UNIVERSITY OF SOUTHAMPTON

OBJECT PLAY IN THE ADULT DOMESTIC CAT
Felis silvestris catus

by

Sarah Louise Hall

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ABSTRACT

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The internal and external stimuli which influence the performance of object play are examined with the aim of determining the role of object play in the behavioural repertoire of the adult cat. Three groups of cats were used, two which had no hunting experience (colony cats) and one which had had regular access to live prey (household pets).

The most important classes of external stimuli for eliciting object play were size, texture and movement. The most intensive play was elicited by toys of small size (7x5x1cm), which were moving, and covered in real deer fur, feathers, or fakefur. The main internal factors examined were hunger and habituation. Cats deprived of food for 16 hours showed an increase in close contact, 'killing' behaviour patterns, towards a small toy, and an increase in exploratory behaviour towards a medium (12x7x2cm) toy. These changes in behaviour were similar to effects shown by Biben (1979) studying the influence of hunger and prey vulnerability on predation in domestic cats.

The performance of play was shown to stop primarily as a result of increasing habituation to unchanging toy stimuli, and only slightly due to a general decrease in motivation for playing, although these were both affected by the length of time over which habituation occurred. Play inhibited by habituation could be disinhibited by a change to a toy with contrasting stimuli. The combination of rapid, strong habituation followed by a contrasting toy of high sensory value produced a strong post-inhibitory rebound in play, in which play was more intensive than it had been initially.

Using sequence analysis, no clear or characteristic change in frequency of any behaviour patterns could be detected that would characterise the end of a play bout. However, it was possible to relate the degree of elaboration and repetition of behaviour patterns to the cat's motivation level.

It was also possible to alter the quality and quantity of object play using positive reinforcement with food rewards under a variety of schedules.

The similarity of internal causation and structure between non-hunting adult cat object play and predation supports the hypothesis that the two share the same motivational basis, and that object play may be more correctly classified with predation than with play per se.

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INTRODUCTION

There were probably two major factors that resulted in the domestication of the cat *Felis silvestris catus*. Initially, they may have been attracted to human settlements by surplus animal protein in refuse and by the rodent pests which ate stored grain. The benefits of the latter to man led to the cat's maintenance as a rodent killer (Clutton-Brock 1988). Subsequently, in ancient Egypt cats were kept in temples and were maintained for religious rites and worship as deities. However, as the association of cats with humans continued, their appeal as pets, with more aesthetic qualities than utilitarian uses, became important. Part of the appeal of a cat as a companion must be the pleasure derived from watching cats play, both as kittens and adults. Play behaviour has been subject to widespread investigation in many fields from animal behaviour to psychology, involving numerous mammalian species. It is also the cause of almost endless controversy and widely divergent opinion regarding the definable structure of play, types of play, and functions which would explain its persistence in behavioural repertoires. Many review papers document the diversity of hypotheses concerned with play (for example Loizos 1966, Fagen 1974a). These reviews concern themselves almost exclusively with play in juvenile animals. Although play in adult cats is amusing to watch, it is difficult to explain. Few studies have focussed upon adult play and little headway has been made concerning its causes and role in the animal's behavioural repertoire. Every owner of a pet cat recognizes and has an anthropomorphic interpretation of their cat's play behaviour, but in more scientific terms play remains difficult to define and to explain. The research presented in this thesis attempts to describe the causes and motivation of play in the adult cat.

1.1: DEFINITION AND FUNCTION OF PLAY BEHAVIOUR

Tinbergen (1963) identified four basic approaches to ethological study. These were proximate causation, ontogeny, evolution, and function. In the case of play behaviour the former three have received the most attention, but function remains the most elusive. The structure of play has been defined by the characterisation of its structure, for example, by the use of behaviour components used in other types of behaviour, such as predation, but involving repetition of some inexplicably favoured behaviour components. Random ordering of these components and lack of any consummatory end behaviour is associated with the performance of behaviour components from other behaviour systems performed out of their usual context (Bekoff 1976, Fagen 1981). A structuralist approach to defining play predominated in earlier play literature (Loizos 1966).

Generally, play behaviour is associated with 'high arousal' behaviours; animals rarely incorporate components from maintenance or everyday activities, such as grazing, rumination or grooming, into play (Barber 1991). This high arousal associated with animal play is easily expressed anthropomorphically. For example, Rasa (1984) described dwarf mongooses *Helogale undulata rufula,* as squeaking "excitedly" when playing.

Criteria more specific than the identification of high arousal have been proposed. For example, Fagen (1981) provides a list of activities commonly described as 'play'. These are:

1) Nonagonistic fighting and chasing maintained by social cooperation;

2) Solo locomotor and rotational movements performed in the absence of threatening predators, parasites and conspecifics;

3) Developing locomotor or manipulative behaviour repeated with slight variation at a previously established level of mastery;

4) Divertive effector interactions with an inanimate object subsequent to the termination of

an initial phase of sensory and mastery activity, including exploratory manipulation, directed toward the object.

The most controversial method of definition of play is by function. The possible functions of play still evade researchers, and are the cause of much disagreement. Initially functional definitions of play were negative. Play is easily regarded as something superfluous and unnecessary to the animal's survival. It has even been denounced as 'behavioural fat', implying that it is an indulgence on the part of the animal to spend time and energy playing (Muller-Schwarze et al 1982). Barnard-Gilmore (1966) states that,

> "In the past play has been a thing to be inferred, not the sort of behaviour that elicits clear agreement with respect to its presence or absence,"

This leaves the evolutionary cause and function obscure. Symons (1978) defines play as a behaviour lacking in immediate function or at least the function of the patterns it resembles, i.e. play may include patterns from predatory behaviour, but without the normal functions of these patterns. Thus play was thought to occur when no other behaviours were in operation, a way of filling in spare time. Further unflattering definitions have been applied by those interested in motivation. According to Meyer-Holzapfel (1965), play is maximal when no motivation is present and the 'general activity drive' has free reign. Thus play was commonly seen as an unmotivated act. Mitchell (1990) states that this is a psychological error on the part of the human observer, such that,

> "Difficulty with defining play results from the general denial of our implicit interpretation of play behaviour as intentional".

This quotation indicates the level of anthropomorphism involved in the casual interpretation of animal play behaviour. Possibly more than any other behaviour, the pleasure obtained from human play, and the care-free circumstances of human playfulness, lead to the belief that animal play is analogous to human play, thus promoting anthropomorphism. However, care must also be taken to avoid the possibly false distinction of play as a separate category of behaviour.

Less dismissive functional definitions come in various guises, and there are various ways in which it can be shown that there is motivation specifically for play. For example, experiments with deprivation of play in domestic goats *Capra hirca* have shown that a play-specific rebound effect occurs, after a period of play deprivation, indicating that motivation for play exists (Chepko 1971).

Many of the oldest functional definitions of play have been documented by Gilmore (1966) and he divided them into four main classes:

1) *Surplus Energy*; (Schiller 1873, Spencer 1873 & Tolman 1932). The animal plays to rid itself of left-over energy, unwanted for other behaviours. Some authors referred to left-over 'nervous' energy, and others to left-over dietary energy. It was proposed that play would be expected in phylogenetically more advanced animals (for example mammals), which had 'mastered the problems of survival', and so had 'leisure' time (Spencer 1855). This is akin to the idea of Meyer-Holzapfel (1956) in which surplus energy not directed to specific behaviour could be used up in play behaviour. A more recent redefinition of this theory has been presented by Burghardt (1988), in which the evolution and taxonomic distribution of play in all mammals is predicted according to the surplus energy of the species in question. This is measured according to criterion including size, basal metabolic rate, level of parental care and altricial or precocial offspring. Burghardt made nineteen predictions for the occurrence of play behaviour throughout the animal kingdom. For example, that,

> "Well-cared-for captive animals should play more than their wild counterparts."

and that,

> "Species that engage in sporadic vigorous behaviour (for example, foraging excursions) should play more than species that are active near the limits of their physiology."

It is important to understand that surplus energy may only permit the evolution of play, but would not cause it to evolve.

2) *Relaxation*; (Lazarus 1883, cited in Gilmore 1966). Animals with no need to perform maintenance behaviours necessary for their immediate survival can 'relax' and play. Burghardt's surplus energy theory also tackled an updated version of this. He suggested that captive animals and animals which are protected with a high level of parental care, and so have reduced exposure to a changing environment, will show more play behaviour. These animals are able to 'relax' and are more likely to exist in an unstimulating environment. This may increase motivation for play.

3) *Recapitulation* of events and behaviours in the animals ancestral repertoire; explaining the occurrence of apparently random behaviour components in a disorganized, varying order (Hall 1906).

4) *Exercise*; physical locomotor training and practice (Groos 1898).

The first three of these are probably less likely to be the solution to the problem. The fourth represents one of the most strongly upheld theories of play function, particularly in the case of juvenile play. For example, locomotor play may build up and strengthen growing muscles, bones, tendons and ligaments. A major argument against this idea comes from the prediction of Fagen (1976) that for play to constitute valuable exercise it should be performed when the muscle is near to fatigue, when muscles benefit most from exercise. The duration of play bouts would be expected to have a non-random statistical distribution if play was to exercise the muscle properly. However, in a study of play bouts in the California ground squirrel *Spermophilus beecheyi*, McDonald (1977) found that the play bouts followed a simple exponential delay curve. This meant that the play behaviour was controlled by random events and was therefore not optimised to promote the growth of muscle.

Practice for the perfection and possible elaboration of other behaviours is disputed as the chief function of play, but likely to be more applicable to young animals than to adults. Practice can be necessary for a number of important categories of behaviour in an animal's life, from honing motor and perceptual skill (in young animals), practice for predation (in predators), escape from predators (in prey species), and for social skill development (Fagen 1974a, 1981, Caro 1979, Leyhausen 1979; Mendoza & Ramirez 1987; Sen Gupta 1988). These ideas are more easily applied to young animals, and it may be the case that a direct relation between juvenile play behaviour and the adult analogous behaviour can be found. Caro and Alawi (1985) studied the play of two species of hyrax *Heterohyrax brucei* and *Procavia johnstoni* and found that adult *Procavia* showed higher scores than adult *Heterohyrax* on three measures of play. This was found to correspond to differences between play of the young of the species. Such examples can be used to argue that play is not necessarily an immature version of the 'serious' adult behaviour, since there appears to be little difference between the two. There are also instances when the young animal shows 'serious' behaviours without having practised them with play. For example a domestic pig *Sus scrofa* must fight for dominance and one of its mother's teats in the first days of life. This fighting can be very vicious, and only after the piglets have sorted out their dominance arrangement do they begin to play together (McBride 1963).

Adult play presents an even more difficult problem. The common argument against the practice function of play in adults is that it is not necessary for the animal to practise in play. An adult animal could practise a particular behaviour simply by performing it, rather than playing (Loizos 1966, Biben 1979). A more compromising attitude toward play as practice is that play is unnecessary for the practice of the instinctive motor patterns of behaviours, but may affect overall proficiency (Poole 1966, Fagen 1981). Thus play enables the adult to practise an already fully-formed basic motor skill while adding variation to the behaviour. Accordingly, play would be expected to appear in animals which have a greater behavioural repertoire, necessitating the perfection of more skills in the animals' social, predatory or other behaviour (Bateson & Young 1979). Sex differences in adult play also imply that play could be practice for other behaviours which have sex differences (Biben 1982). This is only likely for adult social play. Poole (1966) found sex differences in adult ferret *Mustela putorius furo* play-fighting, a form of social play. Males showed greater aggression in play, which could be practice for serious fighting. However, play in adults of some species bears no resemblance to any other behaviours. This is the case for adult Harbour seals *Phoca vitulina* in which solitary play has no features in common with other adult behaviours (Renouf 1993).

Another suggested function of play is one of exploration and learning. When observed in children, play has been described as a 'self-initiated experiment in exploration' by Sylva (1977) and 'buffered learning' by Miller (1975). The child is able to learn about its environment via play, and to assess the potential of parts of its environment by using them in games, thus learning through play. This has lead to the suggestion that play is a child's way of thinking (Barnard-Gilmore 1966). For other animals, examples of play as exploration are often cited with a similar reasoning, for example by Ferron (1975) referring to locomotor and object play in adult ground squirrels *Spermophilus townsendii*. Exploration is a function often suggested for object play in adult domestic cats (Leyhausen 1979). The animal is exploring and learning about its environment by playing with it. This is especially applicable to novel objects within a familiar environment. But there are occasions when the opposite has been seen. Schiller (1957) noticed that one chimpanzee *Pan troglodytes* given a stick with which to retrieve food, did not learn to retrieve the food despite playing with the stick. Learning did not occur even after the chimp had been deprived of food.

Exploration and play are still distinguishable as two different behaviours. According to Sylva (1977) exploration is investigation of the properties of the environment, whereas play is oriented towards the potential use of properties of the environment in self-devised 'plans'. Play has also been shown to reinforce learning of a maze in rats (Humphreys & Einon 1981). This suggests not only the use of play as behaviour to promote learning, but, since the rats ran through the maze to reach a playful rat or play object, it also indicates that there is specific motivation for play.

The final major possible function of play is its role in the behavioural flexibility of individuals. Fagen (1982) has suggested that this may be an important factor in the evolution and persistence of play behaviour. Fagen defines flexibility as,

> "the capacity of an animal to alter its behaviour or its ecology through behavioural means when faced by novel challenges so as to increase its chance of leaving surviving offspring or kin."

He states that through play the individual becomes,

"versatile, resourceful, creative, and able to cope productively with the novel and the unexpected." .

Thus animals which play may have a competitive advantage over those which do not when faced with unexpected and unpredictable change in the environment, and are better able to adapt skills to new requirements. Criticism of this hypothesis attacks the necessity of such versatility with respect to evolution. The costs of such play and resulting flexibility may not be viable when compared with a more efficient fixed strategy. Also, there is no experimental evidence which clearly supports this hypothesis.

1.2: PLAY IN DOMESTIC CATS

The majority of play studies with the domestic cat have had kittens as their focus, including investigations of form and function, but play in the adults has received little attention. Adult cat play is a phenomenon responsible for much controversy when it appears in play literature, since its infrequent observation has not enabled the ready formation of ideas concerning its structure and function. Juvenile play has been divided into two distinct components, social play and object play (West 1974 & 1979; Caro 1979 & 1981), which can be distinguished in terms of characteristic components, the circumstances under which they occur, as well as the obvious difference in interaction with littermates or objects. On the basis of this distinction various suggestions for the functions of play as an important part of kitten development have been proffered according to the theories above. Both social and object play can be treated as a form of exercise for young animals and practice in the interactive use of motor and perceptual skills (West 1977). Mendoza & Ramirez (1987) suggested that play benefits motor-training, socialization and cognitive training. Leyhausen (1979) suggested that certain components of both types of play, such as rolling on one side to tackle a littermate or object, is practice for handling prey, especially large prey. West (1974) suggested that social play is important in keeping the litter together in one place, so that their mother is always aware of their location and can, therefore, protect them more easily. However, the general opinion is that social play is probably related to various adult social behaviours, from fighting to mating, and that object play is related to predation. This applies to other species as well as cats, for example Poole (1966) noted that social play in European polecats *Mustela putorius* was structurally more similar to adult fighting than to adult predation.

In adult domestic cats social play is rarely seen, and has never been the subject of scientific study. This may be due to a variety of factors including a general lack of interest in adult social play, the rarity of social play between adult cats, or because of the traditional, and only recently discredited, view that the domestic cat is a solitary species. Object play, however, persists into adulthood but has still been the subject of little attention or study, despite the structural similarities with predatory behaviour. The possible relationship between object play and predatory behaviour forms one focus of my study. Because of this possible relationship between play and predation, to understand object play it is also necessary to understand predatory behaviour. From this point the term 'play' will refer to object play, unless otherwise stated.

1.3: PREDATION

Predation has generally been studied as part of feeding behaviour, and rarely as a behaviour of interest in itself, and the relationship between predation and object play is even less well understood.

Despite being an easily identifiable behaviour, predation has not been defined particularly succinctly. Taylor (1984) gives a basic definition of predation covering different levels as;
1) an organism killing another for food,
2) individuals of one species eating living individuals of another species; this also includes parasitism.
3) one population benefitting at the expense of another and
4) the ecological process by which energy and matter flow from animal species A to animal species B.

The study of predation suffers from practical problems, the most obvious being the difficulty of observing carnivores performing predatory behaviour. In their natural environment they often hunt irregularly, at night and may kill in different areas each time, making behaviour difficult to observe and record. Laboratory study of predation is usually performed using rats as model predators, since these are small and easily lab-reared and maintained. Literature concerning predation in mammals tends towards descriptive accounts, mostly from field workers or game hunters. Examples include, lions *Panthera leo* (Schenkel 1966, Schaller 1972, Elliott et al 1977); domestic cats *Felis catus* and other wild cat species for example, serval *Felis serval* and ocelot *Felis pardalis* (Leyhausen 1965, Lorenz & Leyhausen 1973, Ewer 1973, Liberg 1981); mongooses *Helogale parvula* (Rasa 1973); cheetahs *Acinonyx jubatus* (Eaton 1970); African wild dog *Lycaon pictus* (Estes & Goddard 1967); spotted hyaena *Crocuta crocuta* (Kruuk 1972); cougars *Felis concolor*, (Robinette et al 1959, Saunders 1963, Hornocker 1970); and leopards *Panthera pardus* (Johnson et al 1993).

The domestic cat has featured in several studies concerned with predation. The main aims of these studies have been;

1) To elucidate the relationship between play during development and the cats' subsequent predatory behaviour (West 1974, 1976, Barrett & Bateson 1977, Caro 1979, Adamec 1980a,b,c, & 1983, Bateson 1986).
2) To consider other factors during development which may affect adult predation (Kuo 1930, Chesler 1968, Caro 1980a,b).
3) To determine the stimuli which induce hunting (Curio 1976, Leyhausen 1979).
4) To quantify the effects of the cat's ecology and environment upon its predatory behaviour (Sunquist & Sunquist 1989, Liberg 1981),
5) To clarify the relationship between hunger and predation (Flynn 1967, 1970, Polsky 1975, Adamec 1976, Leyhausen 1979).

1.4: OBJECT PLAY, PREDATORY PLAY AND PREDATION

The function of object play in the adult domestic cat is probably related to predation.

However, there are problems in the use of the word function when applied to a domestic species. Function can be simply defined as,

> "the consequences of a behaviour which currently increase the individual's chances of survival and reproduction in the natural environment and upon which natural selection acts to maintain that behaviour" (Martin & Caro 1985).

For domestic animals the effects of behaviour on reproductive success are not relevant, because the animals are not subject to natural selection. Therefore the function of their behaviour is less significant, and has less influence on their survival. However, domestic cats often exist in a state of semi-independence, in which their association with humans fluctuates from one generation to the next (Macdonald 1991). Thus, function may be a more relevant term for cats which are only semi-dependent. However, it is still unwise to apply an adaptationist explanation to the behaviour of a domestic animal. Domestic cats have changed little since domestication, but their environment has, making caution on the subject of function and adaptation necessary (Church 1994). It is necessary to have a thorough understanding of the causation of a particular behaviour before making any inference about its function.

Play in adult domestic cats may be structurally related to predation, since predation and object play have certain behaviour patterns in common. Based upon this observation it has been hypothesised that predation and play may also be causally and motivationally related. However, although this relationship has been little explored, it has been the subject of both great support and vigorous denial.

Caro (1979) advocated the importance of object play in kittens and its relationship to later adult predatory behaviour. He noted the change in prevalence of particular play components over time. Components such as rearing, arching, and chasing, which he maintained had an agonistic function, became more distinct from object-oriented components, and appeared less in the kittens' behaviour as they grew. He associated agonistic components with social play, and predation with object play, and proposed that the two may be regulated by different motivational systems. He also found that many measures of object play over the 4-12 week age period correlated with predatory components seen at 6 months. Bateson (1981) supported these findings by singling out object play in kittens and proposing that it is the output of a different system to those influencing other types of play.

Other studies have provided evidence for the relation between object play and predatory behaviour (including predatory play with the prey, and the normal predation components). Sen Gupta (1988) studied object play of ferrets *Mustela putorius* and domestic dogs *Canis familiaris* and concluded that there was no difference between object play and predation in structure or motivation of the animal. It is a widely held belief that object play can be distinguished from true predation by the inhibition of the killbite (see Appendix for definition), which is the supposed 'consummatory' act of predation bringing about the death of the prey (Bekoff 1976). However, Sen Gupta recorded the performance of the killbite during object play, suggesting that lack of a consummatory behaviour component cannot be used to define play. Russell (1990) also failed to notice any difference between object play or predation in ferrets, and attempted to explain this in terms of the benefits of object play. According to Russell these are; reduction of fear of the prey by prolonged handling, reduction in latency to approach prey, improvement of paw and bite placing, reduction of the total time taken to kill and enabling specialization of predatory behaviour to common prey through the exploitation of flexibility, as discussed earlier.

Egan (1971) also noted the close relationship between the two, but maintained that object play was distinct from actual predation because of the lack of the consummatory act (killbite). She explains this by suggesting that the lack of necessary stimuli from inanimate objects causes the consummatory act never to be expressed.

Whether there is a killbite or not in the play repertoire appears to be a matter of the observer's personal preference. It sometimes appears that the distinction between object play and predation is more of a human invention, especially when the distinction is narrowed down to the absence or presence of the killbite. Objective human definition of the behaviour being performed may be simply based upon the presence or absence of a prey animal. The usual practise of dividing behaviours into an appetitive and consummatory part has led to the assumption that the prey itself is the consummatory stimulus in predation. Since play is often characterised as behaviour without an obvious goal requiring a consummatory stimulus, the lack of a prey causes the definition of the behaviour to be changed to 'play' (Symons 1978, Smith 1982). Watching cats 'playing', this sometimes appears to be an arbitrary decision which requires the implicit assumption that there is a difference in motivational state, or even system, for predation and object play.

It is also difficult to classify a stimulus as either appetitive or consummatory. This property of a stimulus is defined by the way in which the animal behaves towards it, its appetitive or consummatory nature is not an independent characteristic (Nevin 1973). The denotation of both stimulus and associated behaviour as appetitive or consummatory may thus be just a decision of the observer.

There are also various arguments against the importance of play to predation which have a more scientific basis. Biben (1979) suggested a different means of linkage between play and predatory behaviour in adults. She found that the probability of a kill could be predicted with known hunger and prey size. Conflict between hunger and prey size (for example, high hunger level, but large and, therefore, fear-evoking prey) caused the cat to play, before, after, or instead of killing. This play she categorized as inhibited play, resulting from fear or conflict in the cat. This play behaviour could have several functions. It could enable a cat unfamiliar with the particular prey at hand to become familiar with it through the time spent in close contact with it. It could increase motivation to kill the prey via this exploratory play. It could enable a fearful cat to assess the strength and possible aggression of the prey and to overcome its fear. Finally, it might frighten a fierce prey animal. Martin (1984) also suggested the same role for play with prey. Here play has more than one function- exploration, practice and to inspire increased motivation for predation in the animal.

However, there are problems concerning adult play as 'practice'. Biben (1979) states that play is unnecessary for predation, since prey, once caught, can easily be killed without play. Also play involves predatory components, but in random order, and with emphasis on components favoured by individual cats. Thus its value as practice is questionable. Caro (1980) changed his ideas about the relationship between object play in kittens and adult predation, after noting that experience with a particular prey item or object during development has little effect on later predatory ability. He concluded that predatory play has little effect on adult predation. However this can be countered by Bateson (1981) who provides an explanation for variation in individual behaviour in his equifinality model, whereby various factors in the animal's development interact, not necessarily in the same proportions, in different individuals. Cats that play with objects exclusively may therefore be using play to compensate for some deficiency in other factors contributing to the development of effective predatory behaviour. The end result in terms of adult competence is therefore similar in all cats, and bears no simple relationship to the time devoted to play.

If play is directed at objects lacking a consummatory stimulus (Leyhausen 1973, Martin 1984) it is unclear why cats should play with live prey, since live prey would be expected to have the consummatory stimulus. A possibility is that the animal lacks the internal motivational cues which may link hunting and killing in a hungry cat. If the cat is well-fed it may still hunt but not be motivated to kill because it is not hungry, resulting in play with live prey. On a similar line, West (1979) noted that play resembles behaviour with captured rather than uncaptured prey. Since hunting precedes capture, play cannot be relevant to this part of predatory behaviour. He continued by stating that the best practice for hunting and killing is probably hunting and killing themselves, and that play with captured prey is too ' 'functionally ambiguous' to assign a definite theory.

Mitchell (1990) asks whether object play is simulative of, or actually is predation. He defines simulative play as play enacting another behaviour intentionally, and does not rule out the possibility that the similarity between object play and predation may be spurious, i.e. the animal may not intend to simulate predation when playing with objects. This distinction between action with and without intention may not, however, be easily applicable to animals other than humans.

1.5: AIMS OF THE STUDY

In this study I aimed to achieve an understanding of the external causes and internal motivation of adult play behaviour. I have also attempted an explanation of the existence and maintenance of object play in the behavioural repertoire of adult cats.

Initially I defined adult cat play by constructing an ethogram including the structural components of play. This ethogram is described in the Appendix. Using this ethogram, I investigated the external stimuli which elicit play behaviour in experiments in which I presented cats with a range of types of stimuli, in the form of different toys.

I then investigated the internal factors which both constitute and affect the cat's motivation to play. The assessment of motivation to perform a behaviour can probably only be attempted by judging the relative effects of the component factors. With this in mind, the aim was to determine the important internal factors which alter the eventual expression of play, and to determine their inter-relationship. Internal factors which are known to influence motivation for various categories of behaviour are hunger level, fatigue and habituation, in addition to more straightforward factors such as diurnal effects.

The central hypothesis of this study is that adult object play is motivationally related to predatory behaviour, in addition to being structurally similar. By presenting external stimuli which are similar to those of prey animals, I hoped to find out whether play and predation are elicited by the same stimuli. Since live prey could not be presented to the cats (for ethical reasons), comparison of play behaviour was made with accounts of domestic cat predatory behaviour found in literature. Many past studies have described cat predation and the stimuli that elicit it (for example, Leyhausen 1965, Biben 1979). Likewise, the findings from my experiments in which I manipulated the internal causes affecting the motivation of play behaviour were related to past studies of the motivation of predation, of which there are many (for example, a review by Polsky 1975).

1.6: STRUCTURE OF THE THESIS

Chapter 2 describes the experimental methods used throughout the study, and the statistical tests used to analyse the data.

Chapter 3 describes a series of experiments which were designed to investigate the external causal factors of object play using toys.

Chapter 4 describes an experiment to determine the influence of hunger on object play.

Chapter 5 describes a series of experiments aimed at examining the internal motivation of play, and factors which may affect a cat's motivation to play.

Chapter 6 describes the analysis of play sequences with different toy stimuli; at different levels of hunger and of play at different points throughout a play bout. I undertook these to determine whether changes in the structure of play occurred which could be used to measure play motivation or predict its endpoint.

Chapter 7 describes a study of the flexibility of object play. Training schedules were used to investigate whether it was possible to modify the quality and quantity of play. A study of social transmission of newly learnt play responses was also attempted.

Chapter 8 presents a final discussion of the findings of this study.

2

MATERIALS AND METHODS

2.1: SITES AND SUBJECTS

The domestic cat is an ideal subject for the study of object play behaviour by adult animals. Social play is often found in adult animals, both domestic and wild, for example in dogs (Fox & Bekoff 1976), sea lions *Eumetopias jubata* (Farentinos 1971), and vervet monkeys *Ceropithecus aethiops* (Fedigan 1972). Object play in adult animals is relatively rare (Russell 1990), but adult domestic cats that readily play with objects are not uncommon. Cats are easy to house, they are tractable, and interact playfully with humans. Populations of cats kept under different environmental conditions, ranging from those kept in catteries for scientific research to pet cats, enable experiential effects to be studied.

