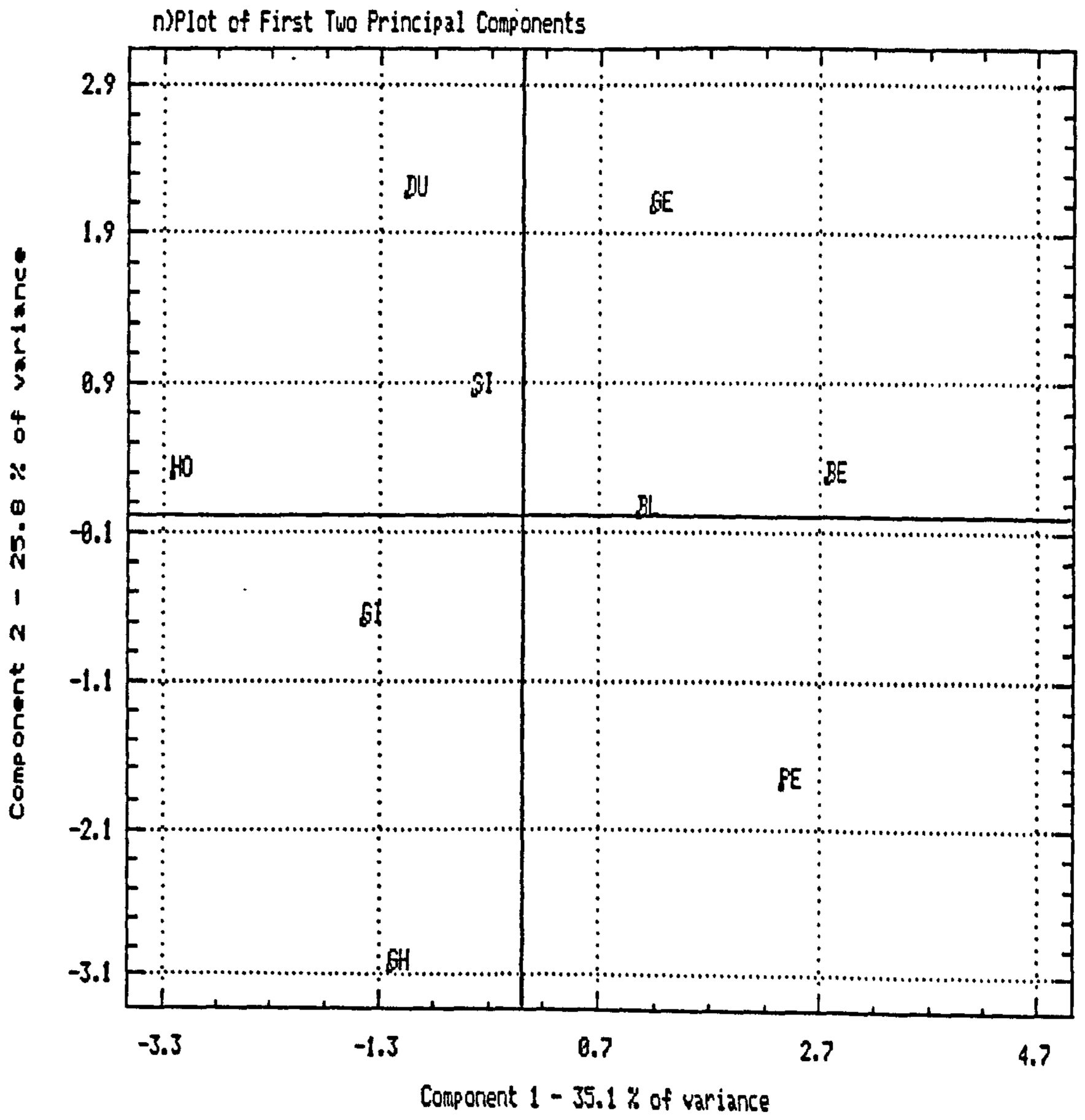
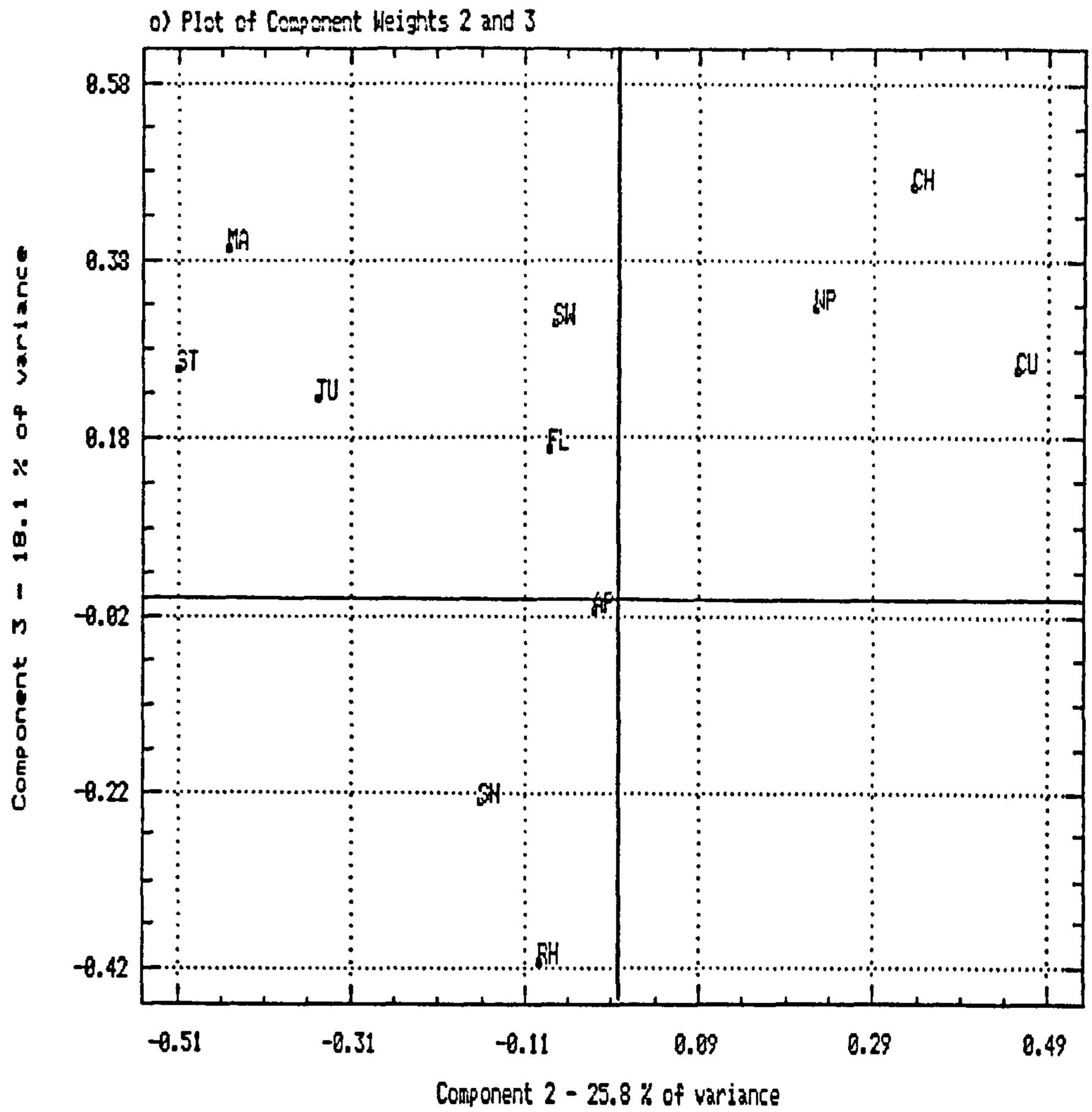


Figure 5.3.1. o & p. *PCA on behaviour patterns received by cats during Period 2 at Chilworth. Components 2 and 3.*



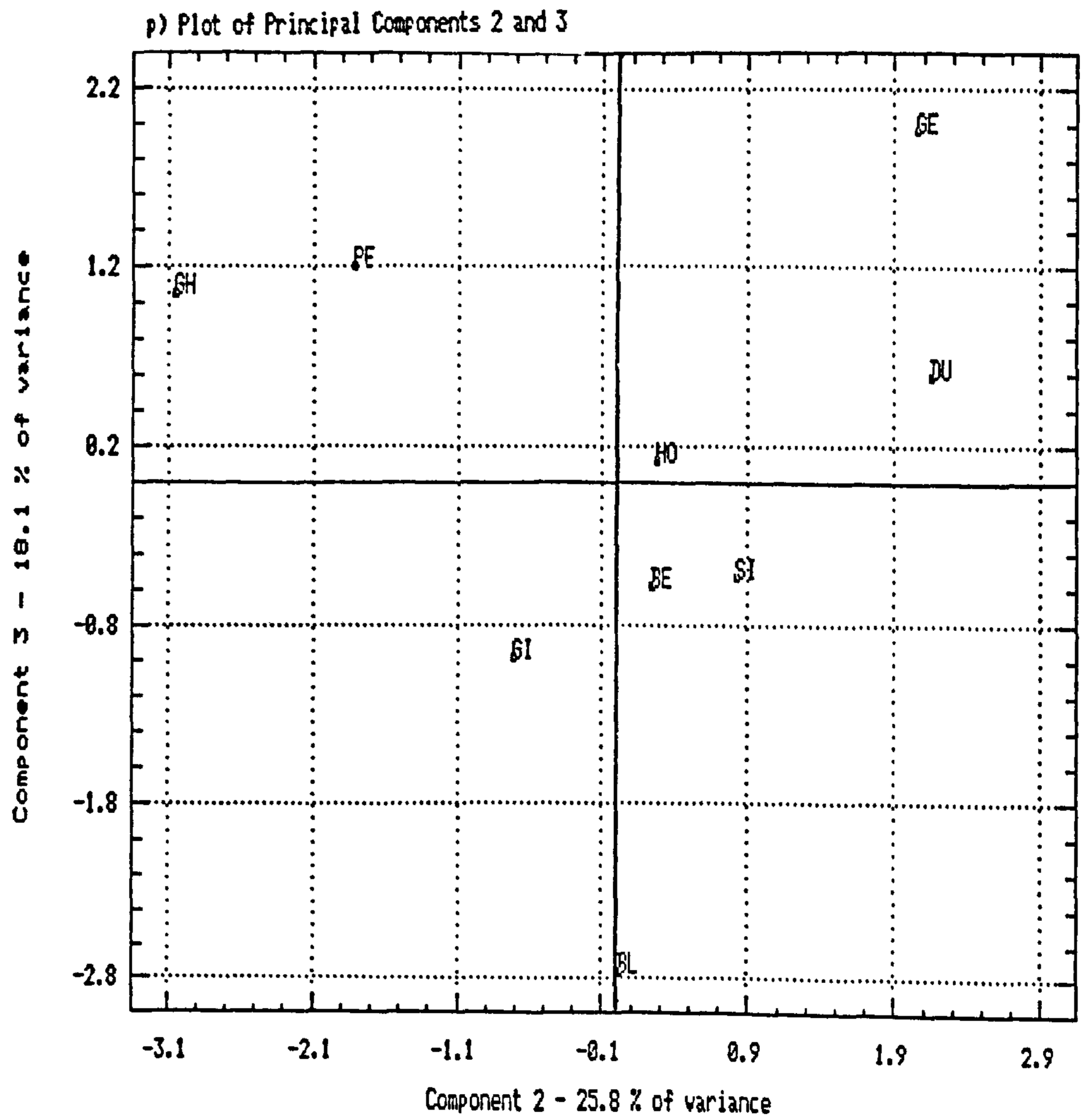
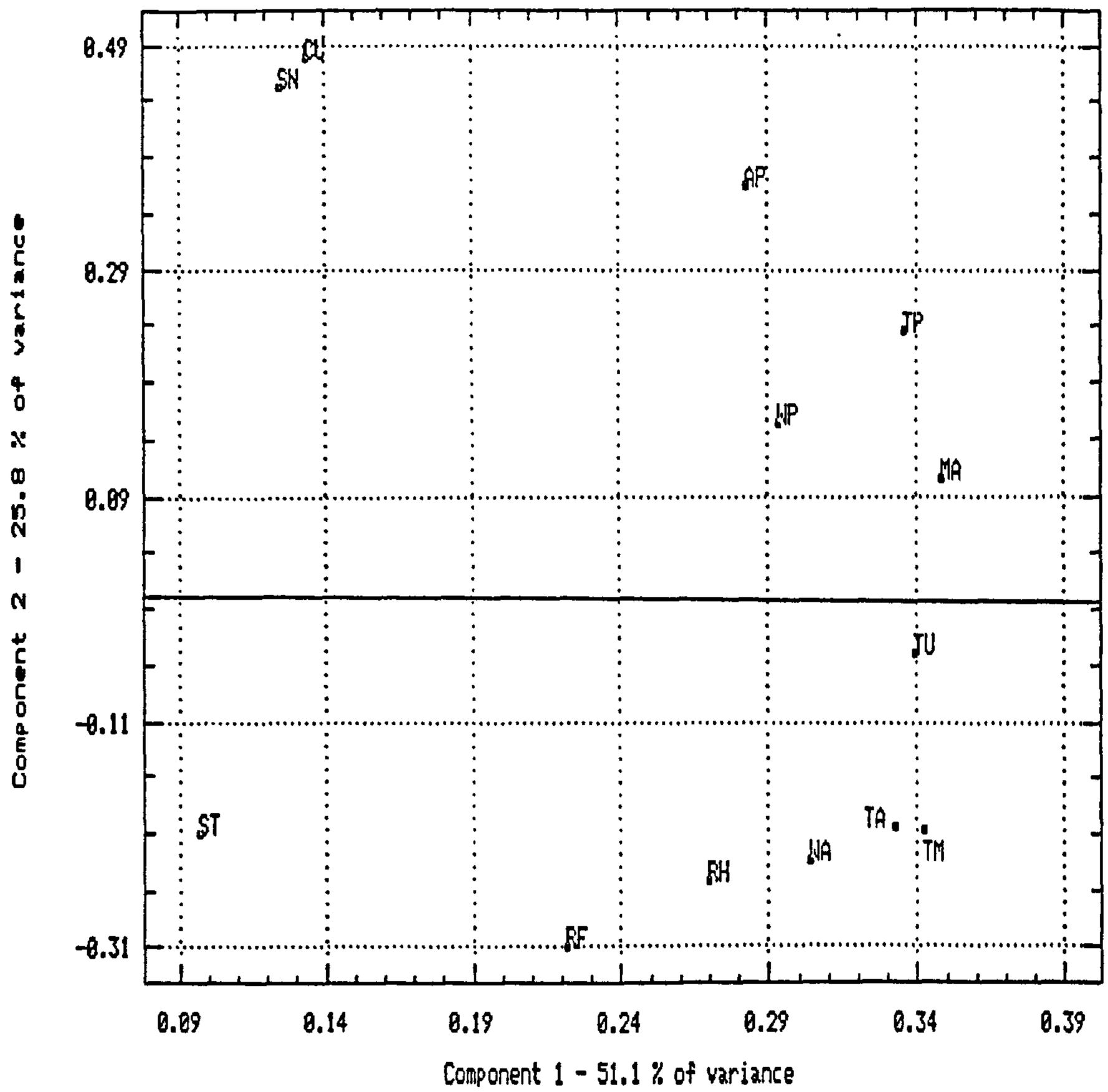