A large number of subjects, essential for a valid study, was easily located and data were collected from a total of 103 different cats. These were drawn from two distinct types of location: cattery cats at two sites and pet cats. Cats from these two backgrounds were chosen partly because they had different histories, particularly with respect to the probability of hunting experience. Since one aim of the study was to form an understanding of the relationship between play and hunting, it was important to have some idea of the cats predatory experience when interpreting results. Thus the cattery cats represented populations with known life histories, and no previous hunting experience. In contrast, the pet cats had sometimes unknown life histories, and hunting experience. Some owners had not seen their cats hunting, but the cat may still have been an unobserved hunter.

Cattery Cats

In this study a cattery refers to a population of cats which had been born and lived all their lives in a restricted indoor environment. These are cats which were kept for behavioural studies and for feeding trials. They were all raised and lived in very similar environments, which should reduce subject-to-subject variability caused by variations in experience. In catteries the history of each cat is known, although it can not necessarily be quantified since the developmental factors leading to more or less play when adult are largely unknown. Two cattery colonies were used, one at the Waltham Centre for Pet Nutrition and the other at Southampton University.

The Waltham Centre for Pet Nutrition (WCPN):

Data were collected from 50 cats in the food palatability unit of WCPN (Waltham on the Wolds, Melton Mowbray, Leicestershire). In this unit approximately 150 cats are housed in ten groups, known as panels. Six large panels comprised approximately 25 cats each, and four smaller panels had six to ten cats. Neutered males and entire females were kept together, and the groups were of mixed ages, varying from just under a year to 12 years old. All of the cats were bred at WCPN and were British Shorthairs. The palatability unit cats were used routinely for trials involving preference and measured intake of standard pet foods, but not for other types of experiments.

Each panel was kept in two large, connected rooms. The inner room was centrally heated, with a raised heated strip on one side of the floor, and had air-conditioning and a supply of fresh water. There were a number of shelves at various heights, and numerous beds and boxes. The rooms were also filled with toys and scratching posts. The outside room had no central heating, and contained nothing but one shelf, litter trays and water, and a view of the outside world. Experimental observations were carried out in one of the smaller inner rooms. The size of the room was decreased with a wooden partition, so that observations took place in an area of approximately 180cmx120cm, approximately the same area as the observation cubicle in the Southampton cattery.

WCPN operates a system of socialization for all the cats bred, in which kittens are handled and played with from an early age. Thus all the cats are well-socialised and easily handled. Staff play with all the adult cats every afternoon, to provide them with the opportunity for human interaction and exercise. The cats at WCPN proved to be unusually playful. Well over 50% of the cats in the colony played extremely vigorously, without obvious fatigue, compared with only 25% of the cats in the Southampton University colony, which played less vigorously and for less time. None of the cats had any hunting experience.

Southampton University:

Data from 19 different cats were collected. The Southampton colony consisted of 26 cats which were born and raised under identical conditions, and which were all aged 5 or 6 years when the study was started. There were both males and females, and all were neutered. The cats lived in two large rooms (23m^2 and 28m^2), a corridor (14m^2), and an outside yard (96m^2). The inside rooms were centrally heated, air-conditioned, contained litter trays, water, and were filled with shelves, beds, and a variety of toys. The outside yard was walled and had a concrete floor. The cats were prevented from escaping over the walls by a wire mesh roof. The yard contained logs, branches, tubes and shelves, and trays of turf. The cats were used for feeding trials and for other behavioural studies. In common with the cats at WCPN, these cats had all been raised in the same environment as each other and none of them had any previous hunting experience, except for occasional insects which entered the yard through the chicken wire. They had all seen and heard birds flying over the yard and appeared to recognise these as potential prey, as many exhibited the typical "teeth-chattering" response when birds were sighted. The experiments took place in a walled cubicle within one of the large rooms. This cubicle was 135cmx155cm with blank white walls and a wire mesh door. A closed-circuit camera fixture was positioned on top of the door. During observations no other cats were allowed into the room containing the cubicle.

Pet Cats

Fifteen pet cats belonging to members of the Southampton University Biology Department were recruited for some parts of the study. The cats were all crossbred and consisted of neutered males and females, and varied in age from one to seven years. Some were kept singly and others were kept in groups of two or three. Most of the pet cats had been observed hunting by their owners, although some owners considered that their cats were 'outdoor' and hunted regularly, while others said that their cats were 'indoor' and hunted infrequently. However, this distinction is subjective, since unless prey is brought to the house, owners may not be aware of the hunting activities of their cat.

2.2: METHODOLOGY

An ethogram of play behaviour

The behaviour patterns included in an ethogram can be defined in terms of their actual structure, their consequences or their spatial relation with other objects (Martin & Bateson 1993). The behaviours were defined with reference to the ethogram used by Biben (1979) for predatory behaviour and play. All three ways of describing behaviour were employed. For example 'recline' is a structural description, 'killbite' describes the consequence of a behaviour and 'avoid' describes the spatial relation with a particular object (the toy in this study). The ethogram used throughout the study is described in the Appendix.

Assignment of cats

Before including individual cats in the study it was necessary to find out which cats were playful. This was done by playing with each cat using a standard commercially available cat toy on a string to see if it would play. Cats which were either not playful or which were stressed by being separated from their colony were not used in any experiments. The latter was an important consideration at the Southampton and WCPN catteries only. Here many cats were playful when in a familiar room with the rest of their group, but were distressed when either removed to an unfamiliar room or separated from the other cats.

Experimental design

All treatments were presented according to randomized Latin Squares, as described in Cochran & Cox (1957), where letters were assigned to toys, rows to the cats, and columns to days of the experiment. The use of Latin squares permits the effects of subject-to-subject and day-to-day differences in play behaviour to be separated from the effects of the applied treatments (for example, type of toy). Table 2.1 is an example of a Latin Square.

Cat	Day1	Day2	Day3	Day4
1	A	C	D	B
2	B	A	C	D
3	D	B	A	C
4	C	D	B	A

Table 2.1. *An example of a 4x4 Latin Square, in which four cats receive four toys (denoted by letters) in a randomized sequence.*

When treatments are presented in sequence it is possible that the response to a treatment will be affected by the preceding treatment. To minimise this possibility an interval of one day was left between experimental days to allow for any effects of the previous treatment to have died out. Thus in an ordinary week, the cats were tested on Monday, Wednesday and Friday. Where learning an association was the aim of the experiment (see Chapter 7) the cats were used daily to strengthen the effect of the experiment protocol.

The majority of the experiments described in this thesis included four, six or eight different toys. Each cat received one toy on each day of the experiment, the toy being determined by the Latin Square. The experiment therefore took either four, six or eight days, plus intervening 'rest' days, to carry out. Experimental observations took place in the morning, after the cats' rooms were cleaned. Cats were fed once a day at approximately 1600 hours. The number of cats in each experiment varied; sometimes the same number of cats as toys were used, for example six cats each received six toys; in other experiments the number of cats was double the number of toys, for example eight cats each received four toys. In some experiments the toys were presented twice to each cat, for example eight cats received the same four toys twice, making the experiment eight days long (not including rest days).

Preliminary play sessions which lasted for five minutes showed that many of the cats lost interest in play after three minutes; one-way ANOVA was used to compare play in the first three minutes with the last two minutes, six out of 25 behaviour patterns were significantly different, three at $p<0.05$, three at $p<0.001$. Avoiding behaviour was greater in the last two minutes, and play behaviour was greater in the first three minutes, as was general activity. If observation sessions were any longer very little additional play behaviour was recorded. Durations of experimental play sessions were therefore fixed at either two or three minutes, depending upon the experiment.

Cats were always tested on their own in the same room for every session, separate from the rest of the cats in the cattery or other pets in the home. I presented the toys on the end of a piece of string, moving them in a standardized way, moving the toy back and forth in front of the cat, to gain the attention of the cat and to elicit play. Once the cat had caught hold of the toy and started to play with it I stopped moving it. If the cat then discontinued play I moved the toy again immediately. Thus all experiments involved interaction with me, as the experimenter.

In rewarding experiments (Chapter 7) each observation was not of a set length of time, but ended when the cat had stopped playing. An arbitrary cut off point was used to determine the difference between a brief hiatus in play, and actual stoppage of the play bout. If the cat did not show any play behaviour components for 20 seconds or more the observation ended.

2.3: THE EFFECT OF THE EXPERIMENTER

As stated earlier, all play behaviour involved interaction with the experimenter. It is possible that the cats may play differently according to the person playing with them, since cats sometimes show slight differences in behaviour when different people are present (McCune 1992). This may produce a bias in the data, and so a preliminary experiment was designed with the aim of determining whether there was an 'experimenter effect'.

Two people, with whom the cats were familiar (one person was the author, the other a co-worker within the research group), played with eight cats from the Southampton colony, using two contrasting toy types, one made from real deer fur and the other covered in polythene. There were four treatments (each experimenter with both toys), which were presented to the cats according to a Latin Square design. Observations were two minutes long, and data were recorded and analyzed as detailed above and below.

ANOVA tests of the independent variables toy and human showed that while six behaviours were significantly different with toy type, only one behaviour was significantly different with human (both at $p<0.05$, as explained earlier). This result was not considered significant for human interaction since at this probability level one significant result is likely to occur purely by chance, as explained earlier.

All other experiments were therefore carried out by the author.

2.4: DATA COLLECTION

In every session the frequency of each behaviour pattern in the Appendix was recorded along with the time when it occurred and, if relevant, the duration of its performance. The duration of the final behaviour pattern in each observation period is curtailed by the end of that timed period. However, for the purposes of this study this was not considered important because the focus was the comparison of behaviour under different stimulus conditions, not the detailed and complete description of the behaviour.

This method of continuous recording allows accurate measurement of frequencies and durations of behaviour components, and enables the exact sequence of the behaviour components to be analyzed if required (Martin & Bateson 1993).

In the rewarding experiments (Chapter 7) only one rewarded behaviour pattern was recorded. The rewarded pattern varied between experiments; if the pattern had no duration, only the frequency was recorded. If the pattern had a duration, its total duration during the session was recorded.

Data from observations were collected either on videotape or dictaphone. In the Southampton and WCPN catteries it was possible to have a closed-circuit T.V camera, monitor and video recorder. In pet cat houses and in some experiments with the cattery cats, behaviour was recorded onto dictaphone. All recorded behaviour was then transcribed onto computer using the Observer system (Noldus Information Technology b.v) for collection and analysis of observational data.

2.5: STATISTICAL ANALYSIS

Data collected in the Observer was then prepared for analysis in Lotus spreadsheets. Behaviour patterns which were not performed at all or occurred only once in the experiment were removed from the analysis. Data were imported into Statgraphics or SPSS.PC for analysis.

Analysis of Variance (ANOVA)

Two-way or multi-factor ANOVA is used to estimate the effect of two or more independent variables on a dependent variable (in this study the independent variables were the toy treatments and the dependent variables were the frequencies or durations of the play behaviour patterns). Multi-factor ANOVA is also used to detect interactions, when the effects of the independent variables are not simply additive, but depend upon the value of each other. Much behavioural data does not fit the ANOVA assumption of normal distribution. Preliminary experiments indicated that the means and variances of frequencies of common play behaviour patterns were reasonably independent of each other. Frequencies were therefore analyzed as raw data. Variances for durations were found to be dependent on the means; this could be largely eliminated by applying a square root transformation, which was then used for all analyses.

To ensure that any difference between treatments in each experiment was not simply difference between cats, the cat by treatment interaction term was used as the error term instead of the residual, wherever possible, see Table 2.1. When each cat was presented with each treatment only once, the cat by treatment interaction term could not be separated from the residual, which therefore had to be used as an approximation to the error. This interaction term is a result of the cats responding differently to the treatments, and is thus a measure of how different they are. By using this as the error term the overall (mean) difference in behaviour with different treatments can be compared with these qualitative

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Cat	338.78	11	30.79	
Treatment	105.58	2	52.79	52.79/6.41=8.23
Cat*treatment	141.08	22	6.41	
Residual	286.50	36	7.96	

Table 2.2. *Sample two-way ANOVA table, showing recalculation of treatment F-ratio.*

differences between the cats. Significant results (large values of F) are thereby only obtained when the treatment effects are substantially larger than the qualitative differences between cats.

Data from all experiments were tested with ANOVA. Probability levels were not adjusted to allow for multiple comparisons within each experiment, but the number of patterns expected to give a 'significant' result by chance was taken into account in interpreting the results of each experiment. Approximately forty patterns were analyzed in each experiment. If four or less were significantly affected by treatments the result was interpreted as not significant because four significant patterns out of 40 analyzed could be expected to occur by chance at 10% probability. Otherwise behaviour patterns significantly affected by the treatments at the $p<0.05$ level were then combined and analyzed in order to determine the direction of the main effects, and to examine any interactions between treatments in multifactorial experiments. This was carried out in Principal Components Analysis (PCA). In multifactorial experiments those Principal Components accounting for a substantial amount of the overall variance were themselves examined by ANOVA to compare main-effect and interaction effects.

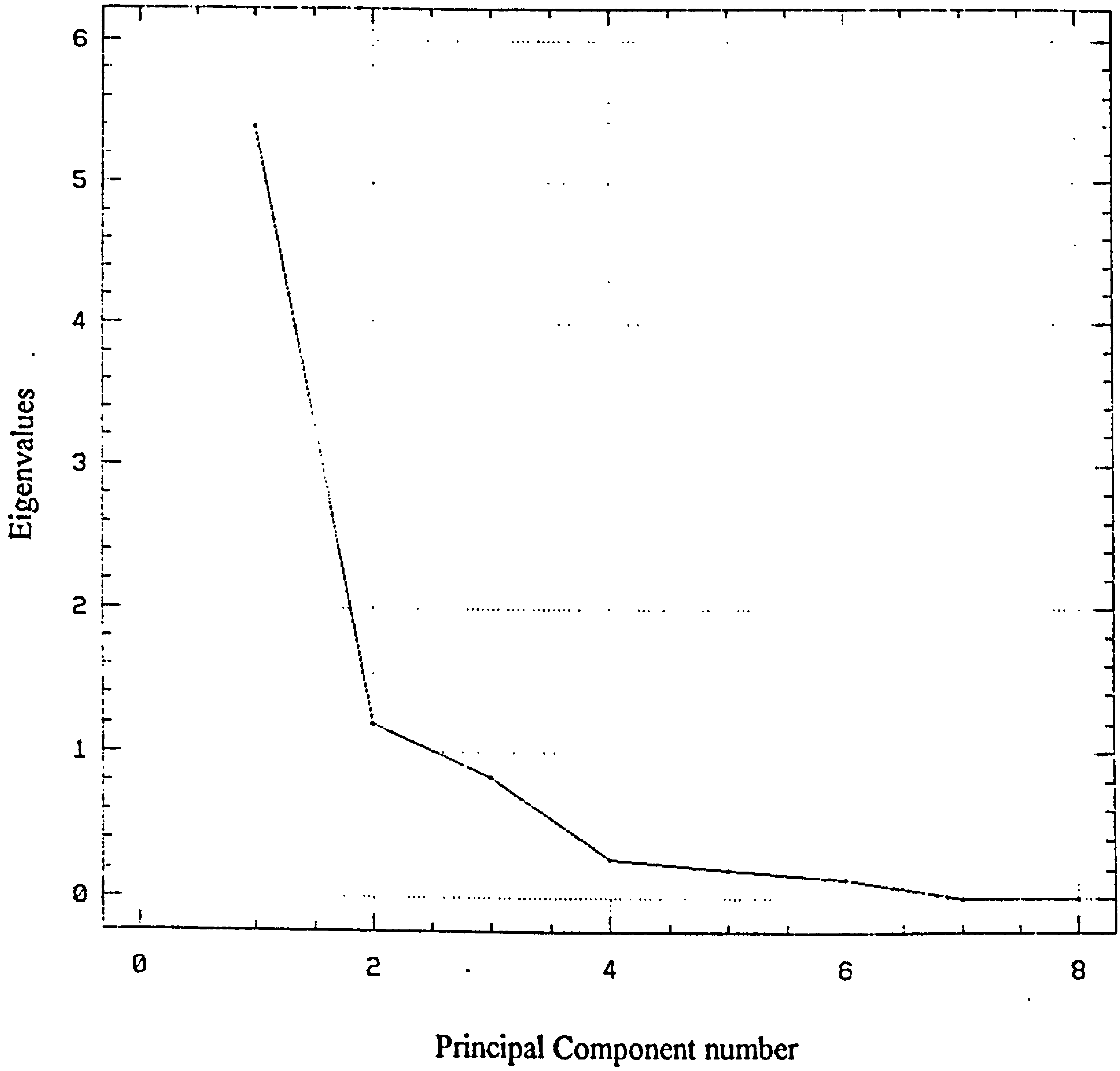
Principal Component Analysis (PCA)

PCA is a multivariate test used when more than one dependent variable has been measured. Since the performance of many of the play behaviour patterns is linked in sequences (see

Chapter 6), many will be affected in the same way by the treatments applied. Conversely, if one pattern is expressed repeatedly, it will prevent the expression of other patterns. In order to describe these relationships it is helpful to group the individual patterns as a smaller number of underlying factors which account for a large amount of the variance of the original variables using Factor Analysis techniques. PCA is one method of factor analysis in which the main linear effects are separated into principal components. The first component accounts for the largest proportion of variance within the data. This first component is removed and the component which accounts for the largest proportion of variance within the remaining data becomes the second component. This second component lies on an axis perpendicular to that of the first, so that they are uncorrelated. This is repeated, and succeeding components account for less and less variance, and are all uncorrelated with each other. Having generated the components it is possible to determine which ones are of value by examining a scree diagram- a plot of the eigenvalues of each component (a measure of the variance explained) against the component numbers. The gradient of this plot generally has a break in it; above this break the number of points corresponds to the number of components of value (see Figure 2.1). Usually only the first two or three components, which account for most variance (usually over 75%), are worth examining. In each component it is possible to determine the relationship between the dependent variables (behaviour patterns) and independent variables (sessions). Dependent variables are given a weighting, either positive or negative. These weightings correspond to a separate distribution of the independent variables. These distributions are displayed graphically in PCA and visual comparison reveals the relationship between the dependent and independent variables (behaviour patterns and sessions, comprising combinations of cat and treatment).

For each experiment PCA was used to look at the effect of the toy treatments on the play patterns they affected significantly (see above). Means tables contain information which is as useful in determining the direction of a treatments effect (for example, did a pattern increase or decrease in frequency and duration with the change from small to large toy size?), but PCA enables a clearer, visual interpretation of all the changes in play, simultaneously.

Figure 2.1. *An example of a scree diagram. Eigenvalues are shown on the Y axis, and Components on the X axis. Only components above the break in the plot, when the graph is read from right to left, are examined, in this case Component 1, 2 and 3.*



Sequence analysis

Analysis and comparison of play sequences elicited by different toy stimuli was carried out using the MatMan program (de Vries et al 1993). MatMan is designed for the ethological analysis of frequency matrices and behavioural transition matrices. Data from Observer files were imported into MatMan for conversion into transition matrices. These contain the frequencies with which the preceding behaviour patterns (in the rows) are followed by succeeding behaviour patterns (in the columns). Once in the transition matrix format, Chi squared tests are used to estimate the significance of each transition pair of behaviour patterns, by measuring the difference between expected and observed values, where the expected value would be a random probability. Any variance between the data and a normal distribution becomes the adjusted residual, the final value used in the analysis; transitions which have adjusted residuals (z values) significant at $p<0.001$ are recorded. These significant transitions can be used to construct a kinematic diagram which illustrates likely behaviour pattern transitions, even though these are based upon first-order transitions only (that is, no reliance can be placed on relationships between patterns not directly connected by an arrow). The kinematic diagrams were used in this study (in a descriptive way only) to split play behaviour into patterns which appeared to occur close together in time, and which seemed to represent different levels of intensity of play. This was useful in determining the transitions which appeared to mark the end of play bouts and those which were characteristic of low intensity or high intensity play. It was possible to use the kinematic diagrams to lend some support to arguments pertaining to the pattern of motivation change throughout play bouts.

A more detailed discussion of the uses, requirements and limitations of sequence analysis is included in Chapter 6.

3

INVESTIGATION OF PLAY-ELICITING STIMULI

3.1: INTRODUCTION

The first step in this study was to define the stimuli which elicit adult cat play, since the stimuli that elicit a behaviour can be used to characterise a type of behaviour. It is possible to identify the 'sign-stimuli' which elicit the performance of a behaviour. Sign-stimuli are the essential stimuli of an object that elicit a behaviour; animals commonly respond to a few aspects of an object presented to them. These are usually particular features to which animals are instinctively responsive, for which no learning is necessary; for example the bill colour of adult herring gulls *Larus argentatus argentatus* elicits the food begging response from chicks (Tinbergen 1950). The instinctive response to sign-stimuli usually occurs where it is important that the animal always responds to the stimulus, for example calls warning of predators, and where false responses are not important, as in the case of responding to a false predator alarm (Manning 1979). An object may have more than one sign-stimulus, and in this case the response of the animal is usually not additive, but more complex. Stimuli are often interactive and have a synergistic effect on the response they elicit (Curio 1975, Manning 1979).

The responsiveness of animals to particular stimuli and not to others can be a result of either central or peripheral filtering (Manning 1979). Peripheral filtering occurs when the animal's sensory structures respond only to distinct stimuli, for example the antennae of the male silk moth *Bombyx mori* are selectively responsive to the pheromones of females, but to no other chemicals (Schneider 1966). Central filtering can occur when animals appear to have an 'inborn' or 'innate' response or preference. For example, newborn garter snakes *Themnophis sirtalis* which have never fed before show definite food preferences which are the same as those of their mother, suggesting that there is a genetic influence on their responses (Burghardt 1970). Similarly, newborn Peking ducklings *Anas platyrhynchos* exhibit a colour preference for green in their pecking response (Oppenheim 1968). Such inborn preferences are often difficult to alter, even with rewarding and learning schedules: Burghardt could not alter the food preferences of garter snakes even when he fed them only with food for which they showed low preference.

Central specification for a response to external stimuli is referred to as a 'releasing mechanism', and this is often specific enough to discriminate between a group of stimuli (for example prey from non-prey items), but is unspecific enough to enable response to all potential prey items (Curio 1975). The releasing mechanism can respond differently to various combinations, or configurations of stimuli encountered, showing 'configural selectivity' (Ewert 1987). This configural selectivity can be modified by learning and differences in motivation. Even limited experience with certain stimuli can lead to 'perceptual sharpening' which can modify an animal's configural selectivity, for example observing one prey species more than another (Curio 1975). Conversely, naïve animals often respond to a wider range of objects which possess a particular sign-stimulus. For example, naïve Loggerhead shrikes *Lanius ludovicianus* attack a wide range of moving dummy prey objects because motion is the most important stimulus in prey detection. Experienced hunters respond less to moving dummies which lack some other stimuli characteristic of prey, preferring moving stuffed and live prey (Smith 1973).

Studies to determine the sign-stimuli which elicit a behaviour have traditionally focussed upon the construction of artificial stimuli; for example Tinbergen (1950) constructed numerous dummy adult herring gull bills in order to determine the sign-stimuli that elicit the food begging response in chicks. An enormous number of variations in the size and shape of the bill were accepted by the chicks, but the sign stimulus was eventually narrowed, by repeated variation of all possible bill stimuli, to the colour of the bill tip.

A few studies of the stimulus parameters which elicit adult play or predation have used this approach. These studies involved changing the stimulus parameters of simulated dummies, and analysing variations in response in order to determine the relative efficacy of stimuli. Dummies have been used to present variations of stimuli and prey features in studies of predation; for example, to determine cues which direct predators to the head of prey, and which enable them to place lethal bites in the correct place (Leyhausen 1965, Rasa 1973). Such studies enabled the ranking of prey stimuli according to the predatory response they elicited. They also indicated that the presentation of stimuli in the form of dummies is an effective method of studying external factors which elicit predation.

In attempting to determine the stimuli which elicit play in adult cats in this study, a similar approach was used. The stimuli chosen were characteristic of prey animals. The physical similarity and possible motivational relationship between play and predatory behaviour lead to the hypothesis that play may be elicited by similar stimuli. Cats must possess a configural selectivity for prey sign-stimuli which enables them to recognise prey animals, and to respond with predatory behaviour. The suggestion that play and predation are closely related would be substantiated if both behaviours were elicited by the same stimuli. Thus the obvious starting point when constructing dummies to elicit play behaviour is to use stimuli characteristic of real prey.

Prey features incorporated into dummies have been used before in the study of play-eliciting stimuli. Russell (1990), working with ferrets, looked at the effects of a range of stimuli on their play behaviour, including movement, shape, size, colour and odour. The variations of these stimuli all included those which were characteristic of ferret prey. The ferrets responded playfully to dummies which had prey-like characteristics, and showed less interest in dummies with novel, unnatural characteristics.

Since prey stimuli have been shown to elicit play in other carnivorous species, it can be reasonably expected that play in cats should be elicited by prey stimuli.

With these studies as a background, the aims of the experiments described in this chapter were to determine the key stimuli, presented as toys (dummies), which elicit play behaviour in adult cats, and to compare them with each other and define the most effective stimuli. In the experiments of part 3.2. variations of discrete stimulus parameters were presented; in part 3.3. the stimulus parameters which were found to elicit the most intensive play behaviour were combined in a multi-factorial protocol to determine which stimulus parameters were the most important when they were all presented in combination.

3.2: THE COMPARISON OF VARIATIONS OF SINGLE STIMULUS PARAMETERS

METHOD

In order to determine the key stimuli which elicit play behaviour in adult domestic cats, a set of experiments were undertaken in which the stimuli were designed to mimic those which would probably also elicit predatory behaviour. This was based on the assumption that since play and predation are structurally similar, they may be elicited by similar stimuli. Toys were designed in order to test discrete stimulus characteristics. Some stimulus characteristics were intended to mimic those of real prey, while others were intended to be as dissimilar to prey characteristics and novel as possible.

Eight experiments were performed over a period of 1½ years, with six or eight cats from the Southampton colony. Two of these experiments were repeated, with slight variations, with two other groups of cats, at Waltham Centre for Pet Nutrition (WCPN) and with the pet cats. All toys were presented to the cats according to a Latin Square design, and each session lasted for two or three minutes. Sessions were recorded on video tape (Southampton and WCPN cats) or on a dictaphone (pet cats).

Size and shape

Studies of predation have shown that the size of an object determines whether it is treated as prey or not; for most predators there is an upper size limit to potential prey objects, above which evasive action is more likely to be elicited. This has been shown in various species, for example cats (Biben 1979), toads (Ewert 1987) and rats (Polsky 1976). It is likely that size is an important factor in determining the play response of cats.

Three sizes of toy were presented to six WCPN cats. A small toy measured 7x5x1 cm (mouse size), a medium toy measured 15x9x2 cm (rat size), and a large toy measured 30x10x9 cm (cat size). Each cat received the three toy sizes twice. The experiment was repeated with 12 pet cats. Each cat received the three sizes twice.

Three different sizes of toy were presented to six Southampton cats, and were combined with two different shapes; the sizes were small (7x5x1 cm), medium (12x7x1 cm juvenile rat size) and large (15x9x2 cm). The cats received two toys of each size, one with a constriction at one end, representing a 'neck', and one without.

Texture

Six different textures were presented once each to six Southampton cats, five designed to be similar to prey, and one totally artificial and unlike real prey. The textures were real fur (fallow deer), fakefur, feathers, felt, towelling and polythene. The toys were made the same size as the small (7x5x1 cm) toys above. The feathers were yellow, the real fur was brown, but the remaining toys were white. The experiment was repeated with 12 cats at WCPN. The same textures were presented, once to each cat.