Figure 5.3.1. q & r. *PCA on behaviour patterns performed by cats during Period 3 at Chilworth. Components 1 and 2.*

q) Plot of First Two Component Weights



r)Plot of First Two Principal Components

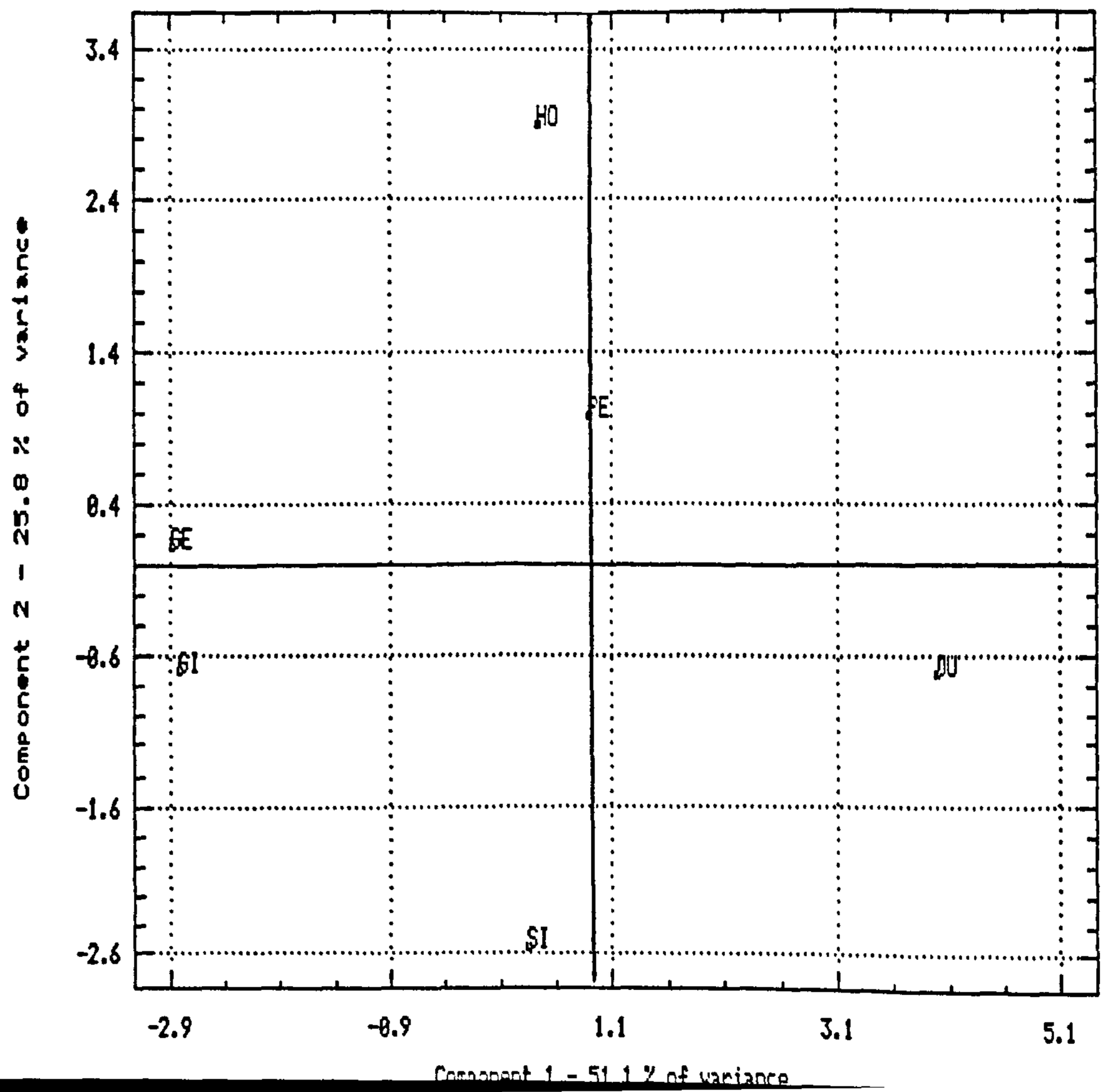
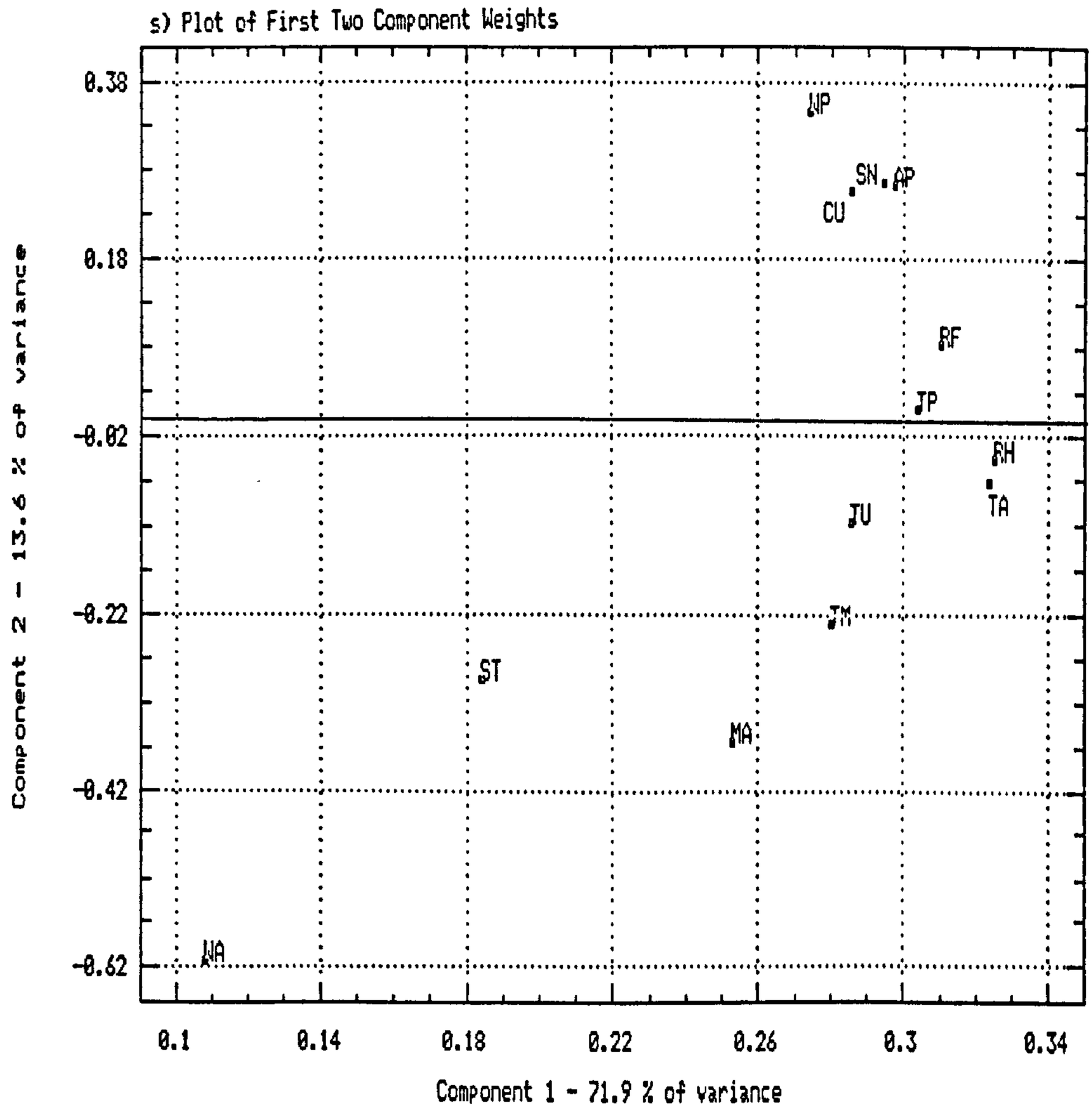


Figure 5.3.1. s & t. *PCA on behaviour patterns received by cats during Period 3 at Chilworth. Components 1 and 2.*



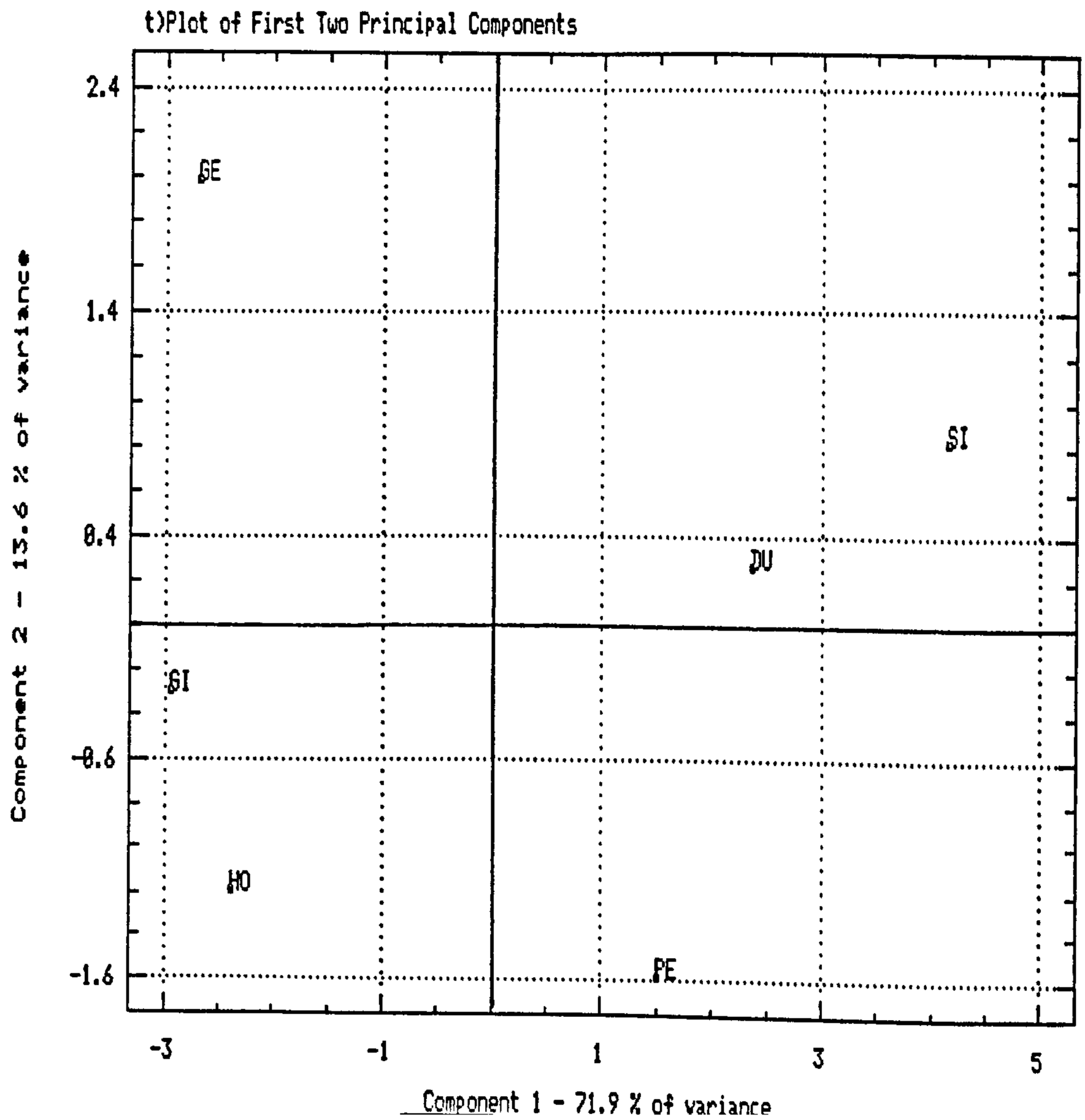
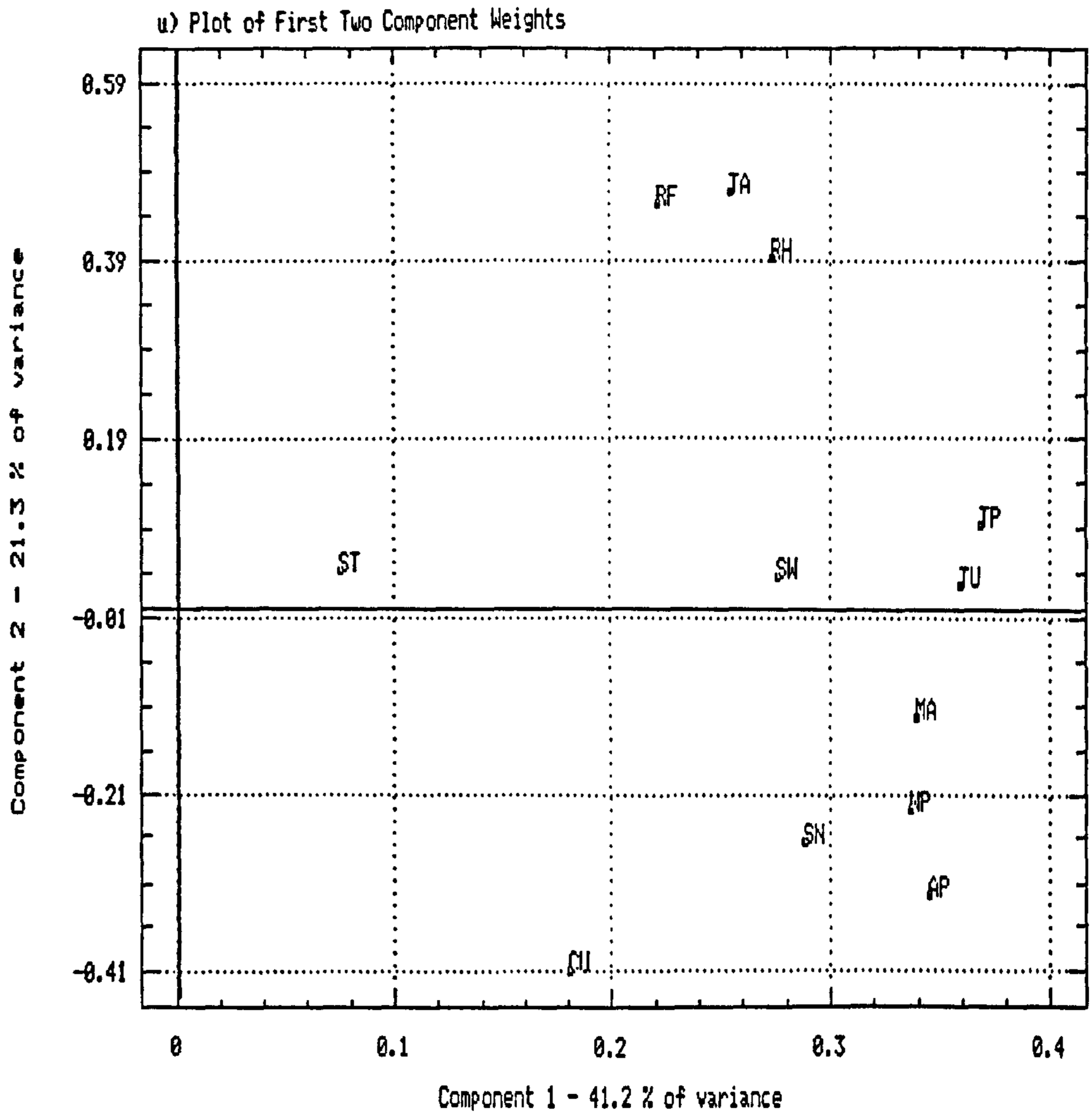