The trial with the pet cats was varied slightly. It had been noted that a new toy in the Southampton colony elicited intensive play; this toy was a small (8cm diameter ball) black, fakefur 'spider' with pipecleaner legs. A new toy was made which had pipecleaner legs, the 'body' of the toy was small (7x5x1 cm), white fakefur. A preliminary experiment showed that it elicited as much play as the feather and fakefur toys. In this trial this new toy was introduced as another variation of complex texture and replaced towelling. The textures presented were; smooth, felt, feathers, fakefur, real fur and the new toy, 'legs'. The 12 cats received each toy once.

Size and texture

An unreplicated experiment with 18 cats at WCPN combined the three sizes with the three of the textures which elicited intensive play. The three textures were fur, fakefur and feathers. Thus nine toys were presented, each of the three textures covering a small, medium and a large toy. The cats received each toy once.

Pattern

Cats are highly sensitive to differences in tone and to 'edges' (Bradshaw 1992). When an object moves the cat is able to detect it rapidly because of this sensitivity. A toy with a greater contrast between its colours, and with a more complex pattern, might therefore elicit intensive play. To test this six toys were made, covered with patterned fakefur. These were; white with black polka dots; white with large black patches; light brown with dark brown stripes, light brown with dark brown spots, plain white and plain black. The toys were all 7x5x1 cm. Six cats at the Southampton colony were presented once each with each toy. The experiment was not replicated.

'Skin' looseness

An unpublished study at WCPN suggested that toys with a loose-fitting covering elicited more play behaviour than toys with tighter covering (Robinson, personal communication). It was suggested that loose-fitting covering would be easier to grasp and bite than a toy with a tight-fitting covering. To test this idea two toy sizes, small (7x5x1cm) and large (30x9x10cm) were presented, either with loose-fitting 'skin' or with tight 'skin'. The toys were all made from white fake fur, and were presented to eight cats at Southampton, each cat received each toy twice. The experiment was not replicated.

Sound

Toys were made which contained small buzzers designed for use in doorbells. Each buzzer was hidden inside a small (7x5x1cm) white, fakefur toy. The buzzer was connected to a battery and switch box by a long lead which acted as the string by which the toy was held. The switch box was held in the hand so that it could be activated easily. There were three sounds; a continuous tone; a pulsed tone and a two-tone. Two sound durations were presented. The short duration sound was for one second with a ten second pause before the next sound, a long duration sound was for five seconds with a ten second pause before the next. A silent small white, fakefur toy was presented as a control. Eight cats from the Southampton colony were used to test these toys. The cats received each toy once.

Odour

Five different odours were tested for their ability to elicit play. Two were food-like; **fish** (John Burgess and Son Ltd anchovy essence), and **chicken** (PFW Ltd, P.O Box 18, Greenford, Middlesex.). Three were plant derivatives; **dried catnip** (Hagen dried catnip, Rolf.C.Hagen (USA) Corp, Mansfield, MA 02048.); **peppermint** (Safeway Foodstores Ltd, Aylesford, Kent. Natural Peppermint Essence.); **vanilla** (L.Noel and Sons Ltd, Oswaldtwistle, Lancashire,BB5 4PR.). Finally, no odour was used as a control.

Subjective tests were undertaken to match the strengths of the fish, chicken, peppermint and vanilla odours. Co-workers were given samples of the odours at different concentrations, and asked to match up the four smells according to concentrations which were roughly compatible. The following number of drops of each were found to be approximately equivalent; three drops of vanilla, five drops of fish, seven drops of peppermint and one drop of chicken. A preliminary experiment in which the odours were presented at this strength elicited very clear repulsion from the cats, leading to the conclusion that the odours were too strong. Therefore the odour essences were diluted before being presented again. The equivalent quantities of each odour were then diluted to 1/100th of the original concentration with 0.1% TWEEN solution. One drop of each was then put into a toy for presentation to the cats.

Catnip was not presented to co-workers since to most humans this has no particular smell. Approximately 5g of catnip was put into the toy. This was removed and replaced with unused dried catnip after each experimental day.

The odours were presented to six cats from the Southampton colony in toys which were small white fakefur, with small pouches sewn on one side. The drops of diluted essence were put onto a piece of cottonwool and this was inserted into the pouch so that the cat would not be able to extract it. Each prepared toy was wrapped in cling film to prevent it from contaminating the other toys and to prevent the odours from being detectable in the experiment room before and after it was used. The cats received each toy once. The experiment was not replicated.

Movement

Toys were designed to test the effect of movement and of movement quality upon play. The cats received the following toys; one toy with a string attached (small, white fakefur), was swung during the experiment, as in all past experiments; the second toy was a clockwork mouse of the same dimensions, covered in white fakefur. This mouse moved at $15 cm sec^{-1}$, and changed direction at random intervals and in random directions; finally a third small white fakefur toy had no string attached to it, and was simply left on the floor of the experimental room, in the same place for every cat. Six cats from the Southampton colony received each of the three treatments twice.

RESULTS

All data were analysed using the appropriate ANOVA test. Behaviour patterns which were significantly affected by treatments at $p<0.05$ were analysed in Principal Component Analysis in order to visualise the direction of trends in behaviour (see Chapter 2). For every component, each behaviour pattern is given a weight, shown on a plot of component weights. For each individual play session's combination of cat and toy type, the data for each behaviour pattern is multiplied by the weight for each pattern. This is used to produce a scatterplot of each play session (labelled with cat and toy type). These two plots can then be visually compared to determine the distribution of cats and toy types in relation to the distribution of behaviour patterns on each component. Which components are examined depends upon the scree diagram, as explained in Chapter 2. In general only the first two components are useful, that is, account for a large proportion of variance, although component 2 usually shows only cat variation.

Size and shape

WCPN cats

In the one-way ANOVA test of the WCPN data 15 out of 32 behaviour patterns were significantly affected by toy size, nine at $p<0.05$, six at $p<0.01$. The 15 behaviour patterns were analysed in PCA. Component 1accounted for 48.5% of the variance. It contrasted stand avoid and walk avoid with the other 13 behaviour patterns, which are all play or watching patterns (see Figure 3.1). This distribution of behaviour patterns on component 1 is typical of the first component in all the PCAs performed in the experiments of this chapter. All contrasted avoiding patterns with play and watching patterns. Figure 3.1 is therefore representative of the distribution for all experiments as well as for the WCPN size repeat.

Behaviour abbreviations for Figure 3.1, and all further figures and tables:

F=frequency measure
D=duration measure

Play patterns: All play patterns are frequency only, except **CL** and **HM**, which also have a duration measure.

SN-sniff
HM-holdmouth
KB-killbite
RE-rear
LI-lick
CW-chew
GR-grasp
HI-hit
BA-bat
CL-clutch
KI-kick

HUNTD-total duration of all behaviour patterns classed as play.

Non-Play patterns: All non-play patterns have a frequency and a duration measure.

<u>Primary</u>	<u>Secondary</u>
Wawalk	**AV**-avoid
ST-stand	**GO**-groom
SI-sit	**WT**-watch
CR-crouch	
RC-recline	

Primary behaviour pattern codes precede secondary behaviour pattern codes, for example, **WAWTF**=walk and watch frequency

All behaviour patterns are defined in the Appendix.

Figure 3.1. The distribution of behaviour patterns on components 1 and 2 for the WCPN size experiment repeat.

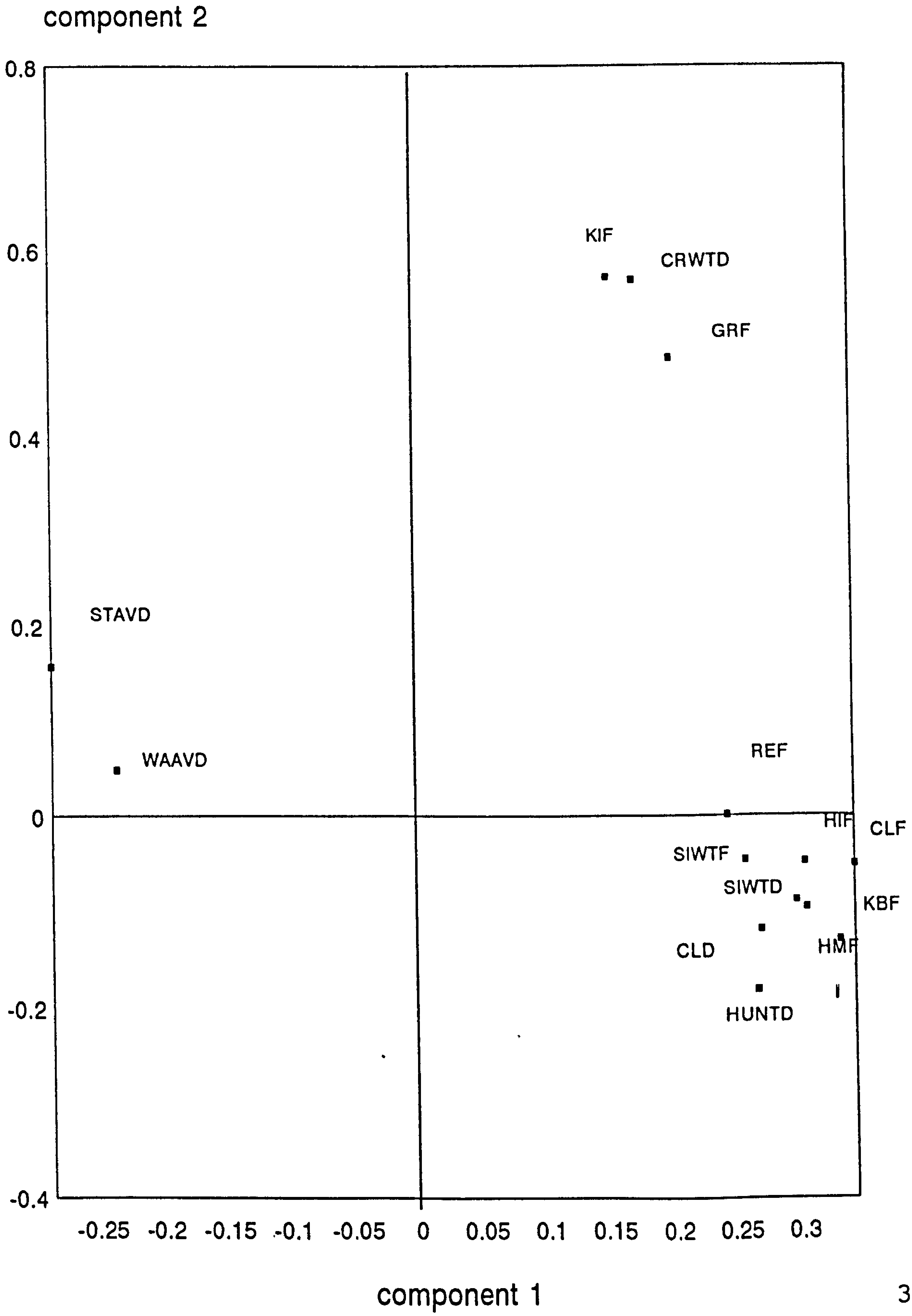
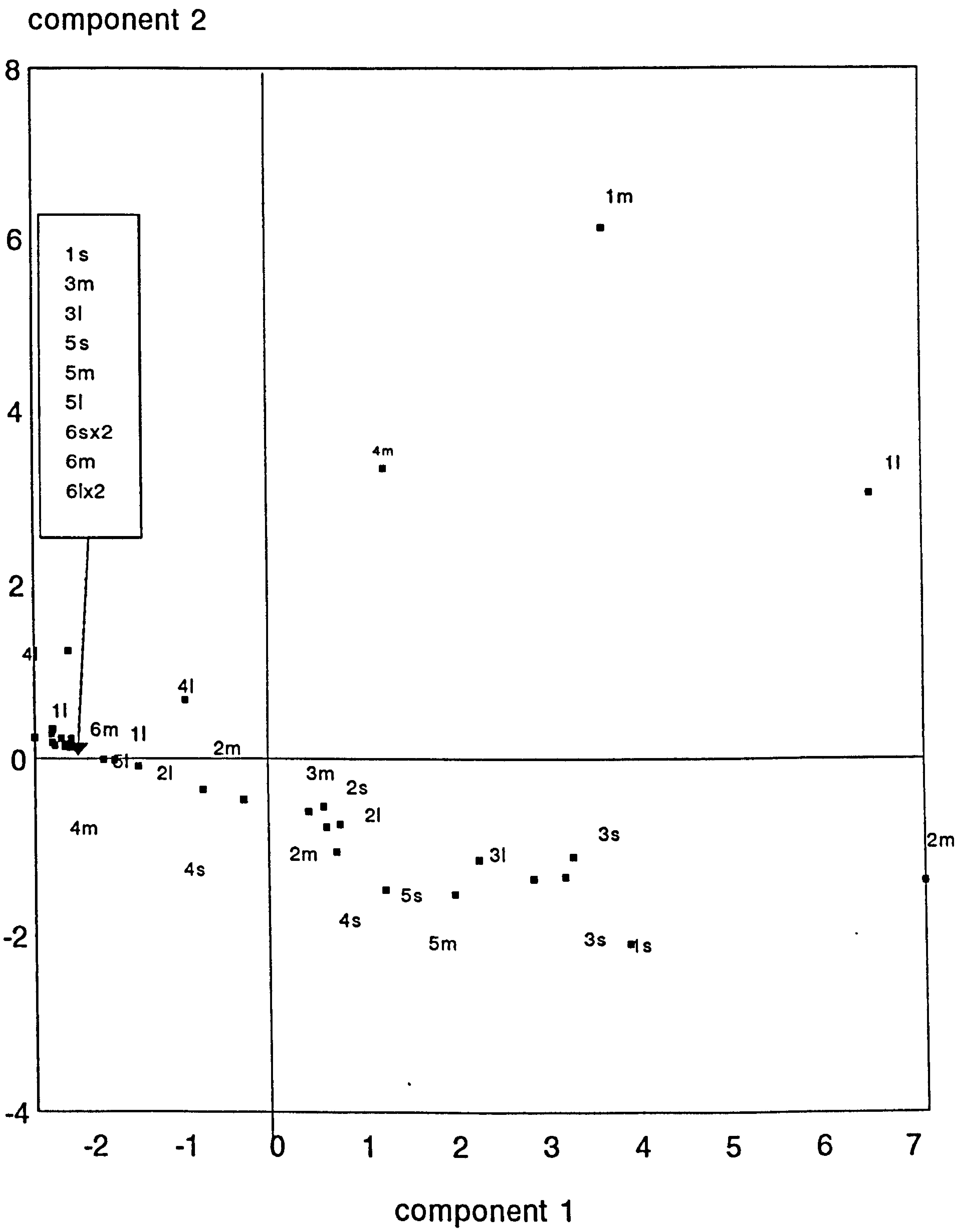


Figure 3.2. The distribution ofindividual sessions, coded by toy size and cat on components 1 and 2 in the WCPN experiment.



s=small; m=medium; l=large

The three toy sizes were distributed on component 1 as shown in Figure 3.2. This distribution can be compared with the distribution of behaviour patterns (Figure 3.1), enabling visualisation of the behaviour patterns that each size elicited.

The three toy sizes were found on the 'avoid' and 'play' side of component 1 as shown in Table 3.1:

Toy size	Play	Avoid
small	9	3
medium	8	4
large	3	9

Table 3.1. *The distribution of individual sessions using each of the three toy sizes on the negatively loaded 'avoid' side, and the positively loaded 'play' side, of component 1.*

It is clear from this table and from Figure 3.1 and 3.2, that the small toy elicited more play than either of the other toys, and that the large toy elicited mostly avoiding behaviour.

The distribution of toy types on component 1 for all further experiments is shown in Tables 3.2 to 3.13. In all PCAs only component 1 provided information about the play elicited by the different toy types. The tables show the values on component 1 for behaviour patterns which were significantly affected by the different toys in each experiment. These values correspond to the distribution of behaviour patterns shown in Figure 3.1, in which play behaviour patterns are positively loaded, and avoiding behaviour patterns are negatively loaded. Results from all experiments are shown in similar tables.

Component 2 was a result of individual differences in 'style'. An example of this is shown in

Figure 3.2, which shows the distribution of cats on components 1 and 2. When compared with the behaviour pattern distribution in Figure 3.1, it is clear that individual cats behave slightly differently. For example cat 1 showed a tendency to perform 'crouch watch', while 4 showed a tendency towards avoiding behaviour.

Pet cats

In the two-way ANOVA of the pet cat data ten behaviour patterns were significantly affected by the size difference, five at $p<0.05$, and five at $p<0.01$. These were entered into a PCA, the results of which are shown in Table 3.2.

The small toy elicited more play behaviour patterns than the medium and large toys, and the large toy elicited more avoiding behaviour than the others.

Southampton cats

In the two-way ANOVA of the Southampton trial (size and 'neck'), the difference in size affected the performance of seven behaviour patterns at $p<0.05$ and seven at $p<0.01$. PCA test results and the trends in behaviour were the same as the WCPN and pet cats trials (see Table 3.2 and Figures 3.1 and 3.2), except that the smaller difference between the medium and large toys resulted in smaller differences in play. However, the existence of a 'neck' constriction significantly affected only three behaviour patterns at $p<0.05$ (expected by chance), suggesting that it made no difference to the cats' play behaviour.

Texture

Southampton cats

Differences in texture elicited significant differences in five behaviour patterns at $p<0.05$, and four at $p<0.01$ out of 39 tested in a one-way ANOVA of the unreplicated experiment. PCA results are shown in Table 3.3. Real fur and feathers both elicited high frequency and duration of play behaviour, being played with almost continuously throughout trials; fakefur elicited slightly less play than these two, but more than felt. The polythene and towelling toy both elicited low intensity play, and more avoiding behaviour.

WCPN cats

In the one-way ANOVA test of the WCPN data, 12 behaviour patterns varied significantly ($p<0.05$) with the toy textures. PCA results are shown in Table 3.4. The trends in response to the textures was similar to the Southampton experiment, except that real fur elicited higher intensity play than feathers.

Pet cats

The one-way ANOVA test of pet cat data showed that nine behaviour patterns were significantly ($p<0.05$) affected by toy textures. PCA results are shown in Table 3.5. Behaviour trends were slightly different; feathers and 'legs' elicited slightly more play than both real fur and felt, which elicited similar play behaviour. Fakefur elicited more avoiding behaviour than any of these, but less than the smooth toy, which was ignored by most cats.

Duration of play

A brief experiment was carried out after the three texture repeats had been completed to determine whether real fur elicits more play behaviour than feathers, another highly effective play-eliciting texture. The same cats from WCPN, Southampton and the pets received the real fur toy and the feathers toy, on separate occasions, and the total duration of play behaviour until the first 20 second break was recorded with each. One-way ANOVA showed that the duration of play for all three groups was significantly greater with the real fur toy, at $p<0.005$. Average play durations with both toys are shown in Table 3.6. Thus real fur is an effective texture, eliciting not only high intensity play, as shown in the texture experiments, but also longer duration of play.

Cat Group	Average play duration (s) with the real fur toy.	Average play duration (s) with the feather toy.
Southampton	487.72	159.84
WCPN	245.29	129.20
Pets	322.98	162.55

Table 3.6. *The average play duration (s) with the real fur and feather toys in the three cat groups.*

Size and texture

A multi-factor ANOVA with interaction between treatments (size, texture) was used to analyse data from this experiment.

Behaviour patterns significantly affected by size, texture and the interaction of size and texture were analysed separately in three PCA tests, the results of which are shown in Table 3.7 and 3.8. The difference in size significantly affected 26 behaviour patterns out of 39 tested, four at $p<0.05$, and 22 at $p<0.01$; texture differences significantly affected seven patterns at $p<0.05$; finally, the interaction of size and texture significantly affected five patterns at $p<0.05$, and five at $p<0.01$.

The PCA tests of size and texture revealed the same trends as noted above (see Table 3.7. and 3.8); play was more intense with the small toy than with the medium, which elicited more play than the large toy. The real fur toy elicited more play than the feathers and fakefur toys, fakefur elicited more avoiding behaviour than the other toys.

The interaction of size and texture showed that the small fur toy was the most successful in

Table 3.2. *The distribution of behaviour patterns and toy sizes on component 1 of the pet trial of the size experiment.*

Patterns	Component 1	Toy	Average value on component 1
walk avoid (d)	-0.257	medium	-1.5305
sit avoid (d)	-0.159	large	-0.2346
walk avoid (f)	-0.0267	small	0.8608
chew (f)	0.245		
clutch (f)	0.261		
holdmouth (d)	0.265		
grasp (f)	0.296		
hit (f)	0.3		
killbite (f)	0.327		
clutch (d)	0.347		

Table 3.3. *The distribution of behaviour patterns and textures on component 1 of the Southampton texture experiment.*

Patterns	Component 1	Toy	Average value on component 1
stand avoid (d)	-0.2268	towelling	-1.3097
sniff (f)	0.0074	polythene	-1.0253
kick (f)	0.1437	felt	-0.5090
grasp (f)	0.2944	fakefur	0.5128
hit (f)	0.3142	feathers	0.8334
clutch (d)	0.3464	real fur	1.9604
hunt (d)	0.3509		
killbite (f)	0.3763		
clutch (f)	0.4292		

Table 3.4. *The distribution of behaviour patterns and textures in the WCPN texture experiment.*

Patterns	Component 1	Toy	Average value on component 1
walk avoid (d)	-0.3012	polythene	-1.6308
stand avoid (d)	-0.2895	towelling	-1.3469
walk avoid (f)	-0.2875	felt	-1.2793
sniff (f)	0.0662	fakefur	0.7143
sit watch (d)	0.2083	feathers	1.3635
holdmouth (d)	0.2547	real fur	2.1790
hit (f)	0.2619		
clutch (f)	0.2800		
holdmouth (f)	0.2893		
killbite (f)	0.3129		
clutch (d)	0.3279		
hunt (d)	0.333		

Table 3.5. *The distribution of behaviour patterns and textures on component 1 in the pet trial of the texture experiment.*

Patterns	Component 1	Toy	Average value on component 1
sit avoid (d)	-0.3936	polythene	-1.4374
sit avoid (f)	-0.3865	fakefur	-0.2544
crouch watch (d)	-0.1751	felt	-0.2533
sniff (f)	0.0359	real fur	0.3906
bat (f)	0.0678	legs	0.7074
hit (f)	0.2958	feathers	0.8471
killbite (f)	0.4082		
clutch (d)	0.4414		
clutch (f)	0.4584		

Table 3.7. *The distribution of behaviour patterns and toy sizes on component 1 in the WCPN size\texture experiment.*

Patterns	Component 1	Toy	Average value on component 1
stand avoid (f)	-0.2390	large	-2.0601
walk avoid (f)	-0.2274	medium	-0.4180
stand avoid (d)	-0.2273	small	2.5193
walk avoid (d)	-0.2246		
recline avoid (f)	-0.0704		
sit avoid (f)	-0.0645		
recline avoid (d)	-0.0642		
sit avoid (d)	-0.0538		
sniff (f)	0.0693		
recline watch (f)	0.1092		
crouch watch (d)	0.1145		
kick (f)	0.1407		
recline watch (d)	0.1427		
crouch watch (f)	0.1466		
holdmouth (d)	0.1648		

Pattern	Component 1		
chew (f)	0.1706		
holdmouth (f)	0.1846		
sit watch (d)	0.2048		
rear (f)	0.2062		
sit watch (f)	0.2111		
killbite (f)	0.2327		
hit (f)	0.2383		
clutch (f)	0.2686		
clutch (d)	0.2786		
grasp (f)	0.2793		
hunt (d)	0.2803		

Table 3.7 continued.

eliciting play behaviour, and the large fakefur toy was the least successful (see Table 3.9). There were some unexpected results, for example, the large fakefur toy elicited slightly more play than the medium fakefur toy, and the medium feathers toy elicited a relatively intense play. To determine which variables out of size, texture and the size and texture interaction were the most significant determinants of changes in play behaviour, a further stage of analysis was undertaken. The PCA was rerun with all significantly affected behaviour patterns (a total of 32). The first three components (selected after reference to a scree diagram) were tested in two-way ANOVA to determine the significance of the three variables. The significance level of each component according to the three variables was noted and shown in Table 3.10. This ANOVA table enabled the determination of the relative influence of the three variable, size, texture and the interaction of the two.

This table shows that the size of the toy and the interaction between size and texture were significant on component 1 (which accounts for the most variance, 34.3%). This indicates that they were the most important determinants of the changes in play behaviour. In component 2 (10.28% of variance) the size and texture interaction was the most important determinant of play behaviour; in component 3 texture was the most important determinant. Since component 3 only accounts for 8.29% of the variance, this indicates that texture had much less influence upon play behaviour than either the size of the toy or the interaction between size and texture.

Pattern

The one-way ANOVA revealed that only one behaviour pattern out of 37 tested was significantly affected (at $p<0.05$, expected by chance) by the pattern of the toy, suggesting that it had no influence upon the cats' response.

'Skin' looseness

In the two-way ANOVA (treatments were size, looseness with no interaction) the difference in

Table 3.8. *The distribution of behaviour patterns and toy textures on component 1 for WCPN size\texture experiment.*

Patterns	Component 1	Toy	Average value on component 1
crouch avoid (f)	-0.1095	fakefur	-0.4060
crouch avoid (d)	-0.1043	real fur	0.0662
crouch watch (d)	0.1763	feathers	0.3372
sniff (f)	0.1831		
walk watch (f)	0.2302		
grasp (f)	0.4938		
clutch (f)	0.5553		

Table 3.9. *The distribution of behaviour patterns (all significantly affected by the size*texture interaction) and toy textures and sizes on component 1 of the WCPN size\texture experiment.*

Patterns	Component 1	Toy	Average value on component 1
walk avoid (d)	-0.2879	medium fakefur	-1.2449
walk avoid (f)	-0.2821	large real fur	-0.2982
stand avoid (d)	-0.2774	large feathers	-0.1123
crouch watch (d)	0.1202	large fakefur	0.0025
rear (f)	0.2814	medium real fur	0.1351
hit (f)	0.3033	medium feathers	0.2285
grasp (f)	0.3082	small fakefur	0.2876
clutch (d)	0.3361	small feathers	0.3630
hunt (d)	0.3370	small real fur	0.5935
clutch (f)	0.3560		

Table 3.10. *The significance levels of each of the first three components for the three variables, size, texture and the size and texture interaction (size*texture).* NS=p>0.05

Significance level for each variable.

Variable	Component 1	Component 2	Component 3
size	p<0.005	NS	NS
texture	NS	NS	p<0.005
size*texture	p<0.005	NS	NS

Table 3.11. *The distribution of behaviour patterns and toy odours on component 1 in the Odour experiment.*

Patterns	Component 1	Toy	Average value on component 1
sit avoid (f)	-0.1586	no smell	-1.1537
recline watch (d)	0.3084	vanilla	-0.8831
walk watch (d)	0.3132	peppermint	-0.6995
lick (f)	0.3288	chicken	-0.5115
walk watch (f)	0.3615	fish	-0.5066
sniff (f)	0.3962	catnip	3.6223
clutch (d)	0.4366		
hunt (d)	0.4418		

Table 3.12. *The distribution of behaviour patterns and toys on component 1 of the Movement experiment.*

Patterns	Component 1	Toy	Average value on component 1
walk avoid (f)	-0.2870	mouse	-0.6375
walk avoid (d)	-0.279	stationary	-0.2782
crouch avoid (d)	-0.2772	string	0.9156
crouch avoid (f)	-0.03		
sit watch (f)	0.08		
sit watch (d)	0.134		
grasp (f)	0.231		
rear (f)	0.274		
killbite (f)	0.278		
hunt (d)	0.345		
clutch (d)	0.3486		
clutch (f)	0.3696		

Table 3.13. *The distribution of behaviour patterns and movement on component 1 of the Movement experiment.*

Patterns	Component 1	Toy	Average value on component 1
walk avoid (f)	-0.2763	stationary	-1.9143
walk avoid (d)	-0.2724	moving	1.9143
stand avoid (f)	-0.2673		
stand avoid (d)	-0.2595		
stand watch (f)	-0.0015		
sit watch (f)	0.0912		
sit watch (d)	0.1400		
killbite (f)	0.2716		
rear (f)	0.2720		
clutch (d)	0.3108		
hunt (d)	0.3117		
clutch (f)	0.3405		

Table 3.14. *The distribution of behaviour patterns and toy movement quality on component 1 of the Movement experiment.*

Patterns	Component 1	Toy	Average value on component 1
sit avoid (f)	-0.2772	mouse	-1.1964
crouch watch (d)	0.1345	string	1.1964
crouch avoid (f)	0.2015		
killbite (f)	0.3275		
grasp (f)	0.3486		
hunt (d)	0.3696		
rear (f)	0.4009		
clutch (f)	0.4047		

looseness of the toy covering affected no behaviour patterns. The different sizes, however, significantly affected five patterns at $p<0.05$, and six at $p<0.01$ out of 39 tested. The trends in play which resulted from the different toy sizes were very similar to those found in the size experiment results (see Table 3.2 and Figures 3.1 and 3.2); the small toy elicited more play than the large toy, which was mostly avoided.

Sound

Two-way ANOVA (treatments were sound type, duration, with no interactions) showed that no behaviour patterns were influenced by the various sounds; this was also true when the play with noisy toys was compared with play with silent toys. The two sound durations (one second and five seconds) were also compared with one-way ANOVA, and only one behaviour pattern out of 35 tested was significantly different (at $p<0.05$). This would probably have been a result of chance.

Odour

One-way ANOVA revealed that eight behaviour patterns out of 35 were significantly ($p<0.05$) affected by the various odours. PCA results are shown in Table 3.11. The difference in odours had approximately the same effect as when they were presented at a high concentration in a preliminary experiment: All cats played with the toy containing catnip, (except for one cat which had been previously shown to be incapable of detecting catnip) but did not distinguish between the toys with different odours and the control toy which had no smell, all of which elicited very low intensity play, and were mostly avoided. The catnip response was not thought to be predatory (Cherfas 1987), so was not considered further.

Movement

Three comparisons were analysed in one-way ANOVAs, and t-tests; these were:

1) a comparison of all three toys;
2) to examine the difference in play when a toy is moving or is stationary;
3) to examine the effect of different quality of movement by comparing play with the toy moved by its string, with play with the clockwork mouse;

1) The ANOVA revealed that 12 behaviour patterns out of 41 were significantly affected by the different toys, seven at $p<0.05$, and five at $p<0.01$. PCA results are shown in Table 3.12. Thus the toy moved by its attached string elicited slightly more play behaviour than the clockwork mouse. The stationary toy elicited very little play and elicited most avoiding behaviour.

2) Twelve behaviour patterns were significantly different with moving or stationary toys, eight at $p<0.05$ and four at $p<0.01$. PCA results are shown in Table 3.13. The moving toys (clockwork mouse and string moved) elicited more play behaviour than the stationary toy.

3) Eight behaviour patterns were significantly ($p<0.05$) affected by the quality of movement. However, the PCA test did not reveal any clear differences in quality with the different modes of toy movement, only differences in play quantity were obvious, as found in 1) (see Table 3.14).

DISCUSSION

This series of experiments enabled the identification of some of the stimuli which elicit play. The intensity of play that different stimuli elicited was taken to indicate the importance of that particular stimulus to play behaviour. The strongest stimuli to determine whether a cat would play with a toy or would ignore or avoid it were the size of the toy, its texture and whether or not it was moving.

Size had a pronounced affect on play behaviour. Small toys elicited higher frequencies and durations of play behaviour patterns. Play behaviour decreased, while avoiding behaviour pattern performance increased with increased toy size. The cat-sized toy was avoided by the majority of cats, some of which appeared to be afraid of it, often freezing with ears back, while others appeared simply disinterested.

If play is related to predation this preference for small objects would be expected, since the preferred prey of cats are generally small rodents, not cat-size (Childs 1986). Cats would probably be able to catch prey up to the same size as themselves, but may lack the necessary strength to overcome large prey (Turner & Bateson 1988). Such a size preference is not significantly altered by the individual cat's later experience with hunting and playing; small toys and prey remain preferable to large toys and prey which are more likely to evoke fear (Caro 1980).

Texture is also an important stimulus. There was a large difference between the amount of play behaviour which fur, feathers and fakefur elicited (all elicited intensive of play), and the less intensive play which the felt, towelling and polythene toys elicited. For the Southampton and WCPN cats real fur, feathers and fakefur were the most effective textures in eliciting play behaviour, but the pet cats played with felt as much as with real fur, and more than with fakefur. The Southampton and WCPN cats showed almost unlimited enthusiasm for the real fur and feathers toys, with which they would play even if the toy was not moved. Other textured toys had to be moved to initiate play. It may be possible to draw an analogy with predation again, the real fur and feathers are both stimuli associated with animals which are commonly the prey of cats. However, it is also possible that cats respond to textures of greater complexity, hence more play with real fur and feathers, and less with polythene, a plain, one-dimensional texture.

The pet cats were not as discriminating toward the various textures, and the trends were obscured by high cat variability. It is difficult to explain this; it may be that this is normal variation with cats from varied backgrounds. Since the cats in the Southampton and WCPN colonies have the same life histories as each other, such uniformity in behaviour could be expected, compared with the individual variability of the pet cats.

All cats showed a clear preference for the real fur toy, which elicited higher intensity and longer duration play than any other toys. However, the pets also showed a preference for complex texture; feathers and 'legs' elicited most play, while the polythene toy was either avoided or ignored.

The experiment examining the interaction of size and texture showed that the size of the toy was of more importance in determining the play response of the cat, than the toy's texture. Again drawing an analogy with predation, it is logical that a cat should attack prey primarily according to size rather than texture. If prey were selected according to their texture cats might waste time, and risk injury attempting to tackle prey much larger and stronger than themselves.

Movement is also an important stimulus for play behaviour. Moving toys elicited more play behaviour than stationary toys, which were ignored. The type of movement appeared to be irrelevant, since two types of movement, by attached string and by clockwork, elicited the same quality of play. The fact that the Southampton cats were accustomed to playing with toys on pieces of string may in part explain their preference for the toy moved by string rather than the clockwork mouse with which they were not familiar. The clockwork mice also made a strange noise, which appeared to frighten some of the cats. They were wary of the mouse probably because it was an automatic, non- interactive toy, less predictable than the interactive toys on string. The string may also be interactive.

Movement has also been shown to be a stimulus of primary importance to predatory behaviour in a number of species, including polecats (Apfelbach & Wester 1977), American kestrels *Falco sparverius* (Mueller 1974), and European toads *Bufo bufo* (Ewert 1987). Movement of prey is also of prime importance to cats during hunting. Prey are initially located by their movement, and the cat has a highly developed visual system for this purpose (Bradshaw 1992).

These experiments also indicated several stimuli which are not important in determining play performance. It was concluded that the presence or absence of a neck constriction had no effect on cats' play response. However, a neck constriction may direct biting during prey handling (Leyhausen 1965); cats with no hunting experience may not have learnt the relevance of the neck, and would therefore not be expected to show a preference for any part of a toy.

The pattern of the toy covering and the looseness of the covering appeared to have no influence on the cats play behaviour. This may be because these are details which are too minor to have much effect upon whether or not play is elicited. It has already been shown that size and movement are the most important stimuli for play behaviour; the small, moving toys used in these experiments elicited play despite the other variations in patterning and 'skin' looseness; the effects of these were effectively overridden by the response to a small, moving object. Analogy with expected predatory responses may explain why cats show no change in play response with different patterns; pattern is not a stimulus used as the main parameter for prey recognition. Size and movement appear to indicate whether an object is treated as prey or not (Biben 1979). Selectivity in response to pattern might lead to the unnecessary rejection of potential prey objects, which would not benefit the cat. Thus, the pattern of a prey animal's coat would be ignored. Assuming a common motivational basis for predation and play, this may explain the failure of pattern to influence the play response.

More surprisingly, sound and odour had no effect upon play behaviour. Although sound is an important stimulus for cats, the sounds presented in the experiment were artificial, multi-frequency, loud and novel, resulting in a neophobic reaction from most of the cats. Animals have often been shown to exhibit 'new object effect'; animals which are presented with novel objects when in their familiar environment show excessive neophobia, as a result of the great contrast between their normal surroundings and the new stimulus (Cowan 1976). Such an effect may have occurred in this experiment. A more controlled system for producing sound may elicit a different response. The cats showed the same response of low intensity play towards the toy with no odour as toward the toys with the five different odours, suggesting that the smell of the toy had no influence on play behaviour. The only effect which the smell of the toy had upon play behaviour was seen in the preliminary experiment in which the odours were at a higher concentration, which repelled the cats. Only catnip increased the cats' interest in the toy and elicited more intensive play behaviour than the other odours. However, if a cat does not respond to catnip, a genetically determined ability (Todd 1962), this effect will not be seen. As with the sound, the odours presented may also have been too artificial and irrelevant to elicit any difference in play response.

Although it has been discerned that overall size, texture and movement are the main stimuli which determine the play response of the cats, the experiments so far have only tested variations of particular stimulus parameters against each other. They showed linear trends in the cats' responses to the variations of each stimulus type, but the extent to which these stimuli interest has not been fully investigated.

3.3: THE EFFECT OF COMBINING THE STRONGEST PLAY STIMULI ON PLAY BEHAVIOUR

An experiment was designed to enable any interactions of different types of stimuli to be examined, using toys which had stimulus characteristics which had only the most significant effect on the quality and quantity of play elicited. According to the results already obtained it should be possible to create, for example, a toy possessing all the stimulus characteristics found to elicit the greatest intensity of play, and another possessing all the stimulus characteristics found to inhibit play in the cat. In this way the interaction between the stimuli could be measured.

METHOD

The design for this multi-factor experiment was for partial confounding of higher order interactions between the toy stimuli (Cochran & Cox 1957). The confounding design was necessary because there were too many toy variations to test each one on all cats. Each cat received only 12 of 18 possible toy types.

The three stimuli presented were those which had the most significant effects on cat play in the previous experiments. These were size, texture and movement. From these three stimuli variations of each stimulus were presented, these were; size - small, medium and large; texture - feathers, polythene and 'legs'; and movement - movement by affixed string, and no movement.

Combining these eight characteristics produced 18 toys, which were presented to nine Southampton cats in two blocks of six observations, with a two week break between them to reduce the effects of habituation. This meant that each cat only received 12 out of a total of 18 toy stimulus combinations, because the cats could not be expected to play for three blocks of six observations without excessive habituation to the experiment protocol and toys. Ideally 12 cats should have been used, but only nine could be found which would play and would be useful in the experiment.

The order of presentation of the toys was determined by partial Latin Square designs, and all practical details were the same as in the previous experiments.

RESULTS

Multi-factor ANOVA with interactions was used to test the data. Although there were five independent variables in the test (cat, texture, size, movement and order of presentation), it was only possible to examine lower order interactions as a result of empty cells in the data. These empty cells were a result of the fact that the cats only received 12 out of the 18 possible toy combinations. However, the first order and second order interactions were sufficient for the analysis. The appropriate cat interaction term was used as the error term for each variable, for example, for the variable 'size' the cat by size interaction term was used as the error term. Behaviour patterns significantly different (at $p<0.05$) for any linear effect or two-way interaction (a total of 31) were tested in a PCA.

To examine the interactions, the 31 principal components saved from the PCA were tested in the same multi-factor ANOVA model as before, enabling the sorting of components which discerned significant interactions between the independent variables. Interaction graphs of any components which had significant two-way interactions were constructed. Three first-order interactions between treatments were possible; between size and movement (comprising six variations from three sizes and two movements); size and texture (comprising nine variations from three sizes and three textures); and texture and movement (comprising six variations from three textures and two movements).

The interaction graphs were compared with the matching component weights graphs, labelled with the 31 significant behaviour patterns, in order to visualise the contribution of the behaviour patterns to the interaction graphs.

According to the ANOVA test, the first seven components all showed significant trends in one or more of the linear variables (size, texture and movement), but only three (numbers 1, 6 and 7) for any of the three possible first-order interactions, all of these were between size and movement.

It was possible to determine what aspect of play behaviour each significant component represented by comparing means tables for the significant variable(s), the interaction graph if there was a significant interaction, and the corresponding weights graph showing the organisation of the behaviour patterns. Each component contrasted a slightly different type of reaction, enabling a complex layered picture of the response to the toys to be built up as each component was examined.

Figures 3.3 to 3.9 show the distribution of behaviour patterns and any interaction graphs, for each of the seven components examined. Table 3.15 shows means of each of the variables on the seven components. The component graphs labelled with behaviour patterns should be compared with Table 3.15, and with the corresponding interaction graph, for components 1, 6 and 7.

Figure 3.3. *The distribution of behaviour patterns on components 1 and 2 in the combination of stimuli experiment (final experiment). Behaviour code abbreviations are as explained before Figure 3.1 on page 38.*

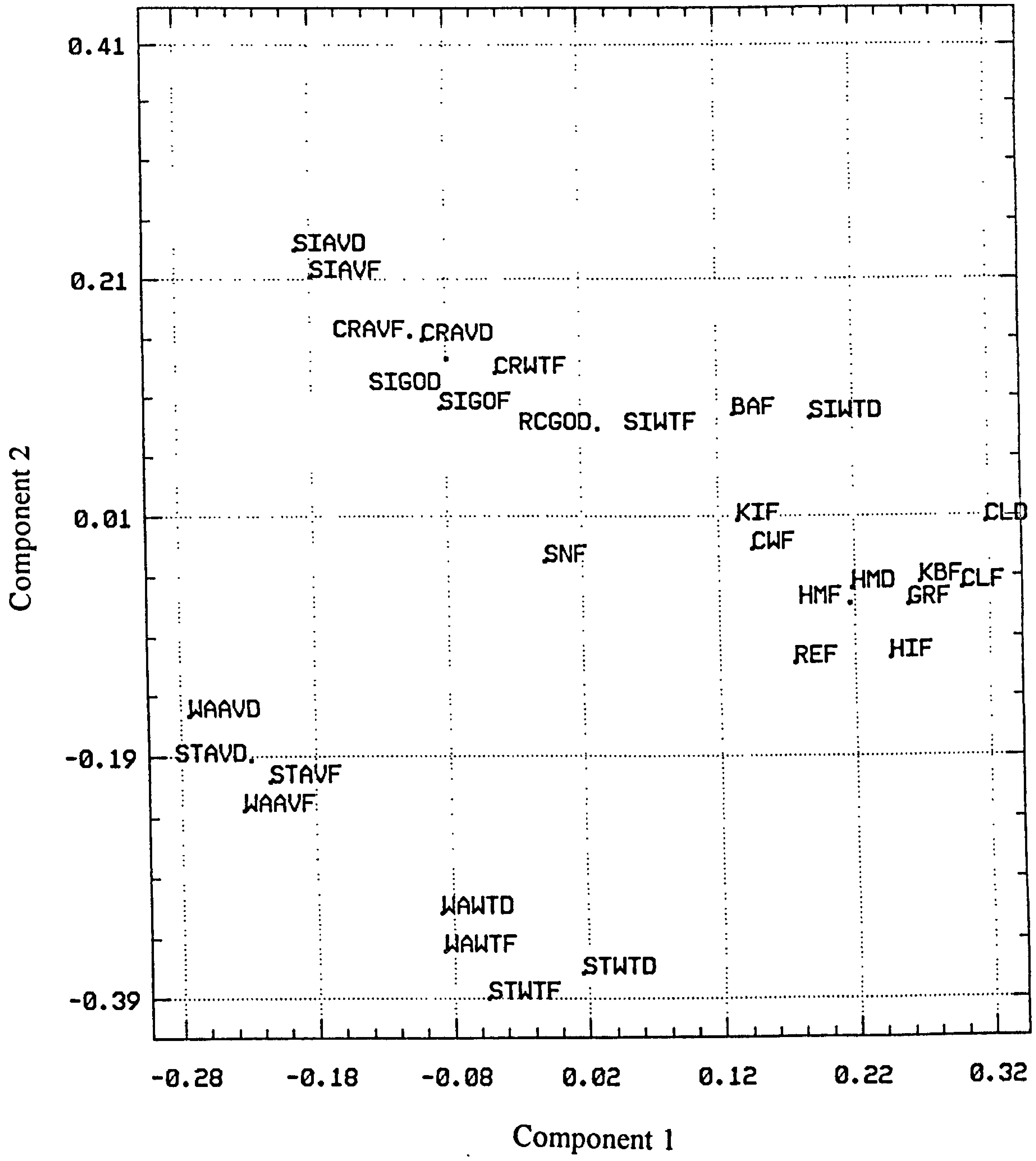


Figure 3.4. The interaction of size and movement on component 1 of the final experiment, compare with behaviour patterns of Figure 3.3

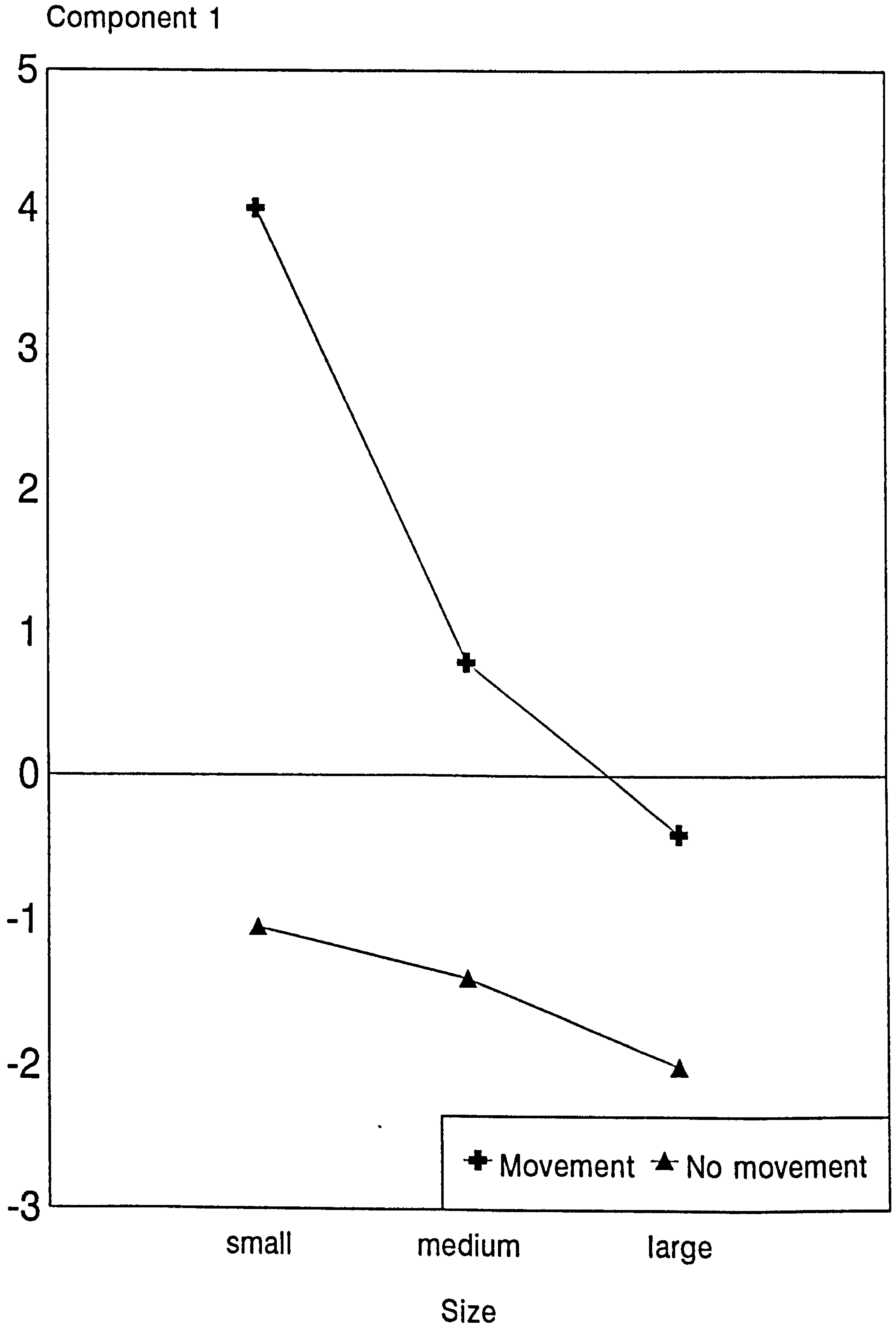


Figure 3.5. *The distribution of behaviour patterns on components 3 and 4 in the final experiment.*

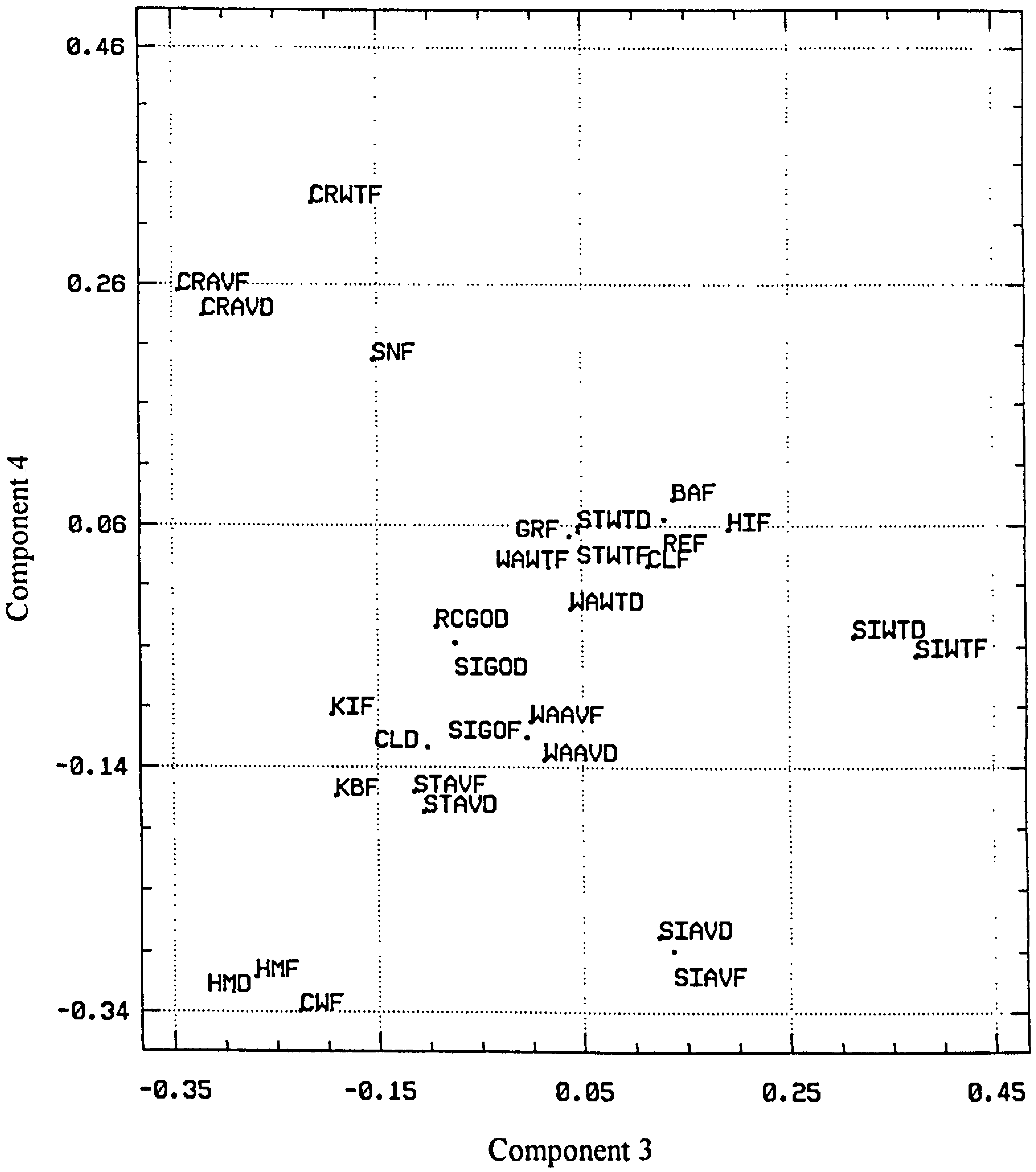


Figure 3.6. *The distribution of behaviour patterns on components 5 and 6 of the final experiment.*

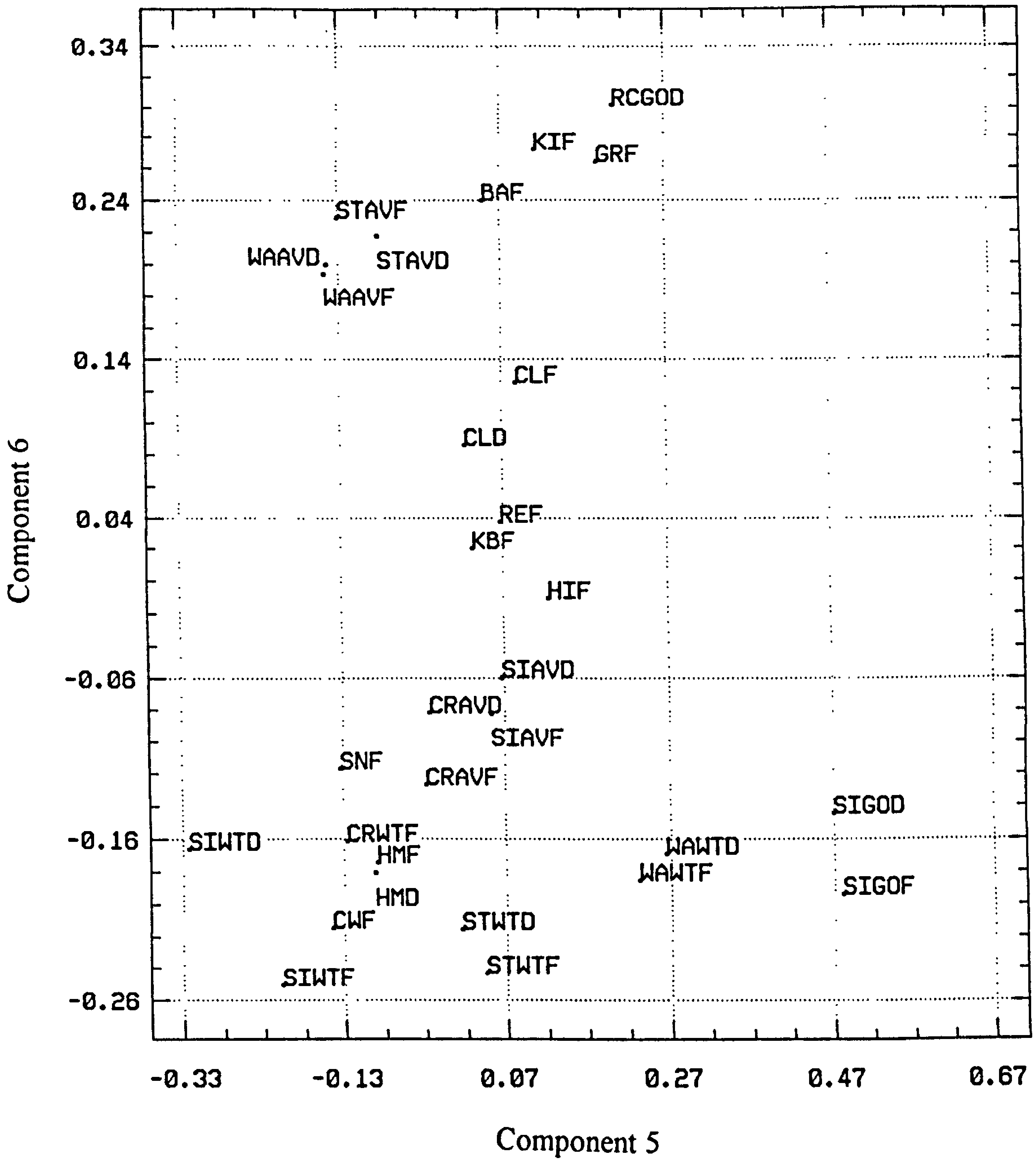


Figure 3.7. The interaction of size and movement on component 6 of the final experiment, compare with behaviour patterns of Figure 3.6.