Figure 5.3.1. u & v. *PCA on behaviour patterns performed by cats during each of the 3 periods at Chilworth. Components 1 and 2.*



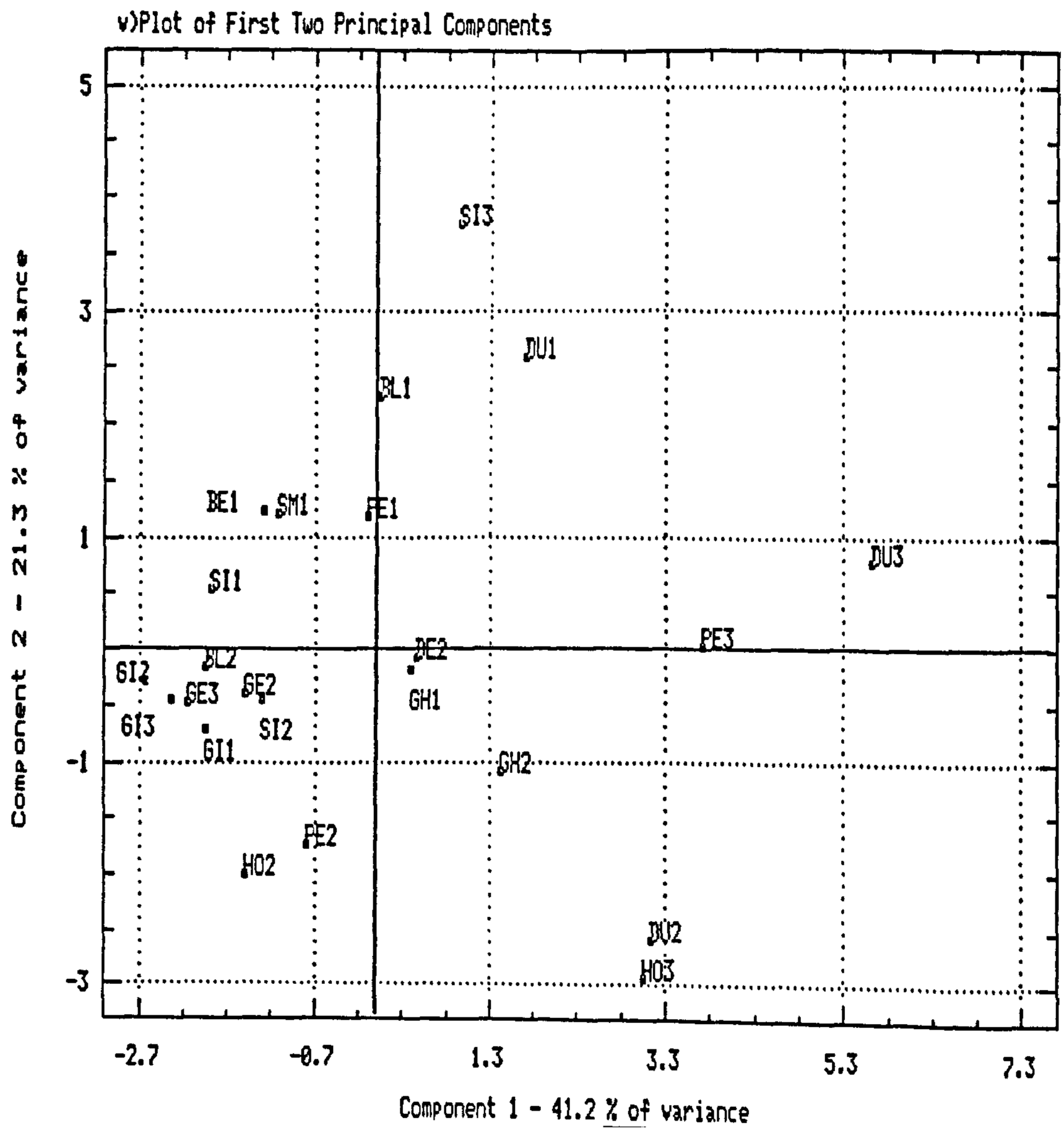
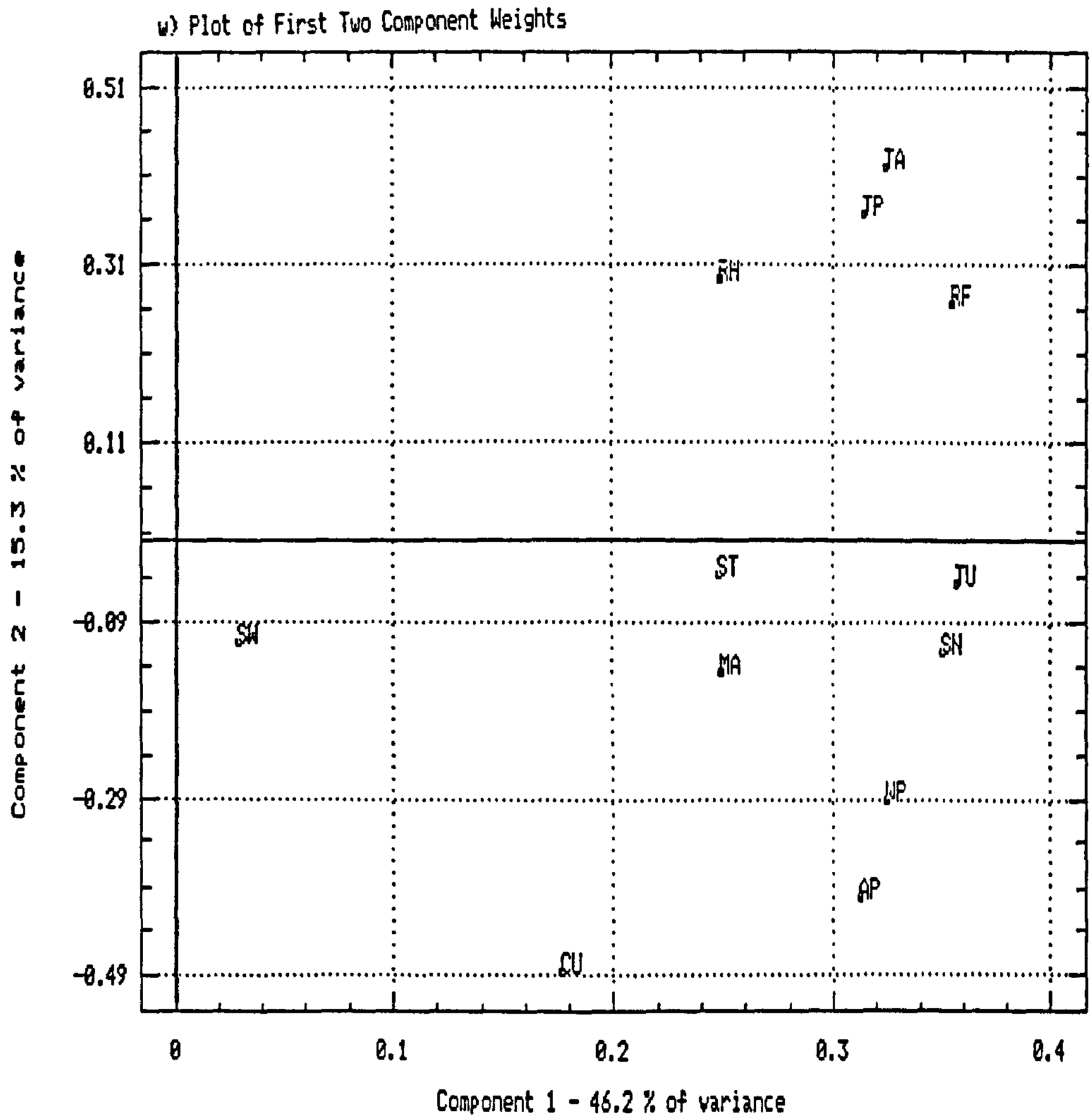
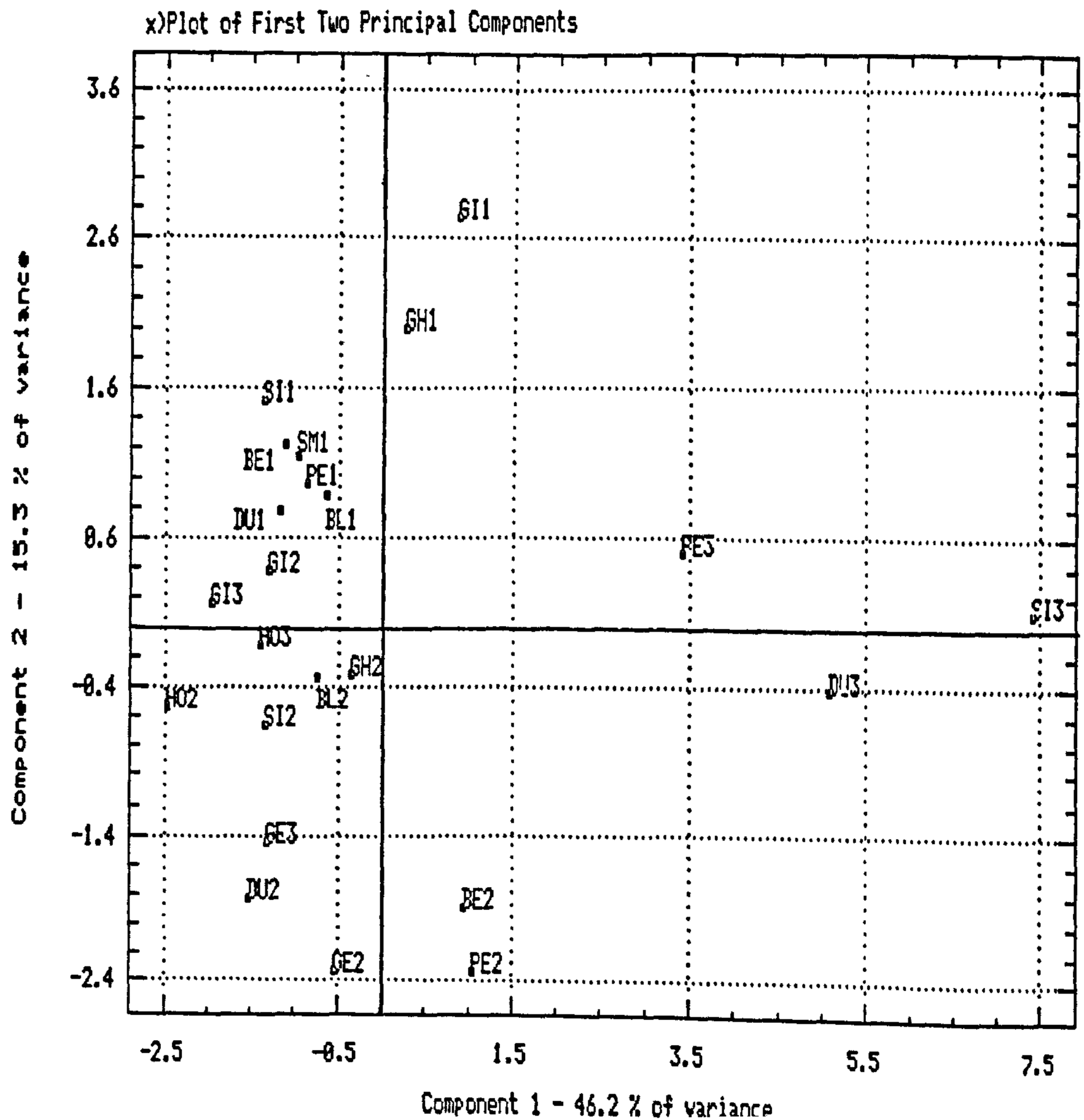


Figure 5.3.1. w & x. *PCA on behaviour patterns received by cats during each of the 3 periods at Chilworth. Components 1 and 2.*





REFERENCES

Alexander, R.J., 1974. The evolution of social behaviour. *Ann. Rev. Ecol. Syst.* 5:325-383.