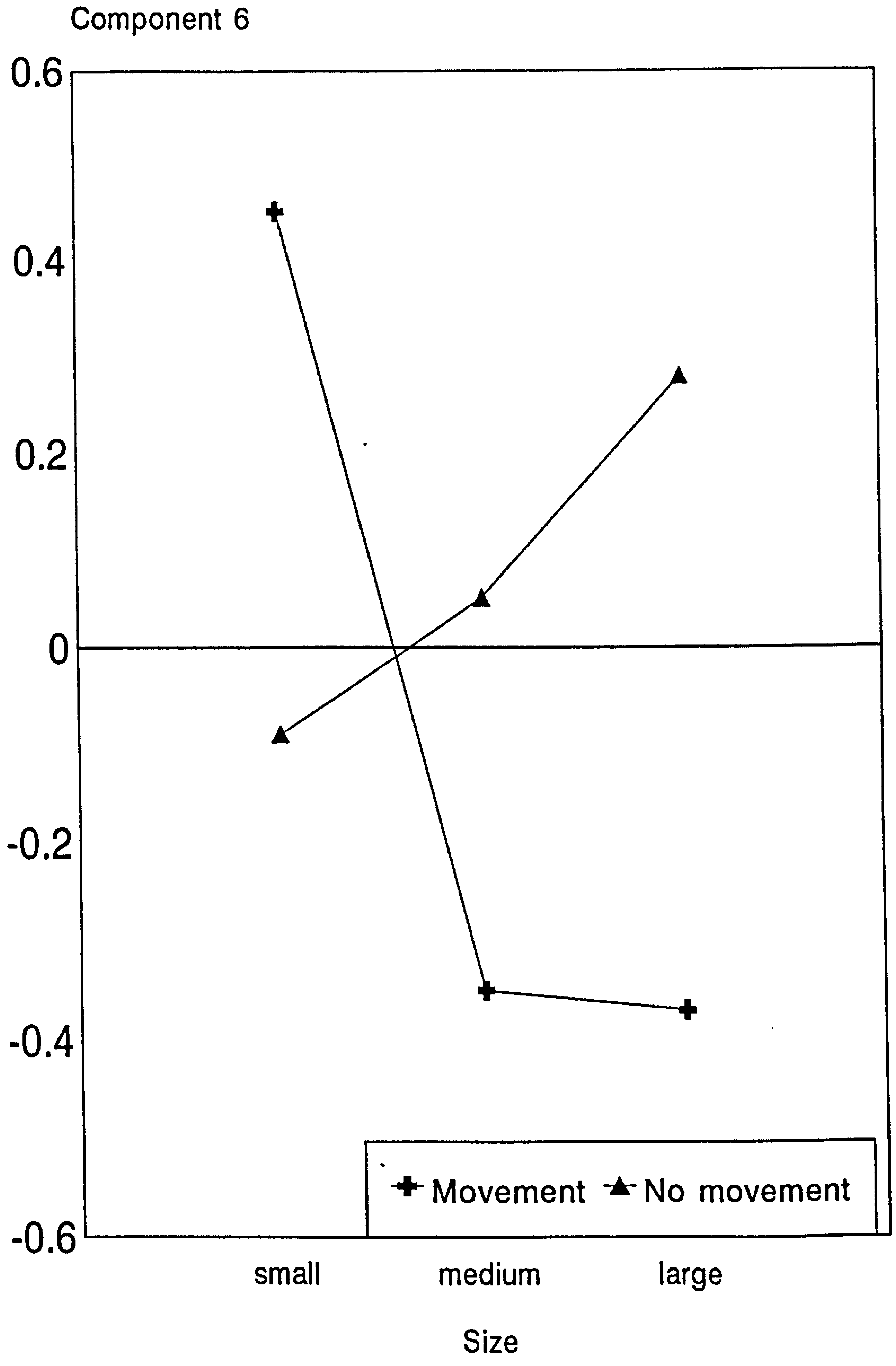


Figure 3.8. *The distribution of behaviour patterns on component 7 (and 1) of the final experiment.*

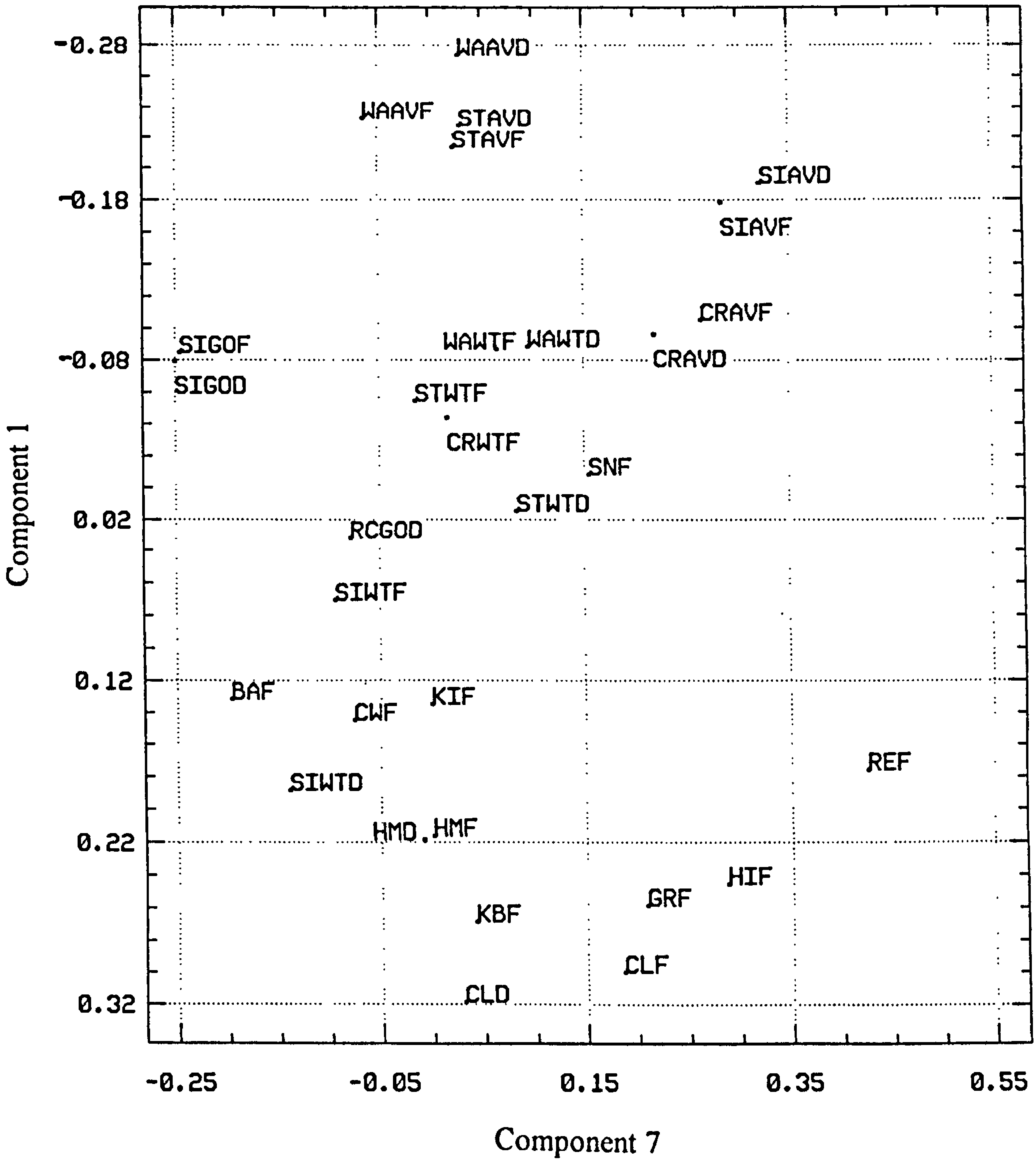
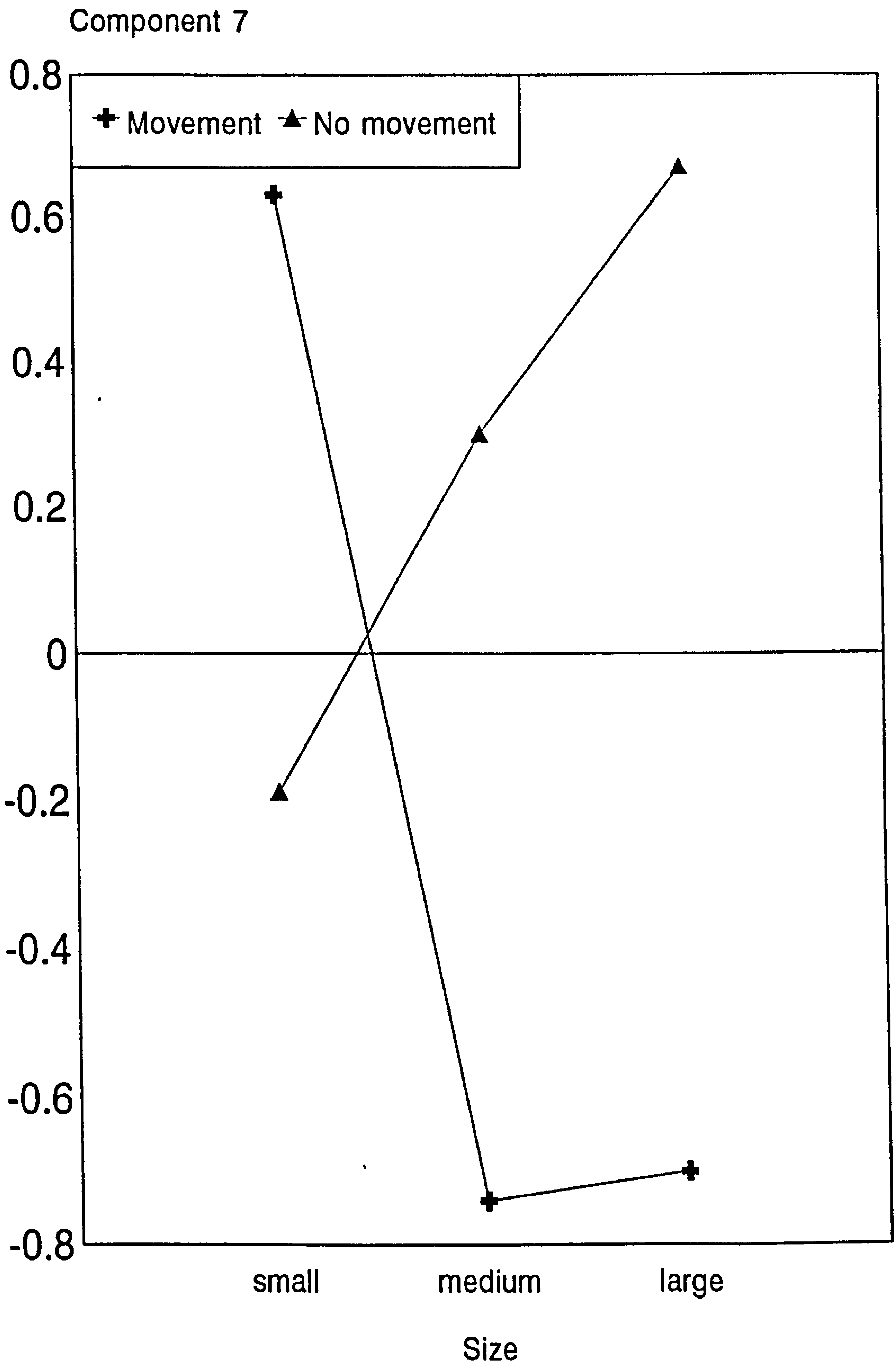


Figure 3.9. The interaction of size and movement on component 7 of the final experiment, compare with behaviour patterns of Figure 3.8 .



The information from these graphs can be summarized as follows:

Component 1 (23.93% of variance). ("General Play")
This component contrasted avoiding and play behaviour patterns, and the toy characteristics were distributed across this showing that the small toy elicited more play than the other two sizes, the large toy elicited more avoiding behaviour. Movement elicited more play patterns and fewer avoiding patterns than no movement. Feathers and 'legs' elicited approximately the same intensity of play, but more than the polythene toy. This component repeats trends seen in the previous experiments where size, texture and movement were tested. The interaction graph (Figure 3.4) indicated that the small moving toy elicited the most play, compared with the large non-moving toy, which elicited the most avoiding behaviour patterns.

		Principal Component number						
		1	2	3	4	5	6	7
Size	small	1.465	NS	-0.425	NS	0.639	NS	NS
	medium	-0.257		0.255		-0.822		
	large	-1.208		0.169		-0.556		
Texture	legs	0.311	NS	0.131	0.332	NS	NS	NS
	feathers	0.676		-0.424	-0.479			
	poly	-0.988		0.293	0.147			
Movement	no	-1.492	0.697	-0.673	-0.320	NS	NS	0.269
	yes	1.492	-0.697	0.673	0.320			-0.269

Table 3.15. *The significantly different means (for main effects only) for components 1 to 7.*

Component 2 (15.08% of variance). ("Disinterest")

Component 2 appeared to contrast patterns associated with disinterest, such as 'sit avoid', with patterns which suggested that the cats were showing interest in the toy, without approaching it, such as 'stand watch' and 'walk watch'. Movement was the significant variable on component 2; moving toys were more strongly associated with patterns denoting interest, while the cats showed more disinterest in the stationary toys.

Component 3 (8.82% of variance). ("Paw Play")

This contrasted 'paw play' patterns such as 'bat' and 'hit', and 'sit watch', with patterns associated with close contact and 'killing', such as 'holdmouth', 'chew' and 'kick'. The 'paw play' could also be interpreted as defensive behaviour towards the toy, since it was associated with sit and watch behaviour, suggesting that the cats were wary of the toy. Certain combinations of stimuli may be threatening for the cats, so that they kept the toy at a safe distance while playing with them; the medium and large toys were associated with this behaviour (see Table 3.15). However, the polythene and legs toys were also associated with paw play, this may indicate that these stimuli were not of sufficient sensory value to elicit close contact patterns. In contrast, the small, feathered and non-moving toy was associated with the close contact 'killing' behaviour; this was expected and corresponded with results in the earlier size, texture and movement experiments. Movement may be a threat to cats when the toys are large, but may elicit play when the toy is small.

Interpretation becomes less clear with further components, which account for decreasing amounts of the variance in behaviour. Components 4 to 7 probably represent an interaction between the 'behavioural styles' of the nine cats and their individual preferences for particular toy configurations.

Component 4 (8.45% of variance). ("Kill/Avoid")

This contrasted 'crouch' with both 'avoid', and also 'killing' patterns, such as 'chew' and 'holdmouth'. The association of avoiding with killing patterns may occur as a cat rests between intensive play bouts. Feathers elicited more killing patterns than 'legs' or polythene, which were treated equally (see Table 3.15). Moving toys elicited more killing than stationary toys, which were avoided. This may have been through a lack of interest in the toys which did not move.

Component 5 (6.48% of variance). ("Groom")
'Sit groom' was contrasted with 'sit watch', the small toy was associated more strongly with 'sit groom', while the large toy elicited more 'sit watch'. Possibly a large, more threatening toy provokes closer monitoring than a small toy.

Component 6 (5.80% of variance). ("Paw Play 2")
This contrasted 'paw play' with 'watch' and 'mouth play'. Grooming was weighted both positively (recline and groom) and negatively (sit and groom). The interaction graph (Figure 3.7) shows that the small, moving toy was more associated with 'paw play', as expected. When the medium and large toys were moving they did not elicit paw play, suggesting that the cats were frightened to approach such large moving objects. However, these toys did elicit more biting, which may have been a defensive reaction when the toys were too close to the cat. Conversely, when these two toys were not moving they were associated with paw play. This may have been because the cats were able to explore the toys, which were not moving and so were not a threat. When the small toy was not moving it was only watched, suggesting that without movement the cats were not interested in it.

Component 7 (4.96% of variance). ("Paw Play 3")
Lastly, component 7 contrasted 'paw play' with 'groom', a possible indicator of lack of interest. The interaction graph (Figure 3.9) is similar to that for component 6: The small moving toy was associated with paw play, as expected. When it was not moving, it was ignored, the cats showing grooming behaviour instead. This may have indicated a lack of interest. Again, the medium and large toys were associated with paw play only when they were not moving, this may have been because the cats were frightened by the toys when they were moving, and so only explored or played with them when they were stationary. When the medium and large toys were

moving they were associated with grooming, which may have been a result of conflict between a desire to escape from the toy, and the inability to do so. It could also have indicated lack of interest in the toys.

DISCUSSION

This rather complex picture reveals an overall, simple trend in play behaviour: Small toys, when moving, received more play, both close contact mouthing and paw play, and also were associated with more grooming. Medium and large toys received similar behaviour to each other, they received more play when moving, more watching, but less paw play and less close contact and mouthing than the small toy. When small toys are still they receive less interest and play than stationary medium and large toys. But when small toys move they receive more play than medium and large toys. This suggests that a small toy which did not move was not a threat to the cat or of any interest, however a large or medium toy could have posed a threat, whether moving or not, and was treated with careful interest. A moving medium or large toy received attention and defensive play when near the cat, and elicited grooming, which may be displacement grooming resulting from conflict between a desire to escape, avoid and to attack or to escape. A small moving toy is an interesting object to play with. It provoked no fear and enabled 'relaxed' lapses in attention and grooming while the cat was recumbent.

Overall size and movement are the most important stimulus parameters, texture having only a small interactive affect when combined in this experiment with size and movement. Preference for textures appears to be shown only when there are no other variables which the cats may use to discriminate toys. In component 1 feathers and legs received more play behaviour than the smooth toy, and were almost equal in the amount they elicited. In component 3 smooth elicited more defensive play than legs and feathers, and legs received more of this behaviour than feathers. In component 4 legs received most play behaviour. These effects are all linear; texture did not interact with either size or movement. It therefore appears to be noted and reacted to independently by the cats.

3.4: CONCLUSION

The experiments of this chapter have identified a small number of stimulus parameters which are essential to play behaviour. These are the size and texture of the toy, and whether or not it is moving. Texture appears to be the least important of the three, having a reduced effect on play when varied along with size and movement; most effects of texture were linear and texture did not modify the main effect of size or movement. However, preference for texture may be shown when other variables used to discriminate between toys are constant.

The stimulus characteristics found to elicit the most intensive play and the greatest duration of play are some of those which typical prey possess; small size, a complex furry texture and movement. The fact that both behaviours may be elicited by similar stimuli hints at a close relationship between play and predation, one that is not just structural, but may also exist at the level of motivation. If play and predation shared a motivational basis, then it may be expected that an animal's play with an object might reflect the extent of the animal's association of the object with real prey (Egan 1976).

4

THE EFFECTS OF HUNGER ON THE EXPRESSION OF PLAY BEHAVIOUR

4.1: INTRODUCTION

The influence of hunger on behaviour has received much attention. The fact that hunger alters behaviour is shown by the extensive use of food deprivation to increase the motivation of animals in conditioning and learning experiments with a food reward (for example Dember & Earl 1957, Cabanac 1985). Past studies of predation often involved keeping the animal hungry in order to maintain its motivation to kill (for example, Ewert 1987). The influence of hunger on play behaviour has inspired little study, possibly because the suggestion that there may be a link is relatively new. The proposed influence of hunger on play relies on the hypothesis that play is related to predation. Since hunger is known to affect hunting behaviour, why not play behaviour as well?

The relationship between hunger and predation

There has been a number of studies which have clearly indicated that hunger has an important and direct effect upon several measures of predatory behaviour. First, hunger has been shown to affect the frequency of killing. For example, in a study of the relationships of food deprivation interval and circadian rhythms to hunger, food consumption and predatory behaviour, Mueller (1973) found that hunger and killing were closely related. He found that sparrow hawks *Falco sparverius* would kill more prey with increasing food deprivation time. Within limits, this relationship was almost linear. After one hour of deprivation 14% of prey presented were killed, but after 35 hours, 92% of prey were killed. Mueller proposed that there was a motivational link between the two which explained this behavioural relationship.

Hunger has also been shown to affect the animals recognition of suitable prey items, providing further evidence for a link. For example, Curio (1976) observed that hunger increased the range of objects recognised and accepted as food by European toads. The upper size limit of prey items accepted increased (while the lower limit remained the same) with increasing hunger. Hunger has also been found to initiate killing in naïve animals, for example in rats *Rattus norvegicus* (Polsky 1975). Thus hunger appears to exert control over several factors controlling predation.

There are also neurobiological data linking killing and eating centres in the lateral hypothalamus, which support the behavioural evidence for an association between predation and hunger (Hutchinson & Renfrew 1966, Biben 1979).

However, debate remains over the strength of this association, and there is evidence for the distinction between hunger and predatory behaviour. It has been suggested that hunger potentiates or initiates a search for prey, and the start of predatory behaviour. But when prey is at close range, the predator will respond with predatory behaviour whether hungry or not (Kruuk 1972, Polsky 1975, Biben 1979). Adamec (1976) found that cats interrupt eating, even of a preferred food, to kill offered prey, demonstrating that lack of hunger does not inhibit predatory behaviour. This finding may also suggest that killing prey may be a self rewarding behaviour and does not require reinforcement by eating of prey. Paul & Posner (1973) proposed that this separation of the two is economically sound, since killing without eating, and vice versa, enables the animal to take advantage of any prey or carrion it finds. They suggested that eating prey is not just the goal of killing, since it is also under the control of palatability. Thus eating prey does not necessarily mark the end of predation, since other factors also control eating; a predator may continue hunting after eating.

Surplus killing is a phenomenon which may be explained in this way. In rare circumstances both domestic and wild predators have been known to kill many more prey than they can possibly eat. Only a small percentage of the killed animals is eaten or stored for later use. Surplus killing has been recorded in domestic cats and dogs, spotted hyaenas, foxes *Vulpes vulpes*, polar bears *Thalarctos maritimus*, leopards, lions, wolves *Canis lupus*, hawks and various other carnivores (Kruuk 1972, Mueller 1973). Kruuk maintained that this occurs when the predators are not hungry, but is the product of the circumstance of numerous, defenceless prey, for example in extreme weather or when prey are calving. The prey become an easy target for the predator, and their closeness initiates repeated predatory behaviour.

Thus hunger may have an incomplete control of predation. It may also depend upon the hunting experience of the animal. Polsky (1975) found that hunger exerted a stronger influence upon the predation of naïve animals, and that experienced hunters were more likely to hunt and kill prey irrespective of hunger.

Hunger and play behaviour

Any relationship between hunger and play is still at the hypothesis stage. The key to establishing a relationship between hunger and play is the assumption that play is closely related to or classifiable with predation in terms of motivation. Thus any effects which hunger has on the motivation to hunt and kill could influence motivation to play in the same way.

Hunger may influence play behaviour in a number of ways. There are several suggestions, some predict that play will decrease with hunger (Muller-Schwarze et al 1982), some that it will increase (Turner & Meister 1988). Predation is the only behaviour reliably not depressed by hunger. Hungry animals may abandon all other behaviours, including play, in favour of searching for food. In white-tailed deer fawns *Odocoileus virginianus*, a minor reduction in food availability led to an immediate reduction in the level of locomotory play (Muller-Schwarze et al 1982). Miller & Byers (1991) found the same effect on the locomotory play of pronghorn deer fawns *Antilocapra americana*. But hunger might also cause an increase in play behaviour; if it is assumed that play has the same motivational basis as predation, then play would also remain undiminished by hunger. Whether or not this would occur is difficult to assess. Food shortage has been found to have no effect on the object play behaviour of domestic kittens (Egan 1971). Play behaviour did not decrease when the kittens were hungry, as would be expected if play was motivationally unrelated to predation. It would be affected in the same way as other categories of behaviour, which all decrease with hunger.

This led Egan to believe that object play could be causally related to feeding behaviour, based on the assumption that play and predation are related. She proposed that the kittens were performing object play in place of predation since they had not yet learnt to hunt properly, and were responding to hunger with play in the same way that a hunting adult would with predation. This hypothesis could also be applied to adult cats which have never hunted. These cats may perform play in place of proper predation, and thus would be expected to show play behaviour when hungry.

More conclusive proof of the link between play and hunger would be to show that play increases with hunger, as does predation. This would provide further evidence for the hypothesis that play and predation are motivationally similar, since both are affected in the same way by hunger. Such an effect has been shown by zoo populations of Oriental small-clawed otters *Anonyx cinerea* which express object play at an increasingly high intensity as they become more hungry and as feeding time approaches. This object play is structurally similar to food capturing and handling behaviour (Pellis 1983 & 1991). Once the otters have eaten, object play wanes and is replaced by social play, which had disappeared as the otters became increasingly hungry (Hediger 1964). Thus the expression of the otters' object play appears to be determined by hunger, increasing with appetite and decreasing with satiation.

Conversely, play may increase as hunger decreases, although supporting arguments are mostly based on conjecture. For example, it has been suggested that play is a facultative response to the animal's nutritional conditions and that it may enable the animal to avoid obesity. Animals which are well and regularly fed might be expected to play in order to 'burn off' excess energy (Barber 1991). If this is true domestic and captive wild animals, which do not go hungry and which are more likely to grow fat, would also be expected to play more than their wild counterparts for whom energy conservation is more important and food a scarce resource. This hypothesis seems a little fanciful. It is unlikely that play behaviour evolved or is maintained as a fat-loss mechanism, although in overweight domestic pets it may have this benefit. Because some animals have sufficient energy to play, it cannot be assumed that the energy is expressly expended for play.

Biben (1979) also suggested that play may occur when the animal is not hungry. She proposed a completely different explanation for play, that it occurs when the animal is in a conflict situation which inhibits normal predatory behaviour. For example, when the animal is not hungry it may not need to kill a prey animal it has captured and plays with it instead. When the animal is hungry the conflict situation does not arise, it kills the prey immediately and does not play. Thus play would not occur if the animal is hungry.

In summary, it is possible that hunger may affect play in three ways:

a) It may cause an increase in play behaviour, which suggests that play shares it's motivational basis with predation, since hunger initiates hunting behaviour.

b) It may cause a decrease in play behaviour, suggesting that it does not share a motivational basis with predation. Play, also being energetically costly, would be expected to decrease if it is motivationally distinct from predation.

c) It may produce no change in play behaviour, either qualitatively or quantitatively. This may occur in a domestic species which does not have to adopt serious energy economising strategies, since humans provide for all nutritional needs and generally do not allow domestic animals to go hungry for long periods of time. The predatory behaviour of inexperienced rats has been found to be unaffected by hunger (Karli 1956), suggesting that lack of hunting experience has prevented them from learning to respond to hunger with predation. Play behaviour, should it share a motivational basis with predation, could be similarly unaffected by hunger in inexperienced animals.

My experiment was based on a study by Biben (1979). Biben investigated the factors controlling behavioural responses of the domestic cat to its prey. Hunger level and the size of prey were manipulated. She detected three trends in the behavioural response;
1) the probability of a kill increased directly with hunger;
2) there was a decrease in the probability of a kill with increased size\difficulty of the prey;

3) it was possible to predict 95% of the variability of the predatory response from the cats hunger and the prey size.

It was predicted that play behaviour should show the same trends if it shared the motivational basis of predation. A similar method was used, but with imitation prey instead of live animals, in which hunger and size of toy were manipulated, and changes in play response analysed.

4.2: DIURNAL EFFECTS (Control Experiment)

Testing in the experiment was planned to occur at two different times of the day. Studies of the general activity of group-housed cats throughout the day have shown that there is a significant "animal house effect" in which the animals show peak activity when they are attended to by animal house staff (usually in the morning), and are surrounded by activity (McCune, pers. comm.). It was predicted that these changes in activity throughout the day might influence the experimental results. Therefore, it was necessary to perform a preliminary experiment in which the effect of time of day was tested. The experiment was designed to be a control for possible diurnal changes in general activity which were predicted to influence the main experiment.

Eight cats from the Southampton colony were tested for two minutes with the small (7x5x1 cm) and medium (12x7x2 cm) toys which were to be used in the main experiment, at either 0930 hours or 1430 hours. The observations were recorded on video and analyzed as usual. The data were tested with two-way ANOVA. Only one behaviour pattern was significantly influenced by the time of day (at $p<0.05$). This would probably have been a result of chance (see Methods in Chapter 2).

It was concluded that the time of day at which a cat was tested had no influence upon the play behaviour patterns performed. Any differences which occurred in the main experiment can be attributed to the treatments.

4.3: THE EFFECT OF FOOD DEPRIVATION ON PLAY

METHOD

The design of the experiment required that the cats would be tested at different times of the day, according to the hunger level treatment. Home Office regulations require that cattery cats cannot be left hungry for more than 16 hours. The three hunger levels were expressed as deprivation; 0 hours, 5 hours and 16 hours since the last meal. The necessary practical arrangement was that the cats at 0 hours and 16 hours of hunger were tested at 0930 hours, and that the cats at the 5 hour hunger level were tested at 1430 hours. Nine cats were tested at three hunger levels. Two different sizes of toy were presented, small (7x5x1 cm) and medium (12x7x2 cm); both were made of white fakefur. Thus each cat received six treatments, both toy sizes at the three hunger levels, for two minutes using the same methodology as in Chapter 3.

RESULTS

Data were tested first in two-way ANOVA to determine patterns which were affected by hunger, size and the interaction of hunger and size. Significantly different behaviour patterns were then analyzed in PCA. In the PCA only the first two components were meaningful according to the scree diagram, accounting for 62.7% variance between them. Component 1 contrasted negatively loaded play and watching behaviour patterns with positively loaded avoiding patterns. The distribution of behaviour patterns was visually compared with the scatterplot distribution of cats, hunger level and toy sizes on Component 1. Component 2 showed only individual variation.

The effect of size

Eighteen behaviour patterns were significantly affected by size, ten at $p<0.05$, and eight at $p<0.01$. The results were as predicted, and confirmed those of the size experiments in Chapter 3. In the PCA the first component showed a very clear trend in which the small toy elicited more intensive play than the medium toy, which elicited more avoiding behaviour. The distribution of behaviour patterns and of sizes on component 1 was similar to that of the size experiment recorded in Chapter 3. Table 4.1 shows the loadings of the behaviour patterns and toy sizes on component 1.

The effect of hunger

Ten behaviour patterns were significantly different with hunger, five at $p<0.05$, and five at $p<0.01$. These behaviour patterns were loaded on component 1 as shown in Table 4.2.

From this table it can be seen that hunger had an effect upon the play behaviour of the cats. An increase in hunger was associated with an increase in play behaviour and a decrease in avoiding behaviour. When the cats were least hungry, at 0 and 5 hours of deprivation, the avoiding behaviour was at its highest. Avoiding behaviour decreased as hunger increased.

The interaction between hunger and size

Seven behaviour patterns were significantly affected by the interaction between hunger and size (five at $p<0.05$, two at $p<0.01$). Graphs of hunger and size interaction for each of the seven behaviour patterns enabled a clearer interpretation to be made. The clearest effects were shown for the two patterns significant at $p<0.01$, 'sniff' and 'killbite' (Figure 4.1). These were the only two play patterns significantly affected. The other five were non-play patterns, for example 'stand watch' and 'sit groom' (the grouping of types of patterns in the ethogram is shown in the Appendix). Table 4.3 shows the means for these patterns.

Table 4.1. *The distribution of behaviour patterns and toy sizes on component1.*

Patterns	Component 1	Toy	Average value on component 1
walk avoid (f)	-0.2661	small	0.6016
walk avoid (d)	-0.2601	medium	-0.6016
stand avoid (d)	-0.2345		
stand avoid (f)	-0.2301		
sit avoid (d)	-0.2196		
sit avoid (f)	-0.2109		
sniff (f)	-0.096		
chew (f)	0.1259		
recline watch (f)	0.1684		
holdmouth (f)	0.1693		
recline watch (d)	0.1867		
rear (f)	0.2065		
kick (f)	0.2309		
hit (f)	0.2791		
killbite (f)	0.2846		
grasp (f)	0.3012		
clutch (d)	0.3067		
clutch (f)	0.3300		

Table 4.2. *The distribution of behaviour patterns and hunger levels on component 1.* Hunger level is shown as hours since the last meal.

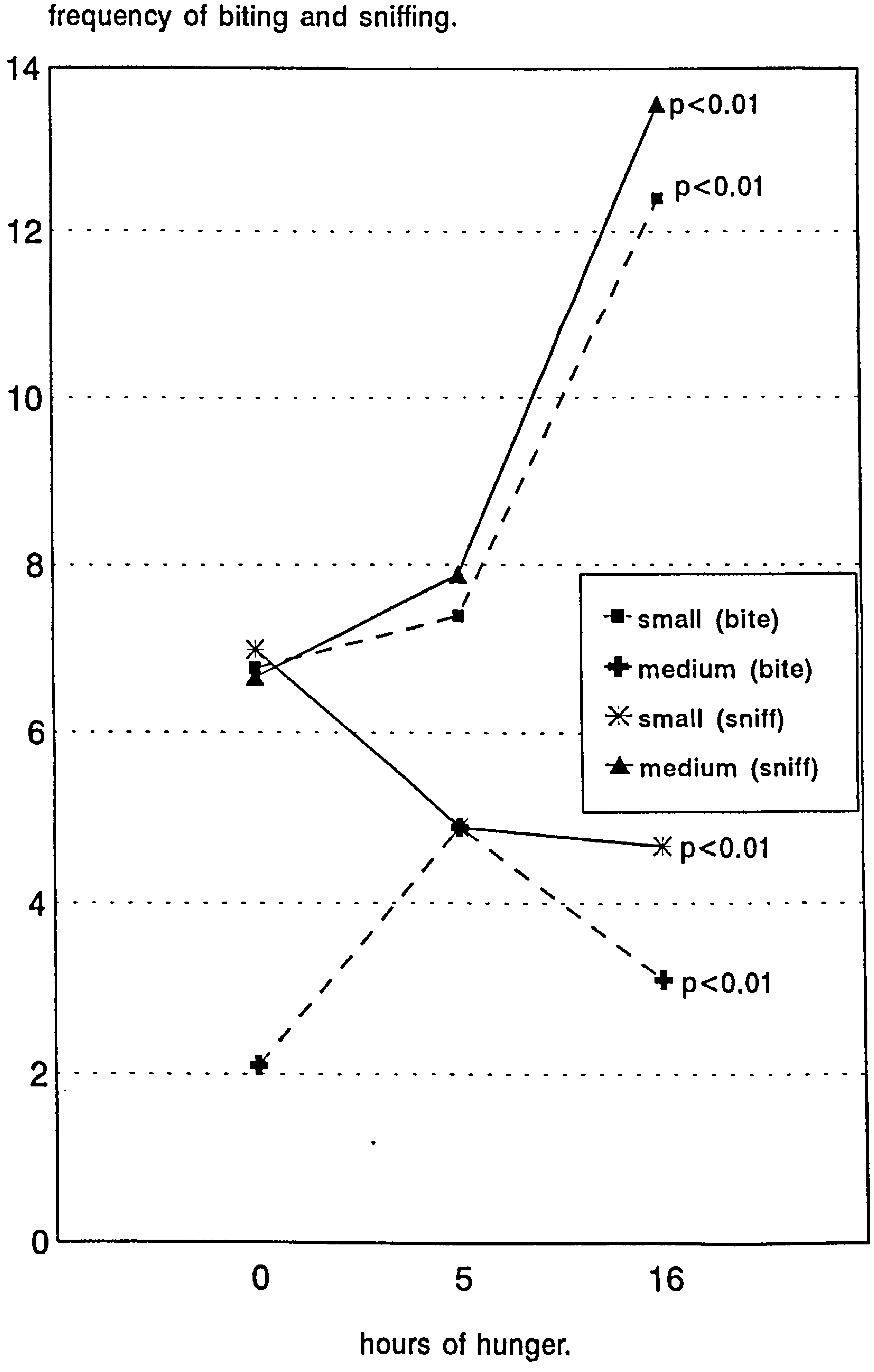
Patterns	Component 1	Hunger level	Average value on component 1
stand avoid (d)	-0.2801	16	0.140
stand avoid (f)	-0.2746	0	-0.1263
sit avoid (d)	-0.2367	5	-0.1411
holdmouth (f)	0.1732		
recline watch (f)	0.2467		
recline watch (d)	0.3052		
killbite (f)	0.3451		
grasp (f)	0.3888		
clutch (d)	0.4010		
clutch (f)	0.4235		

Table 4.3. *Means table for the behaviour patterns significantly different at p<0.05 with the interaction of hunger and size.* Hunger level is given in hours since the last meal; m=medium and s=small.

		Behaviour patterns						
Hunger level	Toy Size	sniff (f)	killbite (f)	sit groom (f)	sit groom (d)	stand watch (d)	walk avoid (f)	walk avoid (d)
0	m	6.67	2.11	0.11	0.51	32.15	2.44	6.20
0	s	7.0	6.78	0.44	2.60	38.38	0.66	1.52
5	m	7.89	4.89	0.67	3.35	33.44	1.33	3.33
5	s	4.89	7.44	0	0	23.50	1.11	3.71
16	m	13.56	3.11	0.33	0.95	33.21	3.11	6.46
16	s	4.67	12.44	0	0	28.45	0.67	2.18

Figure 4.1. The changes in biting and sniffing response elicited by the 2 toy sizes with increasing hunger.

Significance levels are for frequency differences between 0 & 16 hours



Overall the small toy elicited a greater frequency of response from the 'play' behaviour patterns than the medium toy. The medium toy elicited more from the non-play behaviour patterns ('stand avoid', 'sit avoid', 'stand avoid' and 'recline watch'). This trend had already been noted in the analysis of the size variable.

The response to the three different hunger levels was more complex when separated according to the size of toy:

*Medium toy; the occurrence of 'walk avoid' and 'sniff' increased from 0 to 16 hours of hunger. At 16 hours of hunger the medium toy elicited significantly ($p<0.01$) more sniffing than the small toy (Figure 4.1) At 5 hours of hunger frequencies of 'sit groom', 'killbite' and 'stand watch' were at their highest.

*Small toy; the frequency of 'killbite' increased steadily with hunger, and was at its highest after 16 hours of hunger. At 0 hours the cats directed slightly more sniffing at the small toy than the medium, but this decreased steadily as hunger increased. At 0 hours they also showed a higher tendency to perform 'sit groom' and 'stand watch'.

DISCUSSION

The results show three main trends in this experiment. Firstly, the small toy elicited more play behaviour patterns than the medium toy, which elicited more avoid patterns. Secondly, there was an increase in performance of play behaviour patterns as hunger increased from 0 hours since the last meal, to 16 hours afterwards. Finally there was an interaction between hunger and size which suggested that there were some qualitative differences in the changing response to each size of toy as hunger increased. The small toy elicited more intensive 'close contact' patterns such as 'killbite' with increasing hunger. The cats showed increased general interest and investigation of the medium toy; patterns such as 'sniff' increased with hunger.

Although a number of behaviour patterns were significantly affected by differences in size and hunger, the patterns 'sniff' and 'killbite' were probably the two most important ones in the interpretation, since they were the only two 'hunting' patterns significantly affected at $p<0.01$, and were more relevant to the aims of the experiment than changes in general activity patterns. Hunger increased the performance of sniffing directed towards the medium toy. Sniffing is a behaviour pattern used by cats to investigate novel objects. However, in spite of being hungry, the cats were still inhibited in their play with the medium toy. Close contact play patterns (such as 'clutch', 'killbite' and 'chew') were not performed at any level of hunger; the cats were reluctant even to touch the toy with their paws. The performance of 'killbite' remained unchanged by increasing hunger. If hunger could be increased beyond sixteen hours perhaps 'killbite' and other close contact patterns would eventually increase and exploratory sniffing would decrease.

With the small toy, close contact behaviour patterns, especially 'killbite' increased with hunger; 'sniff', an exploratory pattern decreased. Thus, as the cats became increasingly hungry, and performed play patterns at higher intensity, they dispensed with exploratory patterns, such as 'sniff', performing close contact play instead.

Similar behaviour changes were shown by hunting cats with prey; Biben showed that cats became more active and showed an interest in increasingly large and difficult prey, such as rats, with increasing hunger, until finally overcoming their inhibitions to kill large prey (Biben 1979). In the same way, Curio (1976) showed that increasing hunger leads to the acceptance of larger prey than would normally be accepted in European toads.

The play responses recorded in this experiment were similar to those of Biben's study; as hunger increased, play behaviour changed in the same way as predatory behaviour does, although the cats still did not perform close contact play. Hunger enabled the cats to partially overcome their fear of the larger toy in this experiment, just as the cats in Biben's study were able to overcome their fear of large prey when they were hungry.

4.4: CONCLUSION

Since the play response is similar to the predatory response that Biben found, I suggest that this is evidence to support the hypothesis that play behaviour performed by the Southampton cats (which have no hunting experience), shares the same motivational basis as predatory behaviour. Thus play and predation are effectively the same behaviour for non-hunting cats, and the Southampton cats were hunting the toy.

It is assumed that the non-hunting Southampton cats have no hunting behaviour from which they could distinguish play behaviour, play may be motivationally and physically the same as hunting for them. Thus their reaction to a toy and the interaction between hunger and size is the same as that found for a hunting cat tackling prey. Thus the whole effect of hunger on play might be determined by whether the cat is an experienced hunter or not. If a cat had never hunted play would be expected to increase with hunger, since the cat should react to hunger with play performance as an experienced hunter would with predatory behaviour performance. Conversely, if a cat is an experienced hunter, object play would not be expected to increase with hunger; the cat would hunt instead. However, the hunting cat would not be expected to show the same behaviour towards a toy as the non-hunting cat, since it should have learnt to distinguish between hunting and playing, prey and toy.

As discussed in Chapter 1, it is generally accepted that object play by kittens functions as practice for adult predation. Adult hunting cats, which learnt to hunt through kitten play do not need further play practice, but continue to hunt in order to perfect their predatory skills. However, in adult non-hunting cats play could be represented by either of two concepts: i) They may still be practising predation with play, exactly as kittens. In other words adult non-hunting cats have not developed mature predatory behaviour.
ii) Alternatively, they are performing the same predatory behaviour as hunting cats, but in the absence of prey, hunt toys.

Qualitative differences between adult non-hunting play and kitten object play, and a close similarity between adult play and predatory behaviour (Caro 1980), suggest that the second hypothesis is correct. Adult non-hunting cats are hunting their toys, so play is predation.

Also mentioned in the Introduction was one of the main reasons for the difficulty in accepting this hypothesis hitherto- it is hindered by the human distinction of play with objects from predation with prey animals, which is probably based upon a purely functional distinction, that is, the absence of a dead animal at the end of a play bout. Because nothing has been killed the behaviour has been given a different name.

OBJECT PLAY BY CATS IN THE SOUTHAMPTON UNIVERSITY COLONY

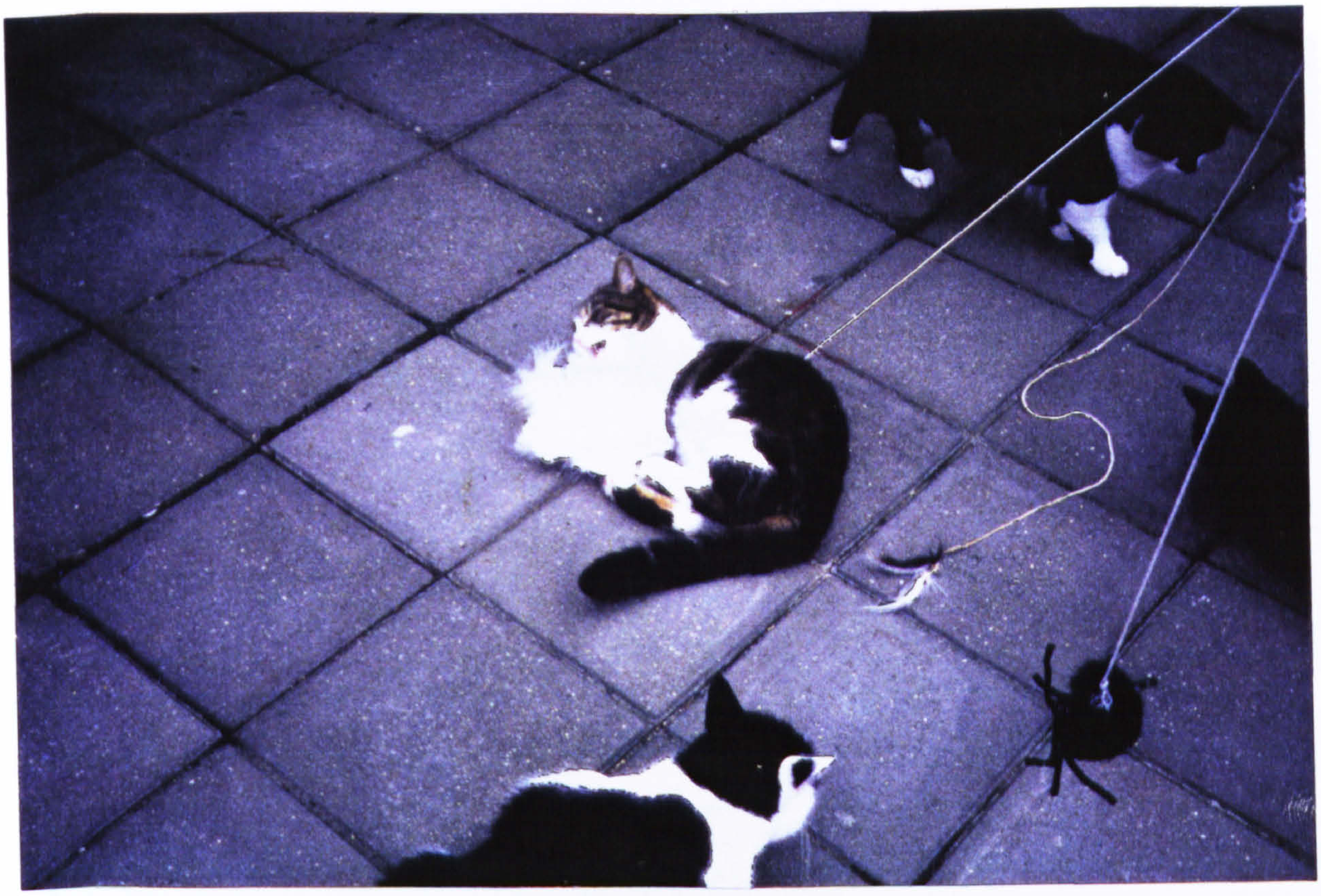


Plate 1. *Cat performing 'kick' and 'killbite'. Also shown are three toys used in this study. From left to right, feather covered toy, real fur toy and fakefur with legs toy.*

Plate 2. *Cat performing 'lick' and 'clutch'.*

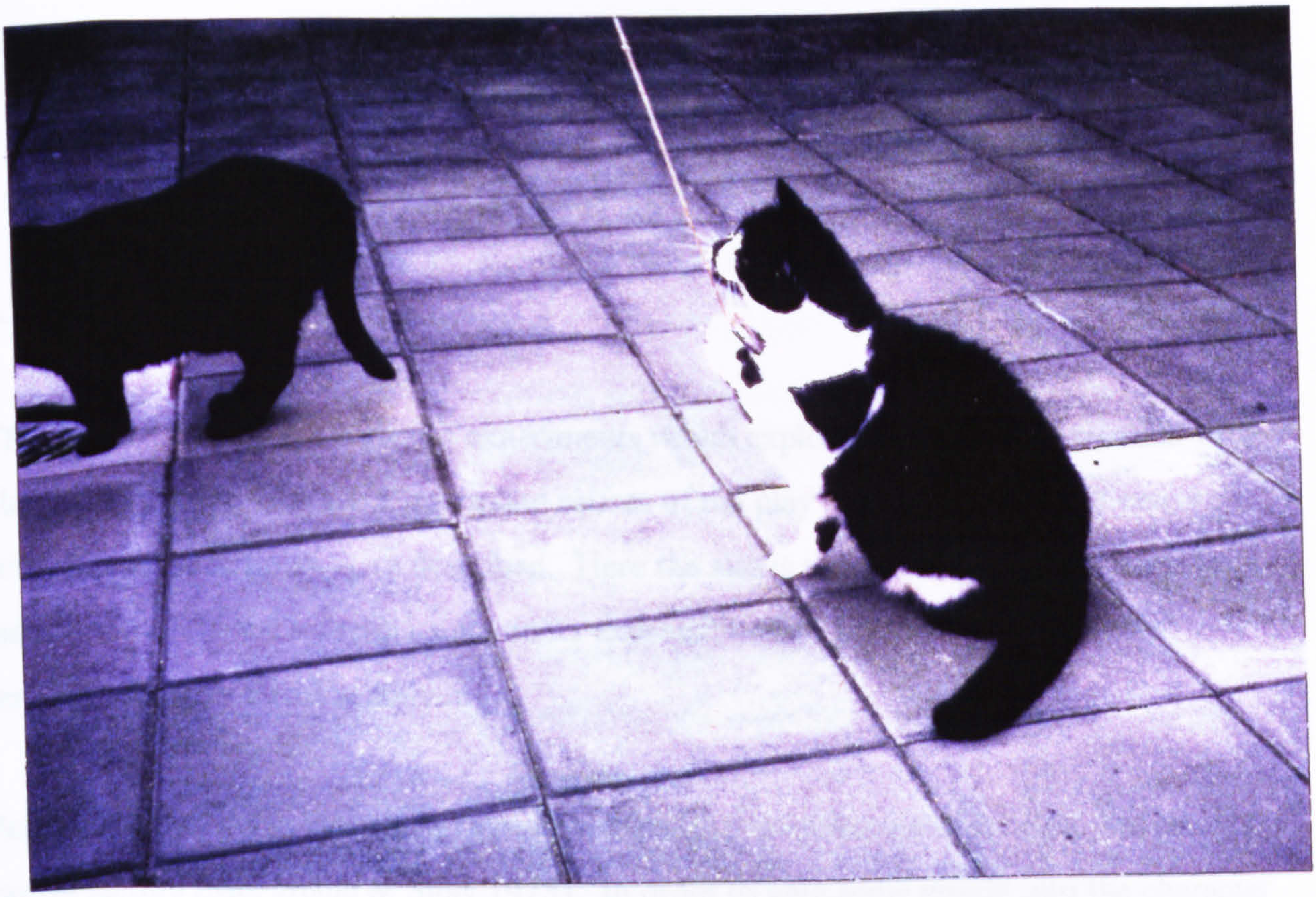


Plate 3. *Cat performing 'clutch' and 'sniff'.*

Plate 4. *Cat performing 'rear' and 'grasp'.*

5

THE MOTIVATION OF PLAY BEHAVIOUR

5.1: INTRODUCTION

This chapter describes a series of experiments which explore the motivation of adult cats' play behaviour. In Chapter 3 proximate causes of the play response in terms of external stimuli which elicit play were described. Here the aim is to investigate the influence and interaction of the cat's internal state on its expression of play behaviour, and on its responses to play-eliciting stimuli.

Performance of behaviour patterns is controlled by a combination of external and internal causal factors (McFarland & Sibly 1975). In order to gain some insight into the character and workings of internal causal factors it is necessary to control as closely as possible the external causal factors. Internal states can be altered by a variety of mechanisms, including metabolic change and proprioceptive feedback. They can also be affected by feedback from external causal factors, even if there has been no performance of the behaviour normally elicited by those causes (Toates & Jensen 1991).

Such a dissection of the characteristics of play motivation was necessary in order to clarify the nature of play behaviour; for example, to determine if play is an appetitive, goal-less behaviour, and in which case, how is it stopped? Despite supposedly lacking a consummatory endpoint, some patterns within play may have a self-rewarding, consummatory role. A cursory examination of definitions of play from past literature hints at the supposed nature of play. The performance of play behaviour has no external consequences, and no apparent consummation, suggesting that it is an appetitive behaviour. Consummatory behaviours usually have external consequences, for example food disappears when it is eaten. Appetitive behaviours which do not have external consequences can only be stopped by physiological changes that result from reaching a goal, and/or from performance of the corresponding consummatory behaviour (Hughes & Duncan 1988). If play is an appetitive behaviour, with no consummatory action or stimulus which stops it, why and how does the animal stop playing? It may be possible that there are consummatory patterns within play behaviour which terminate play. However, if there is a positive feedback mechanism which maintains high motivation, it may simply be stopped by the conflicting motivation to perform another behaviour. Alternatively, the motivation to play may dwindle until it falls below the motivation to perform some other behaviour. For the purposes of this study it is important to remember that apparent inactivity or simply avoiding the toy implies a discrete group of behaviour patterns, not an absence of activity.

Finally, an understanding of the motivation of play behaviour may be relevant to the hypothesis that play and predation have similar motivation.

It is important to remember that the behaviour of an animal at any one time is not solely dependent upon the presence of motivation to perform a single type of behaviour. The motivation for numerous incompatible behaviours will always be present (Lawrence & Rushen 1993). The ease with which a behaviour can be inhibited and the intensity of its performance when disinhibited have been used as the basis for the description of motivation states and processes in various studies (Kennedy & Booth 1963, Kennedy 1966) and form an important part of motivation models, for example, the behaviour switching models of McFarland (1974) and the behaviour of a model animal proposed by Ludlow (1975). The current study of play motivation has been based on some of these theories and models.

There have been very few previous studies of play motivation. It is difficult to examine motivation experimentally, since a method of measuring or tracking motivation is required. With some species it is possible to monitor a particular behaviour pattern, the expression of which is closely related to the motivation state of the animal. In a study of the motivation of object play in juvenile dwarf mongooses, Rasa (1984) suggested that the continuous repetition of squeak pulses was motivation-specific. A high rate of squeaks indicated high motivation, and vice versa. Thus Rasa was able to monitor motivation changes throughout a play session by measuring the squeak pulses. She was able to model an underlying motivational structure which ordered the mongoose's expression of play.

However, such a convenient measure is not always available. At the start of this study attempts were made to find a play behaviour pattern which could be used to indicate readiness to play, and would enable the tracking of play motivation in a way similar to Rasa's use of play squeaks. However, after examining play sequences no such behaviour pattern was found. Therefore, all play behaviour patterns had to be recorded throughout. An alternative approach to the connection between play quality and motivation is examined in Chapter 6 on Sequence Analysis.

The study was undertaken in three phases of experiments. The first phase was designed to describe habituation to the repeated presentation of one toy in a number of sessions and disinhibition by a subsequent change to a contrasting toy. The second phase was designed to examine the effect of delay between sessions on habituation and disinhibition. The final phase was an attempt to measure the motivation of play using habituation and disinhibition.