Altmann, D., 1987. Social behaviour patterns in three wolf packs at Tierpark, Berlin. In: *Man and Wolf.* H. Frank (ed.). Dr W. Junk, Dordrecht, the Netherlands.

Apps, P.J., 1986. Home ranges of feral cats on Dassen Island. *J. Mamm.* 67:199-200.

Baron, A., Stewart, C.N. & Warren, J.M., 1957. Patterns of social interactions in cats (*Felis domestica*). *Behaviour* 11:56-66.

Bertram, B.C.R., 1975. The social system of lions. *Sci Am.* 232:54-65.

Bertram, B.C.R., 1978. Living in groups: predators and prey. In: *Behavioural Ecology: an Evolutionary Approach.* J.R. Krebs & N.B. Davies (eds.). Blackwell Scientific Publications, Oxford, pp. 64-96.

Blackshaw, J.K., 1985. Human and animal inter-relationships. Review series: 6. Behavioural problems of cats: Part 2. *Australian Veterinary Practitioner* 15(4):164-168.

Bloomer, J.P. & Bester, M.N., 1992. Control of feral cats on sub-Antarctic Marion Island, Indian Ocean. *Biological Conservation* 60:211-219.

Borchelt, P.L. & Voith, V.L., 1981. Elimination behaviour problems in cats. *Compend. Contin. Educ. Pract. Vet.* 3:730.

Bradshaw, J.W.S., 1992. *The Behaviour of the Domestic Cat.* C.A.B. International, Wallingford, Oxon, U.K.

Bradshaw, J.W.S. & Smart, F.R.E., 1993. Behavioural differences between kittens homed singly and in pairs. *J. Feline Advisory Bureau* (in press).

Calhoon, R.E. & Haspel, C., 1989. Urban cat populations compared by season, subhabitat and supplemental feeding. *J. Animal Ecol.* 58:321-328.

Caraco, T. & Wolf, L.L., 1985. Ecological determinants of group sizes of foraging lions. *Am. Nat.* 190:343-352.

Carr, G.M. & Macdonald, D.W., 1986. The sociality of foragers: a model based on resource dispersion. *Animal Behaviour* 34:1540-1549.

Chipman, P., 1990. Influences on the home range sizes of domestic cats (*Felis catus*), in an urban environment. *MSc Thesis*, Manchester Polytechnic.

Cole, D.D. & Shafer, J.N., 1966. A study of social dominance in cats. *Behaviour* 27: 39-53.

Corbett, L.K., 1979. Feeding ecology and social organisation of wildcats (*Felis sylvestris*) and domestic cats (*Felis catus*) in Scotland. *Ph.D. Thesis*, Aberdeen.

Crow, J.F. & Kimura, M., 1970. *An Introduction to Population Genetics Theory.* Harper & Row, New York.

Dards, J.L., 1978. Home ranges of feral cats in Portsmouth dockyard. *Carnivore Genetics Newsletter* 3:242-255.

Dards, J.L., 1979. The population ecology of feral cats (*Felis catus* L.) in Portsmouth dockyard. Ph.D. Thesis, Bradford University, Bradford.

DeBoer, J.N., 1977. Dominance relations in pairs of domestic cats. *Behavioural Processes* 2:227-242.

De Waal, F.B.M., 1991. Rank distance as a central feature of rhesus monkey social organisation: a sociometric analysis. *Animal Behaviour* 41:383-395.

Dorn, C., Taylor, D., Schneider, R., Hibbard, H. & Klauder, M., 1968. Surveys of animal neoplasms in Alameda and Contra Costa Counties, California. 2. Cancer morbidity in dogs and cats from Alameda county. *J. Nat. Cancer Inst. 40:307-318.*

Feaver, J., Mendl, M. & Bateson, P., 1986. A method for rating the individual distinctiveness of domestic cats. *Animal Behaviour* 34:1016-1025.

Fitzgerald, B.M. & Karl, B.J., 1979. Food of feral house cats (*Felis catus*, L.) in forest of the Orongorongo Valley, Wellington. *N. Z. J. Ecol.* 9:71-81.

Fitzgerald, B.M. & Karl, B.J., 1986. Home ranges of feral house cats (*Felis catus*, L.) in the Orongorongo Valley, Wellington, New Zealand. *N.Z. J. Ecol.* 9:71-81.

Fonberg, E., Brudnias-Stepowska, Z. & Zagrodzka, J., 1985. Various relationships between predatory dominance and aggressive behaviour in pairs of cats. *Aggressive Behaviour* 11(2):103-114.

Fowler, J. & Cohen, L., 1990. *Practical Statistics for Field Biology.* Open University Press.

Frame, L.H., Malcolm, J.R., Frame, G.W. & Van Lawick, H., 1979. Social organisation of African wild dogs (*Lycaeon pictus*) on the Serengeti Plains, Tanzania 1967-1978. *Z. Tierpsychol.* 50:225-249.

Gittleman, J.L., 1989. Carnivore Group Living. In: *Carnivore Behaviour, Ecology, and Evolution.* J.L. Gittleman (ed.), Chapman & Hall Ltd., London, pp. 183-227.

Hart, B.L. & Barrett, R.E., 1973. Effects of castration on fighting, roaming, and urine spraying in adult male cats. *Journal of the American Veterinary Medical Association* 163(3):290-292.

Hart, B.L. & Cooper, L., 1984. Factors relating to urine spraying and fighting in prepubertally gonadectomised cats. *Journal of the American Veterinary Medical Association* 184(10):1255-1258.

Heistermann, M., Eckhard, K., Ekkehard, P. & Wolters, H.J., 1989. Fertility status, dominance, and scent marking behaviour of family-housed female cotton-top tamarins (*Saguinus oedipus*) in absence of their mothers. *Am. J. Primatology* 18:177-189.

Hepper, P.G., 1986. Sibling recognition in the domestic dog. *Animal Behaviour* 34:288-289.

Izawa, M., Doi, T. & Ono, Y., 1982. Grouping patterns of feral cats (*Felis catus*) living on a small island in Japan. *Japanese Journal of Ecology* 32:373-382.

Jones, E. & Coman, B.J., 1982. Ecology of the feral cat, *Felis catus* (L) in South Eastern Australia 3. Home ranges and population ecology in semi-arid North West Victoria. *Aust. Wildl. Res.* 9:409-420.

Kerby, G., 1987. The social organisation of farm cats, *Felis catus*. *Ph.D. Thesis*, Oxford University, Oxford.

Kerby, G. & Macdonald, D.W., 1988. Cat society and the consequences of colony size. In: *The Domestic Cat : The Biology of Its Behaviour*. D.C. Turner & P. Bateson (eds.). Cambridge University Press, Cambridge. pp.67-81.

Kruuk, H., 1972. *The Spotted Hyena: A Study of Predation and Social Behaviour*. University of Chicago Press, Chicago.

Laundre, J., 1977. The daytime behaviour of domestic cats in a free-roaming population. *Animal Behaviour* 25:990-998.

Leyhausen, P., 1965. The communal organisation of solitary mammals. *Symposium of the Zoological Society of London* 14:249-263.

Leyhausen, P., 1979. *Cat Behaviour: The Predatory and Social Behaviour of Domestic and Wild Cats.* English translation by B.A. Tonkin. Garland STPM Press, New York.