The experiments in the first phase involved four repeats of the same method with three populations of cats. The nature of habituation and disinhibition to particular toy types was examined. The second phase consisted of one experiment with the Southampton cats in which the time for habituation and disinhibition was controlled, so that inferences concerning the internal causal factors of play could be made. The third phase comprised one experiment, similar to the first set, but involving different toys, and was carried out at Waltham Centre for Pet Nutrition (WCPN).

5.2: THE HABITUATION AND DISINHIBITION OF PLAY BEHAVIOUR

METHOD

The idea for the initial experiment arose from the investigation into the effects of different colours and patterns of toys on play behaviour (see Chapter 3). Amongst the toys presented were two small (7x5x1cm), fakefur toys, one plain black and one plain white, both attached to pieces of string. These two contrasting toy colours were then used in this experiment to examine habituation and disinhibition of the play response. Most cats habituate to a toy of only moderate stimulus value, such as fakefur, fairly rapidly. In preliminary experiments, nine minutes of exposure to the toy were found sufficient for the cat to habituate to the toy.

Six cats from the Southampton colony were habituated to either the black toy or the white toy over three, three minute sessions. In a fourth three minute session the cats were then presented with the toy of contrasting colour. In two control treatments the cats were presented with either four sessions of the white toy or four sessions of the black toy. During the course of the experiment all of the cats received their first session, before any were given their second session. This resulted in a delay between the four sessions of approximately 25 minutes for each cat. The four treatments of the experiment were, therefore, to receive three sessions with white, followed by one with black, three sessions with black, followed by one with white, and four sessions with black or with white. The reversal of colour was necessary in order to control for a possible colour preference which would affect the outcome of any habituation/disinhibition observed. The cats received the treatments according to a Latin square design.

This method was repeated for two further groups of cats, once with eight cats at WCPN, and twice with eight pet cats. There were some small variations in the method:

1) These cats received only two treatments. It was determined in the first Southampton colony experiment that the cats showed no significant preference for either white or black (only one behaviour pattern was significantly affected by colour at $p<0.025$), and a preliminary experiment with the pet cats showed that they also had no colour preference (four behaviour patterns were affected by colour at $p<0.05$). As a result of this finding it was only considered necessary to have two treatments; three sessions of white, then one black and four sessions of white.

2) The three minutes allowed for each session was reduced to two minutes since it had been obvious in the Southampton experiment that two minutes would have been long

enough to ensure the cats habituated. This change in time altered the delay between each of the four sessions for each cat. For the six cats at WCPN the delay was approximately 15 minutes, for the pets the delay was five minutes in the first experiment, and less than ten seconds in their second experiment.

3) Finally, the data from the two pet cat experiments were recorded on to a dictaphone, rather than on video, as in experiment with the Southampton and WCPN colonies. This was simply for practical reasons, since it would have been impossible to install video equipment in all of the pet cat owners' rooms. The methods were identical in all other aspects.

RESULTS

The results from these four experiments were analyzed in the same way, and so will be considered together.

Five comparisons of data were made (in paired t-tests for WCPN and pet data, and in two-way ANOVA for Southampton data), in order to examine any effects of habituation and disinhibition of the play response. These were:

1) Session 1 with session 3. By indicating whether play had decreased, increased or remained the same from the first to third session, this would provide a measure of habituation to the toy.

2) Session 1 with session 4 which had a contrast in toy colour. This would reveal the effect of changing to a contrasting stimulus after prolonged exposure to one stimulus.

3) Session 4 with a colour contrast, against session 4 with a toy of the same colour as in the first three sessions.

4) Session 3 with session 4 using a contrasting toy. This would indicate whether a change of toy colour had any affect upon the play response.

5) Session 3 with session 4 with the same colour toy. This acted as a control to comparison 4).

The five tests above were undertaken on each of the four sets of data separately. In the

Behaviour pattern abbreviations for Tables 5.1 and 5.3:

F=frequency measure
D=duration measure

Play patterns: All play patterns are frequency only, except **CL** and **HM**, which also have a duration measure.

SN-sniff
HM-holdmouth
KB-killbite
RE-rear
LI-lick
CW-chew
GR-grasp
HI-hit
BA-bat
CL-clutch
KI-kick

HUNTD-total duration of all behaviour patterns classed as play.

Non-Play patterns: All non-play patterns have a frequency and a duration measure.

<u>Primary</u>
Wawalk
ST-stand
SI-sit
CR-crouch
RC-recline

<u>Secondary</u>
AV-avoid
GO-groom
WT-watch

Primary behaviour pattern codes precede secondary behaviour pattern codes, for example, **WAWTF**=walk and watch frequency

All behaviour patterns are defined in the Appendix.

Table 5.1. *Comparison of behaviour between sessions in the habituation experiments with three populations of cats, showing the behaviour patterns significantly different between sessions, at $p<0.05$, unless stated otherwise.* Behaviour codes are defined on p102. Where F&D=both the frequency and duration measures of the behaviour pattern were significantly different, F=frequency only, D=duration only.

Cat group	Session 1 vs 3	Session 1 vs 4 with a contrast	Session 4 with contrast vs 4 without	Session 3 vs 4 with a contrast	Session 3 vs 4 without a contrast
Soton	**greater in 1**: KIF,REF SNF,KBF CLF&D,HIF HMF,CRWTF BAF STWTF&D **none greater in 3**	**greater in 1**: STWTF KBF HIF,GRF CLF&D **greater in 4**: STAVF&D CRAVF	**greater in 4 with**: HIF,HMF&D GRF,CLF&D KBF,SNF REF,CWF **greater in 4 without**: WAAVD	**greater in 3**: SIGOF RCAVD **greater in 4**: HMF,CLF KBF,REF CLD,GRF RCWTD	**none**
WCPN	**greater in 1**: HIF,HMF CLF,KBF SNF,STWTD **greater in 3**: CRAVF&D	**greater in 1**: STWTD **greater in 4**: RCWTF	**greater in 4 with**: HIF,CLF&D KBF,STWTD **greater in 4 without**: STAVD	**greater in 3**: STAVF&D **greater in 4**: HIF,GRF CLF,KBF SNF,REF SIWTD STWTD CLD	**none**
Pets 1	**greater in 1**: SIWTF&D STWTF,HIF GRF,CLF&D KBF,SNF REF, **greater in 3**: SIAVF&D RCAVF&D	**greater in 1**: SIWTD RCWTD **greater in 4**: CLF,GRF KBF,KIF HMF&D	**greater in 4 with**: STWTF&D HIF,GRF CLF&D KBF,HMF&D **greater in 4 without**: SIAVF&D WAAVD	**greater in 3**: WAAVF&D RCAVF&D **greater in 4**: STWTF, HIF,GRF KBF HMF&D CLF&D	**greater in 3**: CLF,KBF **none greater in 4**
Pets 2	**greater in 1**: KBF,SNF HIF,CLF **greater in 3**: WAAVF&D SIAVF&D	**greater in 1**: WAAVF&D. **greater in 4**: HMF&D KBF CLF&D	**greater in 4 with**: HIF,KBF REF,CLF&D HMF&D,GRF RCWTD,KIF **greater in 4 without**: SIAVF&D	**greater in 3**: WAAVF&D STAVF&D **greater in 4**: HIF,GRF KIF,KBF HMF&D CLF&D RCWTD	**none**

Table 5.2. *Summary of relative scores on the first principal component (all Play vs Avoid) derived from the behaviour patterns significantly affected in Table 5.1.* Where 'with contrast' refers to a change of toy colour in the 4th session, and 'without contrast' refers to no change in toy colour in the 4th session. The time delay between the 4 sessions for each experiment is also given. (No PCA carried out on session 3 vs session 4 without a contrast due to lack of separation by ANOVA).

Amount of play recorded in each session

	Session 1 vs.3	Session 1 vs.4 (with contrast)	Session 4 with contrast vs. 4 without	Session 3 vs. 4 (with contrast)	Session 3 vs. 4 (without contrast)
Pets2 (<10s delay)	1 > 3	1 < 4	contrast > none	3 < 4	3 = 4
Pets1 (5min delay)	1 > 3	1 < 4	contrast > none	3 < 4	3 = 4
WCPN (15min delay)	1 > 3	1 = 4	contrast > none	3 < 4	3 = 4
So'ton (25min delay)	1 > 3	1 > 4	contrast > none	3 < 4	3 = 4

analysis of the second experiment with the pet cats, patterns significantly different at $p<0.1$ were also noted (see Table 5.1), in order to determine the direction of any trend, since the second pet cat experiment was planned as confirmation of results of the first experiment. The behaviour patterns significantly different for the five comparisons listed, for each experiment are presented in Table 5.1.

From Table 5.1 it can be seen that in all four experiments there was no substantial difference in play in session 3 and 4 if the toy colour was unchanged. For the WCPN cats, in the comparison of play in the first and fourth sessions, when there was a colour contrast, only two behaviour patterns were significantly different between the two sessions. In the remainder of the comparisons there were significant differences in the overall play. In order to determine the direction of these differences the means tables for each affected behaviour were examined. Principal Components Analysis (PCA) was used to determine an overall pattern of all the behaviour changes in the four sessions. Examination of component weights and the corresponding distribution of behaviours on the first two components (accounting for 88% of the variance) enabled the direction of changes in play to be interpreted. From the examination of more than 30 PCA graphs accumulated from PCA of the five t-tests/ANOVA tests, for each group of cats, Table 5.2 summarises the trends which appeared in the PCAs of the five comparisons. These trends were all based on several behaviour patterns significant at $p<0.05$ (at least);

1) play always decreased from the start of session 1 through to the end of session 3.
2) play was always greater in the fourth session when the toy colour had changed, than in the fourth session when the toy colour had remained the same.
3) when the toy colour had changed in the fourth session play was always greater than in the third session. If the toy colour had not changed in the fourth, the play levels were similar in the third and fourth sessions.
4) the four experiments showed different trends for the comparison of session 1 with session 4, when there was a change in toy colour in the fourth. Southampton cats showed a **decrease** in play in the fourth session, WCPN cats showed the same level in both sessions, and the pet cats showed an **increase** in play in the fourth session.

DISCUSSION

It was expected that the frequency and duration of play would be initially high in the first session, then show a decrease through to session 3. This expectation was confirmed by the results, and indicated that the cats habituated to the toy as it was presented in each successive session. If the toy colour remained unchanged in the fourth session little play was recorded as the cat remained habituated to the toy.

However, if the toy colour was changed in the fourth session, the frequency and duration of play increased in response to the change of stimulus, so that more play was recorded in the fourth than third session. Thus the comparison of the two fourth session treatments showed that play was greater if the toy contrasted in colour to that encountered in the first three sessions. Therefore all the cats habituated to an unchanging play stimulus. This habituation acted as an inhibitor to play. However, a toy which was identical in all but one feature, colour, was sufficient to disinhibit the play response. The motivation level of play must have been maintained throughout the habituated phase, hence the high level of play response in the fourth session. When the performance of the disinhibited behaviour is at a higher intensity than it was initially, as recorded in the pet cats, the heightened disinhibition is known as a post-inhibitory rebound (Kennedy 1985). If motivation had decreased throughout, the disinhibition would not have resulted in such intensive play in the fourth session, nor could post-inhibitory rebound have been observed. The disinhibited play behaviour is partly dependent upon the underlying motivation, in addition to the effect of changing stimulus.

This is further emphasised by the discrepancy in results which is apparent from the comparison of the first session and the fourth with a colour change. The Southampton cats did not attain their original play level, the WCPN cats achieved the same level, and the pet cats exceeded their original play level. This difference in disinhibition could possibly be explained by innate differences between the three populations of cats in their response to habituation, or perhaps was indirectly due to their different environment and life histories. However, it is also possible that it was the result of the single difference in external causal factors between the three cat groups, the time delay between each session. As stated before the time delays were as follows; for the Southampton cats delay between sessions was 25 minutes, for WCPN cats it was 15 minutes, for pet cats (experiment 1) five minutes and pet cats (experiment 2) less than ten seconds. These differences in time delay may have been sufficient to affect the motivation of the cat groups. It is possible, for example that the group with no delay between sessions would have suffered greater fatigue than the cats with 25 minutes rest between sessions. Alternatively, the play motivation of the cats with 0 minute delay may have been more strongly reinforced by continuous exposure to the toy, leading to increased play in the fourth session relative to the first, when the habituating stimulus (the colour) was removed.

In order to clarify these problems, the affect of time delay was examined in a further experiment with the Southampton cats.

5.3: THE EFFECTS OF DELAY BETWEEN SESSIONS ON HABITUATION AND DISINHIBITION

METHOD

The experiment was simply a repeat of part of the last four experiments, the changing variable being the delay between the four sessions. This was performed in order to test the possible effects of delay between sessions on play, suggested by the results of the previous experiment. Eight of the Southampton cats were presented with the same white toy for the first three two minute sessions, then were presented with the contrasting black toy in the fourth session. There were three different time delays between each session, five minutes (corresponding to the pets), 15 minutes (similar to WCPN cats), and 45 minutes (longer than but comparable with the delay with the Southampton cats). These treatments could not be given to the cats according to a Latin square design as the practical difficulties in keeping to a different delay schedule for eight cats made this impossible. Thus all cats received the same delay time schedule on each day of the experiment. The cats received each treatment twice. The details of the method were identical to those of the previous four experiments. Data was recorded on a dictaphone.

RESULTS

Three comparisons of sessions were tested with two-way ANOVAs, where the main effects were session and cat, as follows:

1) Session 1 with session 3, to measure habituation.
2) Session 1 with session 4, to test for post-inhibitory rebound.
3) Session 3 with session 4, to measure disinhibition.

Each time delay group was tested separately.

1) In the comparison of session 1 and 3, the following number of behaviour patterns were significantly different in each of the three time delay groups;

5 minute delay group, four at $p<0.05$, five at $p<0.1$;
15 minute delay group, eight at $p<0.05$;
45 minute delay group, five at $p<0.05$.

2) In the comparison of session 1 and 4, the following number of behaviour patterns were significantly different;

5 minute delay group, three at $p<0.05$, four at $p<0.1$;
15 minute delay group, two at $p<0.05$ (expected by chance);
45 minute delay group, two at $p<0.05$, five at $p<0.1$.

3) In the comparison of session 3 and 4, the following number of behaviour patterns were significantly different;

5 minute delay group, 11 at $p<0.05$;
15 minute delay group, nine at $p<0.05$;
45 minute delay group, six at $p<0.05$.

PCA analysis of patterns significant in each of the ANOVA tests was used to confirm the pattern of these differences. The trends found repeated those recorded in the previous experiment and are summarized in Table 5.3 and 5.4. The trends were as follows;

1) In all three groups there was a decrease in play performance from session 1 to session 3, indicating that play behaviour had habituated to the toy. This was unaffected by the time

Table 5.3. *Comparison of behaviour patterns between sessions in the delay experiment, showing the behaviour patterns significantly different between sessions, all at p<0.05, except those marked * which are at p<0.1.* See p102 for explanation of codes. Where F&D=both the frequency and duration measures were significantly different, F=frequency only, D=duration only.

	Session 1 vs 3	Session 1 vs 4	Session 3 vs 4
5 minute delay	**greater in 1**: STWTF,SNF STWTD,WAWTF* WAWTD*CRWTD* **greater in 3**: SIAVD,SIAVF* SIGOD*	**greater in 1**: STAVD **greater in 4**: HIF,KBF,GRF*,CLF* SNF*,CLD*	**greater in 3**: SIAVD,STAVD **greater in 4**: SIWTF,STWTF,HIF CLF,KBF,SNF, SIWTD,STWTD CLD
15 minute delay	**greater in 1**: WAWTF,SIWTF,BAF HIF,SNF,STWTD **greater in 3**: SIAVD,SIAVF	**greater in 4**: GRF,CLD **none greater in 1.**	**greater in 4**: SIWTF,HIF,GRF KBF,SNF,SIWTD STWTD,CTWTD CLD **none greater in 3.**
45 minute delay	**greater in 1**: HIF,SNF,STWTD **greater in 3**: SIAVF,SIAVD	**greater in 1**: SNF **greater in 4**: STAVF,SIAVF* CRAVF*,SIAVD CRAVD*.	**greater in 4**: STWTF,HIF,CLF KBF,GRF STWTD,CLD **none greater in 3.**

Table 5.4. *Summary of relative scores on the first principal components (all Play vs Avoid) derived from behaviour patterns significantly affected in Table 5.3.* All results were significant at p<0.05, except those marked *, in which some are significant at p<0.1. (The fourth session toy was always of a contrasting colour). Note that the direction of intensity of play is identical to that in Table 5.2.

	Session 1 vs.3	Session 1 vs.4	Session 3 vs.4
5 minute delay	1 > 3 *	1 < 4 *	3 < 4
15 minute delay	1 > 3	1 = 4	3 < 4
45 minute delay	1 > 3	1 > 4 *	3 < 4

delay between sessions.

2) In all three groups there was an increase in play from session 3 to 4, indicating that disinhibition occurred when the black toy was presented after the play response had become habituated to the white toy over the first three sessions.

3) There was an increase in play behaviour in session 4 compared with session 1 for the 5 minute delay group, indicating a post-inhibitory rebound, as a result of marked disinhibition when the toy colour was changed after habituation to the white toy in the first three sessions.

In the 15 minute delay group there was no large post-inhibitory rebound, although disinhibition had occurred. The play level was the same as that in session 1. Finally, in the 45 minute delay group, there was less play in session 4 than in session 1, indicating that again there was no large post-inhibitory rebound, and that the disinhibition had been smaller than in the other two groups. Its effect on the play level is session 4 was less marked.

The results of this experiment are directly comparable with those of the previous four experiments (Table 5.4; compare with Table 5.2). The 5 minute delay results are equivalent to those of the pet cats; the 15 minute delay results to those of the WCPN cats; and the 45 minute delay are equivalent to the Southampton colony results.

DISCUSSION

These results confirm that the time delay between sessions was the most likely cause of the difference in the amount of play in the previous habituation experiments. Changing the delay between sessions altered the degree of habituation and the effect of disinhibition. A short delay of 5 minutes led to a pronounced post-inhibitory rebound, with more play than in the initial session. A long delay, of 45 minutes, led to much reduced disinhibition, the consequence being less play in the fourth session than in the first session. The intermediate delay, of 15 minutes, led to behavioural changes between these two extremes.

This is most easily explained if it assumed that the underlying mechanisms of habituation, inhibition and eventual disinhibition of play were the same in each case, but were modified by delay between sessions.

When the delay between sessions is short inhibition to the toy stimuli occurs quickly, producing a steep gradient of habituation over the three sessions. When the toy is changed in the final session a post-inhibitory rebound occurs and play is more intensive than in the first session. However, when there is a long break between the play sessions inhibition does not build up to the same extent, leading to a shallower gradient of habituation. When the toy is changed there are three possible explanations for the lack of post-inhibitory rebound and for a reduction in play compared with the first session;

1) The reduced habituation has led to a reduced build-up of 'excess' play motivation. As a result, when the toy is changed disinhibition has a reduced effect on the play expressed. When the delay is short the cat is prevented from playing fully by habituation, thus accumulating 'excess' play motivation which cannot be expressed. It can only be expressed as a post-inhibitory rebound of intensive play when the toy is changed and the play response disinhibited.

2) When the delay is long, the accumulation of 'excess' play motivation which would be expressed as post-inhibitory rebound in play, is interrupted and effectively nullified by the motivation to perform other behaviours in between the play sessions. The 45 minute delay between sessions may be too long for the effect of play inhibition to persist.

3) It is possible that the post-inhibitory rebound is not play specific, although is specifically expressed in play in this instance, and represents an increase in the cat's general arousal. Since different motivational systems interact (Manning 1979), the post-inhibitory rebound may be dissipated in the unusually intensive expression of other behaviours in between the play sessions. The inhibition of play by habituation to an unchanging toy can be dissipated as a large post-inhibitory rebound expressed as very intensive play when the toy is changed, but if the cat is allowed a long break between sessions it is more likely to perform other behaviours, such as social interaction or sudden attack on another object, and the post-inhibitory rebound could be dissipated in the performance of these intervening behaviours. This is more likely to happen if the cat has more time in which to perform other behaviours

between play sessions. With little time between sessions the cat has less time to perform other behaviours and is more likely to remain in 'play state'.

5.4: MEASUREMENT OF MOTIVATION USING HABITUATION AND DISINHIBITION

In the preceding two experiments, the play stimuli (toys) were deliberately selected to induce only moderate amounts of play behaviour. The extent to which a small change in stimulus (colour) re-activated play indicated that over the course of the whole experiment, the cat's motivation to play had scarcely changed. Although this appears to suggest that play contains few, if any, consummatory patterns, it is also possible that the low intensity of the play observed overall had failed to reduce motivation sufficiently. The aim of this experiment was to examine the extent of habituation and disinhibition when the initial play stimulus was a powerful play inducer (the real deer fur toy: see Chapter 3), and when habituation was minimised by alternating this toy with another powerful stimulus (feathers).

METHOD

The subjects were 12 cats at WCPN, tested individually. Each cat was given four play sessions of 90 seconds duration. This duration was selected because in preliminary experiments this was the shortest time in which any cat had habituated to the real fur toy. Both toys were small (7x5x1 cm), one made from real deer fur (RF), and the other covered in yellow feathers (FE) (see Chapter 3). Each cat was presented with the six treatments in Table 5.5 in an order determined from a 6x6 Latin square. Sessions were immediately consecutive, except for a few seconds to make an actual or dummy switch between toys. Play was recorded directly on to a dictaphone for sessions 3 and 4 only.

Data was analyzed using paired t-tests and ANOVA, with the following questions in mind:

1) What effects did the six treatments have upon the play performed in session 4? Six different patterns of habituation and disinhibition were expected. The third and fourth sessions within each treatment were compared.

	Session 1	Session 2	Session 3	Session 4
A	RF	RF	RF	FE
B	RF	RF	RF	RF
C	FE	FE	FE	RF
D	FE	FE	FE	FE
E	RF	FE	RF	FE
F	FE	RF	FE	RF

Table 5.5 *The six treatments comprising different combinations of fur and feathers, where RF= real fur, and FE= feathers.*

2) Does a change of toy stimuli in the early sessions (2 to 3) have any effect upon the play performed in session 3? Play in session 3 after a change in toy from session 2 to 3 (treatments E and F) was compared with play in session 3 when there had been no change in toy from session 2 to 3 (control treatments A and C).

3) Does a change of toy stimuli in the early sessions (2 to 3) have any effect upon the play performed in session 4? Play in session 4 after a change in toy from session 2 to 3 (treatments E and F) was compared with play in session 4 when there had been no change in toy from session 2 to 3 (the corresponding controls, C and A).

Play performed in session 4 within the two treatments in which the toys were alternated throughout (E and F) was also compared, as a check for the analysis above.

4) How much influence does the contrast in toy stimulus from session 3 to 4 have upon play in session 4? Is it possible to predict the relative play response that a toy will elicit in the fourth session according to the type and order of toys in the preceding sessions? Treatments in which there was only a contrast in session 4 (A and C) were compared with their control treatments (B and D), in which the toy was unchanged throughout.

RESULTS

1) The number of behaviour patterns significantly ($p<0.05$) different between the third and fourth sessions for each treatment are shown in Table 5.6, as well as the direction of the differences in play level in the two sessions.

2) Does a contrast in toy from session 2 to 3 affect play in session 3? Comparison of treatments A, C, E and F revealed that 18 behaviour patterns (out of 40) were significantly different in session 3 after a contrasting toy in session 2. This result is the equivalent of results shown in Table 5.6 (for example, treatments C and F) where a change in toy from session 3 to 4 significantly affected play in session 4.

3) Does a contrast in toy from the second to third session have an effect on play behaviour in session 4? In the tests of treatments C, F, E and A, only 2 behaviours were significantly affected by contrast and these may be discounted as expected by chance. The level of play in session 4, enhanced with the toy in the immediately preceding session, is therefore not modified by any contrast presented earlier in the trial.

The comparison of E with F, in which the toy stimuli were alternated in each session gave similar results to treatments A and C. There was an increase in play in the fourth session of F (session 3, feathers, session.4, real fur), and a decrease in the fourth session of E (session 3, real fur; session 4, feathers). This was compared with treatments A and C, in which the toy was unchanged for the first three sessions. The results were similar: an increase in play in the fourth session of F (session 3, feathers, session 4, real fur), and a decrease in the fourth session of E (session 3, real fur; session 4, feathers), as shown in Table 5.6. Sixteen (out of 40) behaviour patterns were significantly different when the two fourth sessions of A with C were compared. Play decreased when feathers followed three sessions of real fur; and increased when real fur followed three sessions of feathers. This comparison demonstrates that a contrast from sessions 1 to 2 and 2 to 3 has no effect upon the play in session 4, since in A and C, and E and F the play in session 4 was affected only by the toy in session 3.

4) Does a contrast between session 3 and 4 have an effect upon the play behaviour level in

Table 5.6. *The number of behaviour patterns significantly different from session 3 to session 4 (all behaviours were significant at $p<0.05$), and the direction of the differences in play.* Only 'play' patterns as defined on p102 were used to determine this. (RF=real fur; FE=feathers).

Treatment	Number of behaviours different from session 3 vs. session 4	Differences in play level from session 3 to 4
A	12	3 (RF) > 4 (FE)
B	0	3 (RF) = 4 (RF)
C	13	3 (FE) < 4 (RF)
D	7	3 (FE) > 4 (FE)
E	11	3 (FE) < 4 (RF)
F	10	3 (RF) > 4 (FE)

Table 5.7. *The mean position in session 4 of the four treatments A to D (shown as toy in session 3 and 4) on component 1 in the PCA.* (RF=real fur; FE=feathers). These loadings should be compared with the loadings of the behaviour patterns on component 1.

Pattern	Component 1	Toy in session 3	Toy in session 4	Mean value
stand avoid (f)	-0.2753	FE	RF	3.13
stand avoid (d)	-0.2688	RF	RF	1.22
walk avoid (f)	-0.2316	RF	FE	-1.17
walk avoid (d)	-0.2254	FE	FE	-2.99
sit avoid (f)	-0.1925			
sit avoid (d)	-0.1764			
recline avoid (f)	-0.1563			
recline avoid (d)	-0.1062			
sit groom (d)	-0.0412			
sniff (f)	-0.0061			
stand watch (f)	0.0792			
recline watch (d)	0.1294			
sit watch (d)	0.1973			
sit watch (f)	0.2206			
walk watch (d)	0.2234			
clutch (d)	0.2387			
walk watch (f)	0.2393			
rear (f)	0.2412			
killbite (f)	0.2694			
hit (f)	0.2771			
grasp (f)	0.2867			
clutch (f)	0.3094			

session 4, of treatments B, C, D and A? Treatments B and D had no contrast from sessions 3 to 4, and treatments C and A had a contrast from session 3 to 4. There were 22 (out of 40) behaviour patterns significantly different at $p<0.05$ when there was a contrast. The direction of trends in play pattern performance was examined in a PCA. Contrast before session 4 led to increased play (see Table 5.7). Corresponding controls (B and D) showed less play in session 4. The order of all four treatments, according to play frequency and duration means in session 4, is shown in Table 5.7.

DISCUSSION

The cats' reactions to the toys in session 4 and throughout the experiment were determined by the combination of three factors; the sensory value of the toy, fatigue from playing for three previous sessions, and finally, habituation to the toy of the previous sessions. The four sets of analyses enabled some elucidation of these three factors:

1) A comparison of the relative sensory values of real fur and feathers revealed that the fur always received more play behaviour and less avoiding behaviour than the feather toy, whether preceded by a contrast or not (see Tables 5.6 and 5.7). The cats also habituated to the feather toy from session 3 to 4 very rapidly. In comparison, habituation was significantly reduced for the fur toy from the third to fourth session. This suggested that the fur toy was more stimulating and of higher sensory value to the cat, as it elicited more intense play for a longer time. There was a marked disinhibition of play when real fur was presented after feathers in session 3. This was enhanced by the high sensory value of real fur.