Liberg, O., 1980. Spacing patterns in a population of rural, free-roaming, domestic cats. *Oikos* 35:336-349.

Liberg, O., 1981. Predation and social behaviour in a population of domestic cats. An evolutionary perspective. *Ph.D. Thesis,* Univ. of Lund.

Liberg, O. & Sandell, M., 1988. Spatial organisation and reproductive tactics in the domestic cat and other felids. In: *The Domestic Cat : The Biology of Its Behaviour.* D.C. Turner & P. Bateson (eds.). Cambridge University Press, Cambridge, pp.83-98.

Macdonald, D.W., 1983. The ecology of Carnivore social behaviour. *Nature,* Lond., 301:379-389.

Macdonald, D.W., 1985. The carnivores: Order Carnivora. In: *Mammalian Social Odours.* R.E. Brown & D.W. Macdonald (eds.). Oxford Univ. Press, Oxford, pp. 619-722.

Macdonald, D.W. & Apps, P.J., 1978. The social behaviour of a group of semi-dependent farm cats, *Felis catus*: A progress report. *Carnivore Genetics Newsletter* 3:256-268.

Macdonald, D.W., Apps, P.J., Carr, G.M. & Kerby, G., 1987. Social dynamics, nursing coalitions and infanticide among farm cats, *Felis catus*. *Advances in Ethology No. 28. Supplement to "Ethology", formerly Zeitschrift fur Tierpsychologie.* G.M. Burghardt, W. Pflumm & W. Wickler (eds.). Paul Parey, Berlin and Hamburg.

Masserman, J.H. & Siever, P.W., 1944. Dominance, neurosis and aggression. An experimental study. *Psychosomatic Med.* 6:7-16.

Mech, L., 1970. *The Wolf: The Ecology and Behaviour of an Endangered Species.* Nat. Hist. Press, New York.

Mertens, C., 1991. Human-cat interactions in the human setting. *Anthrozöos* 4:214-231.

Mertens, C. & Turner, D.C., 1988. Experimental analysis of human-cat interactions during first encounters. *Anthrozöos* 2:83-97.

Natoli, E., 1985a. Behavioural responses of urban feral cats to different types of urine mark. *Behaviour* 94:234-243.

Natoli, E., 1985b. Spacing patterns in a colony of urban stray cats (*Felis catus* L.) in the historic centre of Rome. *Applied Animal Behaviour Science* 14:289-304.

Neville, P.F. & Remfry, J., 1984. Effect of neutering on two groups of feral cats. *Veterinary Record* 114:447-450.

Panaman, R., 1981. Behaviour and ecology of free-ranging female farm cats (*F.catus*). *Zeitschrift fur Tierpsychologie* 56:59-73.

Podberscek, A.L. & Blackshaw, J.K., 1988. Reasons for liking and choosing a cat as a pet. *Australian Veterinary Journal* 65(10): 332-333.

Putman, R.J., 1988. *The natural history of deer.* Christopher Helm, london.

Rabb, G.B., Woolpy, J.H. & Ginsburg, B.E., 1967. Social relationships in a group of captive wolves. *Am. Zool.* 7:305-311.

Rasa, O.A.E., 1977. The ethology and sociology of the dwarf mongoose (*Helogale undulata rufula*). *Z. Tierpsychol.* 42:337-405.

Rees, P, 1980. The ecological distribution of feral cats and the effects of neutering on a hospital colony. In: *The ecology and control of feral cats.* U.F.A.W., Potters Bar, Herts., U.K. pp.12-22.

Rood, J.P., 1975. Population dynamics and food habits of the banded mongoose. *E. Afr. Wild. J.* 13:89-112.

Rudnai, J., 1975. *The social life of the lion.* Medical-Technical Publ., Lancaster.

Schaller, G.B., 1972. *The Serengeti Lion.* University of Chicago Press, Chicago.

Schotte, C.S. & Ginsburg, B.E., 1987. Development of social organisation and mating in a captive wolf pack. In: *Man and Wolf.* H. Frank (ed.). Dr W. Junk, Dordrecht, the Netherlands.

Siegel, S. & Castellan, N.J., 1988. *Nonparametric Statistics for the Behavioural Sciences.* 2nd edition. McGraw-Hill, U.S.A.

Slater, P.J.B., 1973. Describing sequences of behaviour. Chapter 5 in: *Perspectives in Ethology (vol 1).* P.P.G. Bateson & P.H. Klopfer (eds.), pp.131-153.

Smith, R.E. & Shane, S.M., 1986. The potential for the control of feral cat populations by neutering. *Feline Practice* 16:21-23.

Sokal, R.R. & Rohlf, F.J., 1981. *Biometry.* 2nd edition. W.H. Freeman & Co., San Francisco.

Steele, R.G.D. & Torrie, J.H., 1980. *Principles and procedures of statistics - a biometrical approach.* McGraw-Hill, U.S.A.

Tabor, R., 1983. *The Wild Life of the Domestic Cat.* Arrow Books, London.

Tabor, R., 1989. The changing life of feral cats (*Felis catus* L.) at home and abroad. *Zool. J. Linn. Soc.* 95:151-161.

Tobach, E., 1988. Non reproductive aspects of social behaviour: comments on the need to investigate. In: *Evolution of social behaviour and integrative levels.* The T.C. Schneirla conference series, vol. 3. G. Greenberg & E. Tobach (eds.). Lawrence Erlbaum Assoc.

Turner, D.C., 1988. Cat behaviour and the human/cat relationship. *Animalis Familiaris* 3:16-21.

Turner, D.C., 1991. The ethology of the human-cat relationship. *Swiss Archive for Veterinary Medicine* 133:63-70.

Turner, D.C. & Mertens, C., 1986. Home range, overlap and exploitation in domestic farm cats (*Felis catus*). *Behaviour* 99:22-45.

Van Aarde, R.J., 1978. Reproduction and population ecology in the feral housecat, *Felis catus*, at Marion Island. *Carniv. Genet. Newsl.* 3:228-316.

Van Aarde, R.J., 1979. Distribution and density of the feral house cat, *Felis catus*, at Marion Island. *S. Afr. J. Antarct. Res.* 9:14-19.

Van Orsdol, K.G., 1981. Lion predation in Rwenzori National Park, Uganda. *Ph.D. Thesis*, University of Cambridge.

Verberne, G. & De Boer, J.N., 1976. Chemocommunication among domestic cats. *Z. Tierpsychol.* 42:86-109.

Warner, R.E., 1985. Demography and movements of free-ranging domestic cats in rural Illinois. *J. Wildl. Manag.* 49:340-346.

Wilson, E.O., 1975. *Sociobiology.* Belknap/Harvard Press.

Winslow, C., 1938. Observations of dominance-subordination in cats. *Journal of Genetic Psychology* 52:425-428.

Wolski, T.R., 1982. Social behaviour of the cat. *Veterinary Clinics of North America: Small Animal Practice* 12(4):693-706.

Wrangham, R.W., 1983. Ultimate factors determining social structure. In: *Primate social relationships. An integrated approach.* R.A. Hinde (ed.). Blackwell Scientific Publications, Oxford, pp. 255-262.

Zimen, E., 1975. Social dynamics of the wolf pack. In: *The Wild Canids.* M.W. Fox (ed.). Van Nostrand, Rheinhold, New York.