2) A contrast of toy from session 2 to 3 provided a change of stimulus which affected the play performed in session 3. If there was no change in toy, the play in session 3 remained unchanged.

3) Earlier changes in toy (i.e. from session 2 to 3) had no effect on play behaviour in session 4, suggesting that the only toy which might influence the play behaviour in the fourth session was that immediately preceding it. This conclusion is supported by 2) in which the play in session 3 was found to be affected by the toy in session 2.

The comparison of E and F also indicated that the contrast from feathers to real fur elicited more play than from real fur to feathers. This was probably a result of the greater sensory value of real fur, plus disinhibition from habituation to feathers.

Although play in session 4 was shown to be affected only by the preceding session, and none before that, it is possible that, had there been no contrast between sessions 3 and 4, an effect of contrast in session 2 might have been noted (for example, in the sequence FE, RF, FE, FE). The conclusion must therefore be limited to; a contrast between session 3 and 4 removes the effects of preceding contrasts.

4) A contrast of toy stimulus at session 4 was a reliable way of enhancing play. The means shown in Table 5.7 show that play with both real fur and feathers was greater if immediately preceded by the contrasting toy. However, real fur, even if not preceded by a contrast, still elicited more play than feathers after a contrast. As stated earlier, the greater play with feathers after a contrast in session 3 was probably a result of elevation of play motivation by the immediately preceding real fur, rather than disinhibition from habituation to real fur, which has a higher sensory value than feathers. There is probably no disinhibition from real fur to feathers, since there is negligible habituation to real fur over 90 seconds (Table 5.6).

It was possible to order the toy stimuli according to the play elicited in session 4. Play decreased in the order; (RF after FE) > (RF after RF) > (FE after RF) > (FE after FE) (see Table 5.7).

In an effort to clarify the relative importance of habituation and fatigue to the play performed in session 4, a simple additive model was constructed, using the means values in Table 5.7, in which;

a=play with fur,

b=play with feathers,

(a and b are independent of one another, but are arbitrarily defined according to the scale used, which is the that of the behaviour pattern loadings on Component 1).

c=depression of play due to central fatigue (Ludlow 1975), (assumed to be 0 for feathers, this being a less powerful stimulus),

d=depression of play due to habituation.

Accordingly, a, b, c and d can be assigned to the session 4 treatments:

Real fur after real fur; $a-c-d=1.22$
Fur after feathers; $a=3.13$
Feather after feather; $b-d=-2.99$
Feathers after fur; $b-c=-1.17$
(see Table 5.7)

This is solved as follows:

$$3.13-c-d=1.22$$
$$c+d=1.91$$
$$b-d=-2.99$$
$$b+c=-1.08$$
$$b-c=-1.17$$

therefore,

$$2b=-2.25$$
$$b=-1.13$$
$$c=0.045$$
$$d=1.865$$

and, $a=3.13$ as shown above.

Since c is the depression of play due to reduced motivation or 'central fatigue', and d is the depression of play due to habituation, play is affected by habituation from exposure to the toy more than by central fatigue from three sessions of play. This explains why feathers are played with more after real fur, when the cat should be 'tired', than after feathers, when it has habituated to the toy.

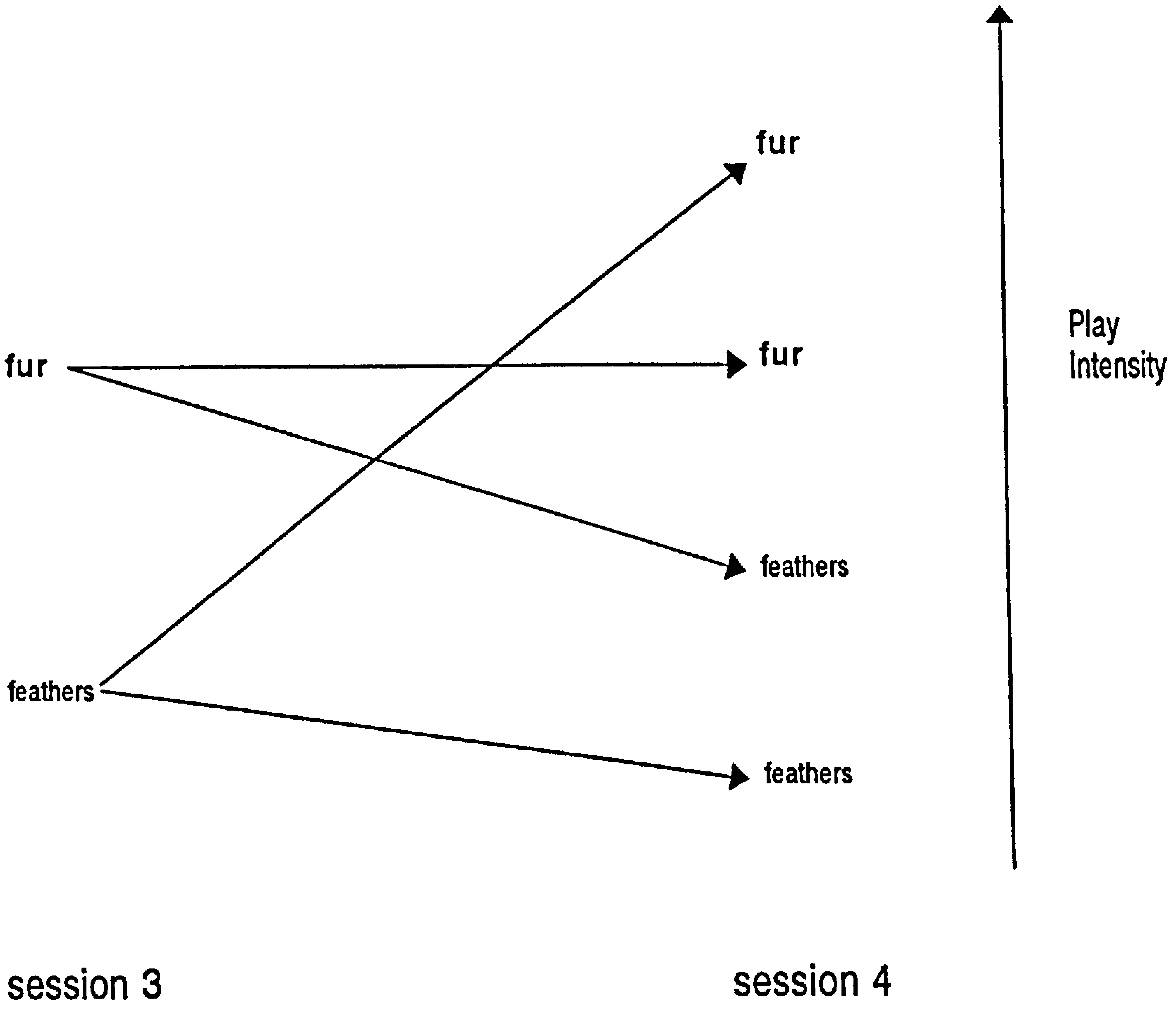
Therefore, it appears that play motivation does not decrease with performance of play, so that cats would play continuously, given a stimulus which does not cause habituation. Fatigue has little effect, but habituation from continuous exposure to the same toy stimulus depresses play.

Play expressed when real fur is presented does not follow motivation to play, because play can increase. When real fur was presented after three sessions with feathers, play was greater than after three sessions with fur. The play level with fur after three sessions with feathers represented a large post-inhibitory rebound after inhibition by habituation to a toy of lower sensory value (feathers), plus the effect of a contrast, and no fatigue. The cats did habituate to the fur toy, but very gradually, and more slowly than to the feather toy. Figure 5.1 describes these effects graphically.

GENERAL DISCUSSION

Motivation is a very complex subject, and numerous theorists and practical researchers have suggested their own definitive solutions to the problem of explaining motivation. As a result, throughout motivation literature there is a plethora of models of various types; behavioural 'black box' models, psychological, welfare, homeostatic, and control system-based models with accompanying negative and positive feedback loops, reinforcers, inhibitors, causal factors, releasers, tendencies, drives, incentives and gradients, amongst a profusion of other terms. The potential for confusion when studying motivation is great, and in order to minimize this a small number of models and studies were chosen, whose terms and concepts could be applied directly to this study.

Figure 5.1. The play intensity in session 4 is determined by the sensory value of the toy and by the effect of the immediately preceding toy (see Table 5.7)



When interpreting the mechanisms involved in the motivation of play I referred closely to Ludlow's model animal (1975), and the work of Kennedy & Booth (1963) and Kennedy (1966, 1985 & 1992) on the internal causation of behaviour changes in aphids.

In an analysis of the behaviour of a model animal, Ludlow (1975) attempts to explain the mechanism of habituation, disinhibition and post-inhibitory rebound. In his terms, an activity for which there is high motivation (for example, play) can become 'centrally fatigued' by inhibition from external factors. Despite being more highly motivated than a second, more weakly motivated behaviour (for example, 'avoiding'), this increasing central fatigue eventually prevents the first behaviour from suppressing the second behaviour. Thus play, with higher motivation, could give way to 'avoiding', despite the fact that play has the higher motivation. Recovery of the first, most highly motivated behaviour, could bring its expression back to its starting level. This recovery could be brought about by a change in external stimuli, which would disinhibit the behaviour.

With respect to the level of expression of the recovering, highly motivated behaviour, after it has been disinhibited by a change in external stimuli, Ludlow notes that almost any conceivable effect may occur. The processes to which he attributed the outcome were fatigue (central fatigue of the behaviour) and summation. He gave the following three examples (in which he referred to disinhibition as 'rebound'):

> 'Suppose for example, that activity A is occurring and is interrupted by activity B. If the inhibition from centre B to centre A is sufficiently strong it may summate and after the interruption activity A may be performed with lowered intensity. If the inhibition from centre B to centre A during the interruption is less strong, less summation occurs and the predominant effect may be rebound because the centre recovers from fatigue during the interruption. If the two processes have different time courses the initial after effect may be depression followed by a delayed rebound, or it may be a rebound which rapidly subsides in to depression.'

Thus the eventual intensity of the behaviour in the disinhibition phase is relative to the motivation for the competing behaviour. The rebound size is determined by a balance of fatigue of the initial behaviour and summation of the second. Kennedy (1966) adds the relative 'strength' of the initial behaviour and the disinhibiting stimulus to this list of influences on this balance determining the disinhibition/post-inhibitory rebound. Strength he defined by the 'excitability' of the stimulus eliciting the response. He noted that a strong behaviour followed by a strong disinhibitor would produce pronounced disinhibition, and that a weak behaviour followed by a strong disinhibitor would produce less disinhibition, which would decline rapidly. This scheme glosses over the underlying motivation mechanisms, but is a straightforward way to categorize behaviours.

In the context of the experiments with contrast of colour, a speculative analogy can be made; strong play behaviour occurs when there was a 0/5 minute delay between sessions. When there was a 45 minute delay between sessions, the play is weak. Both were disinhibited by the black toy i.e. this was a strong disinhibitor. Strong play, when disinhibited, leads to a large post-inhibitory rebound. When the weak play was disinhibited by the strong disinhibitor, there was a weaker post-inhibitory rebound, as predicted by Ludlow. In the fur/feathers experiment the fur toy produced strong play, and the feathers elicited weak play. When strong play was disinhibited with a weak disinhibitor, feathers, the disinhibition was small.

Thus these motivational models allow easier division of the play observed in these experiments into external and internal causes. Examination of the behavioural changes described enabled the relationship between the internal factors of fatigue and motivation in the second and third experiments to be explained. Observed behavioural changes are a resultant of these internal factors and the external stimuli of the toy.

5.5: CONCLUSION

The behaviour changes exhibited in these experiments enable an insight into the nature of the internal causal factors involved in motivation of play, and how they combine to determine the motivational state of a cat when it receives an external stimulus to play. This was possible by manipulation and analysis of the external, causal factors which were the toy stimulus, and sensory habituation. It was discovered that the eventual play behaviour observed was a result of the interaction of the initial stimulus value of the toy, sensory factors contributing to habituation to the toy (both constituting external causal factors), and internal habituation and 'central fatigue'. The influence of any one factor was relative to all the others, so that the expression of play represents the additive effects of these factors.

As shown in the third experiment with the fur and feather toys, the play response and level of habituation to a toy are influenced only by the toy immediately preceding it. If there is a contrast between the two, the expression of play remains at a high level. After habituation to an unchanging toy, play can be disinhibited by a change in stimulus. These two findings suggest that the play response could be maintained at a high level indefinitely if the toy stimuli were changed at regular intervals.

Relationship to predatory behaviour

With respect to the possible relationship between the motivational basis of play and predation, these mechanisms involved in the control of play are presumably applicable to predatory behaviour. The basic mechanism in the response to objects (including prey) appears to be to show very brief initial interest, but to undergo rapid habituation to the object almost as soon as it is perceived. This may be analogous to a method of stimulus filtering; any object which has any stimuli which may be associated with prey, such as small size or movement, may elicit a response initially. However, to prevent unnecessary predatory behaviour with an inanimate or unsuitable object, rapid habituation may inhibit further response, thus acting as a filter.

This habituation may occur as a behavioural default; continued play (and predation) are determined by two mechanisms which can be expressed as being similar to innate releasing mechanisms (IRM). An IRM was defined by Tinbergen (1951) as a neurosensory mechanism which defines the selective susceptibility of a response to a particular set of stimuli. The first mechanism appears to be a stimulus quality selection mechanism. Particular stimuli, such as real fur and feathers, delay the usual habituation. The stimuli have qualities (unidentified in this study) to which the stimulus quality IRM is especially sensitive. If an object possesses any of these qualities habituation is stalled until the object has been investigated further.

The second IRM-like mechanism appears to act as a monitor of the objects 'changeability'. This can be explained in terms of predatory behaviour. If a prey animal is unchanging this could be because the cat has been unable to damage and physically alter unsuitable prey. Habituation to this unchanging object prevents the cat from continuing to attempt to hunt an unsuitable prey animal. This would also occur if the prey had already been killed, causing unnecessary predatory behaviour to stop. Conversely, predatory behaviour would not habituate if the prey stimulus constantly changes as a result of physical damage. Predatory behaviour must be continued until the prey animal is dead, so the cat must not habituate to it, or predation would cease and the cat would not kill the prey.

These two mechanisms of selection for stimulus quality and changeability act in parallel. If an object does not have any of the features selected by either of the mechanisms, the cat will habituate rapidly and quickly ignore the object. Possession of any of the selected stimulus features, changeability or both, prevents the usual habituation from occurring and predation continues further. It is possible that inanimate objects possessing some of the selected features (for example small size and movement) can elicit an initial predatory response. However, lack of other selected qualities and of changeability cause habituation to occur shortly so that predation soon ceases. This would explain a cat's brief attempts to hunt small inanimate objects such as a rubber ball, or a falling leaf.

This system of control effectively enables the cat to distinguish between objects which are dead, inanimate or alive, and live animals which are suitable or unsuitable prey items.

That this system can be suggested from a study of object play supports the hypothesis that predation and object play have similar motivation and control.

6

SEQUENCE ANALYSIS

6.1: INTRODUCTION

The analysis of sequences of behaviour patterns is an objective method of determining the frequency with which each behaviour pattern is followed by another (Rasa 1977). It is designed to enable ethologists to determine whether successive behaviour patterns are independent of one another, or whether an animal's choice of behaviour pattern is influenced by the immediately preceding behaviour pattern (Chatfield & Lemon 1970). It is often used as a means of discerning the causation of behaviour.

Relationships between behaviour patterns can either be probabilistic or deterministic. Most behaviour sequences are probabilistic, so that while the performance of pattern B depends upon the previous performance of pattern A, with a definite probability, it is not possible to predict at what point after pattern A, pattern B will occur. In a deterministic relationship pattern B would always be preceded by pattern A (Fagen & Young 1978). However, deterministic sequences are unlikely in animal behaviour, particularly the complex behaviour of vertebrates. The assumption of a probabilistic relationship also allows for fluctuations in motivation to occur during the performance of behaviour. It is also unlikely that anything higher than first order transitions can be examined in a behaviour sequence; because of the probabilistic nature of the relationship between the behaviour patterns, the sample sizes required to calculate higher-order transitions can rarely be achieved in practice. Sequence analysis is aimed at the identification of these first order transitions between pairs of behaviour patterns. The null hypothesis of a first order model assumes that behaviour patterns do not occur with equiprobability, but that they are ordered randomly (Bakeman & Gottman 1986), that is independent of one another.

Sequence analysis enables precise, quantitative description of the relationships and groupings of behaviour patterns, and can be used as a basis for hypotheses concerning causation. This is possible because the temporal association of behaviour patterns may indicate that they share causal factors. However, other potential explanations for the temporal association of behaviour patterns, in the form of constraints of the external environment, must be taken into account (Slater 1973).

According to Slater there are two types of causal factors which may account for the association of behaviour patterns. These are firstly, that the associated behaviour patterns may be affected by a particular internal physiological state; and secondly, that they may be elicited by the same, or related external stimuli. (The interaction of these two types of causal factors has already been examined in detail, in Chapter 5. Sequence analysis cannot be used to differentiate between the two types of causal factors, internal and external).

Significant pairings of behaviour patterns, as defined by the sequence analysis, can be interpreted in two ways. They can be used as a record of 'sequence effects', in which the probabilities of association between behaviour patterns are regarded as the aim of the analysis. This interpretation assumes that the underlying motivation of the behaviour is static, and explains sequences as the being the result of a particular pattern producing a peripheral state which is conducive to the performance of the next (Slater & Ollason 1972). Conversely, the analysis can be interpreted with the aim of clarifying underlying motivation changes which occur throughout performance of the behaviour. This is based upon the assumption that particular behaviour patterns may have a common causation, so that monitoring the behaviour patterns could describe and characterize changes in motivation level. This interpretation pays little attention to sequence effects. It is important to note that both sequence effects and motivation changes will probably account for behaviour pattern transitions, but most sequence analysis is undertaken with one or the other interpretation in mind.

In this chapter the analysis of sequences of behaviour was used in order to elucidate changes in motivation. By studying changes in the organisation of play patterns throughout play bouts and with different toy stimuli, it was hoped that an insight into the motivation of the behaviour would be gained. Thus, hypotheses concerning the causation of behaviour could be posed.

Two papers by Rasa (1977 & 1984) provide an example of the use of sequence analysis in the investigation of the causation of behaviour. Detailed sequence analysis of the behaviour of the African dwarf mongoose was undertaken and described. The 1977 paper described an extensive study of all the major behaviour patterns shown by the mongooses, but in the 1984 paper the aim was to determine whether play behaviour has an underlying motivational structuring which orders its expression.

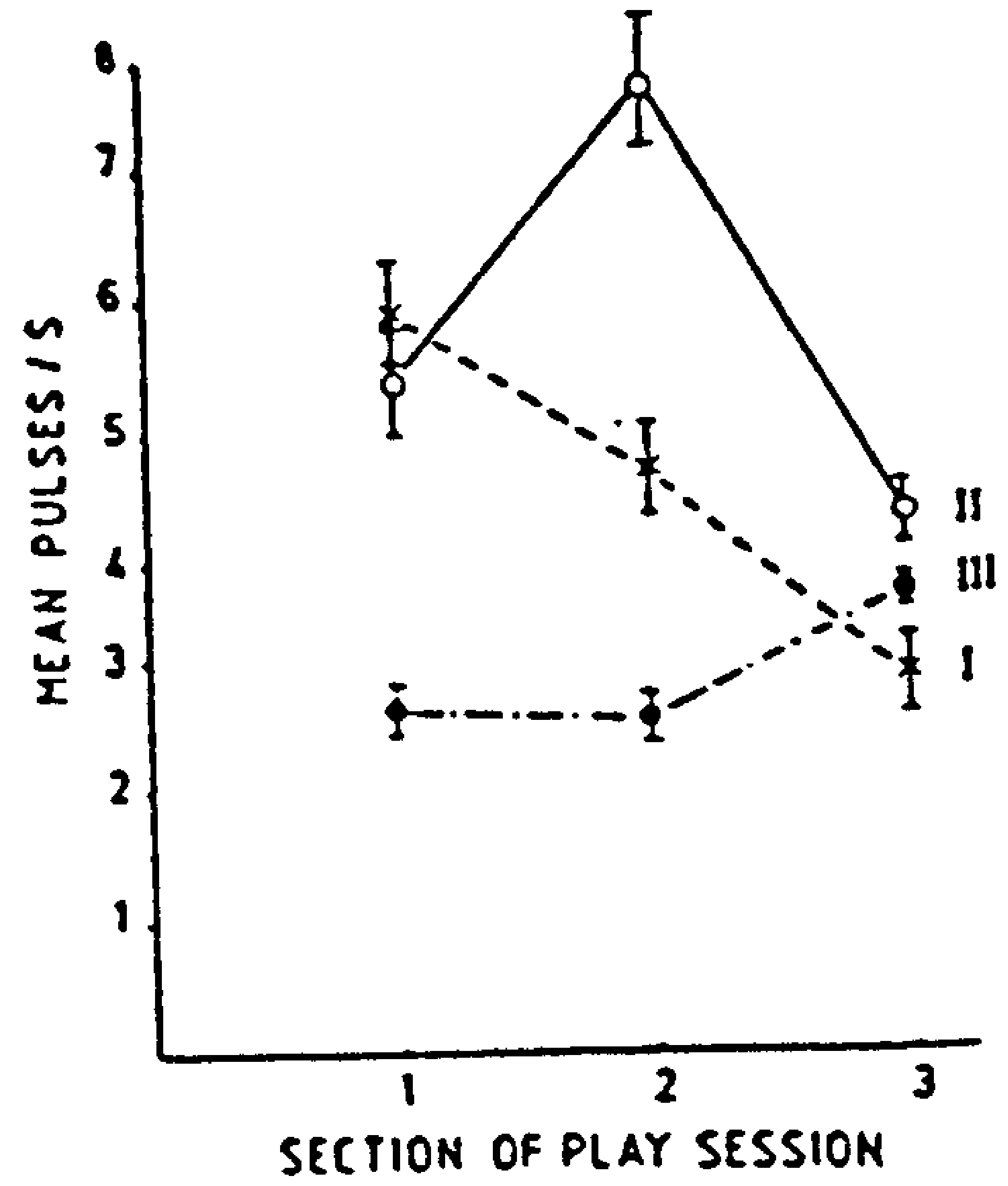
Fortunately for Rasa, mongooses vocalise with high pitch squeaking during play. She found that the repetition rate of squeak pulses was indicative of the animals' motivation intensity, such that a high rate of squeak pulses indicated a high level of motivation and vice versa. Thus Rasa was able to measure the changes in motivation level throughout a play session, by recording the squeak pulse rate while the animal played. From this she discovered three patterns of motivation change characteristic of play (Figure 6.1).

Using this squeak measure, and a sequence analysis, Rasa was able to conclude the following about the nature of mongoose play:

1) Play behaviour patterns appear at particular optimal intensities of motivation. Investigation of the toy, with the first contact (usually sniffing), denoted low intensity. Paw manipulation with one or two paws represented middle intensity of motivation. Finally, biting and close contact with two to four paws was an indication of high motivation intensity.

2) The number of behaviour patterns performed increases with rising motivation intensity.

Figure 6.1. *Three patterns of play motivation in the object play of dwarf mongooses, measured as pulses of vocalisation (Rasa 1984).* In I, motivation decreases throughout the play bout; in II, motivation increases up to a peak in the middle section of the play bout, then decreases; in III, motivation remains stable for the first part of the bout, then increases in the last section.



3) As the play session draws to a close, play bouts become shorter and more frequent, while pauses between play bouts become steadily longer and more frequent before play stops altogether. Thus play becomes more fragmented as it approaches termination.

4) All play sessions end at a 'set point'. The three patterns of motivation change that Rasa found all ended at this same level (Figure 6.1). This point appeared to occur when play motivation had reached a particular low level as indicated by a low frequency of squeaks.

Rasa used these findings to make several hypotheses about the causation of play. She suggested that there was no consummatory end pattern, but that a 'set point' of motivation filled this role of terminating the play bout. Since it seemed to be that a particular set point of motivation determined play bout length, she proposed that there was a mechanism of 'balancing an internal state' in the control of play performance.

According to Fagen and Young (1978), some types of behaviour may tend to terminate independently of the time at which their performance began (for example, distress calling of young animals, which stops when the mother returns, or when the animal is too fatigued to continue). This type of behaviour contrasts with those which depend upon an increasing probability of termination as performance time increases. The latter type is characterised by behaviour patterns which cease to be expressed when a consummatory outcome is reached, at a particular time after beginning the behaviour. Play, however, appears to match the former description. If a behaviour can terminate at any point this suggests that there may be a behaviour pattern which causes termination, and that this pattern may occur with equal probability at any point during the behaviour performance. In play, according to Rasa, the suggested motivation 'set point' may act in lieu of a terminating behaviour pattern.

These analyses and hypotheses described by Rasa exemplify the use of sequence analysis for investigating motivation.

Choice of Methodology

MatMan (Matrix Manipulation and Analysis) version 2.4 was used to carry out all sequence analysis in this study (de Vries et al 1993). The MatMan programme is used for the analysis of frequency matrices and behavioural transition matrices. Of interest in this case are the transition matrix options, which enable the data to be presented as the frequencies with which preceding behaviours are followed by succeeding behaviours (see Chapter 2). Behaviour pattern transitions which have adjusted residuals (z values) significant at $p<0.001$ are noted in order to determine commonly occurring first order transitions between pairs of behaviour patterns.

Figure 6.2 presents an example of a transition matrix generated in MatMan.

Some transitions can occur in both directions, so that pattern A precedes pattern B, and B can also precede A. If the row and column totals of two patterns in the transition matrix are the same, this indicates that the transition between the two is equally likely to occur in either direction. It is also possible to detect asymmetry in reversible transitions. If the row and column totals are unequal the transition is most likely to occur in the direction which has the highest value. It is possible to determine in which direction any reversible transitions occur most frequently, A-B or B-A, by testing the frequencies of both with a Wilcoxon matched-pairs test (Slater & Ollason 1972). However, I did not carry out this analysis here.

Some of the behaviour pattern transition z-values represent repetition of one pattern. These occur in the diagonal of the matrix (Figure 6.2). It is possible to exclude the diagonal values from the analysis if repetition of behaviour patterns is not allowed in a particular behaviour. There are several reasons for excluding the repetition of behaviour patterns (auto-transitions). Firstly, depending on the criterion used to define them, auto-transition frequencies may be artificially inflated (Slater 1973). It is preferable to avoid arbitrary criteria when defining

Figure 6.2. *An example of a transition matrix generated by the MatMan programme.* Behaviour pattern codes on the left precede those across the top. Transitions with z-values >330 are significant at $p<0.001$. For example the transition from **sv** to **st** has a z-value of 627, indicating that this transition is significant at $p<0.001$, and so is very likely to occur. Transitions which have a negative z-value are less likely to occur, for example **st** to **tt** has a z-value of -106, indicating that it is unlikely to occur. Behaviour pattern codes are defined on p102.

	wawt	**waav**	**siwt**	**siav**	**crwt**	**crav**	**stwt**	**stav**	**crgo**
wawt	-52	-22	58	-11	235	-42	631	-37	-11
waav	-19	-8	344	-4	-24	-15	362	748	-4
siwt	-75	-32	-111	627	-98	-60	-106	-53	-16
siav	-11	-5	627	-2	-14	-9	-15	-8	-2
crwt	-66	-28	12	-14	-85	144	-92	-46	-14
crav	-31	-13	-45	-7	2009	-24	-42	-22	-7
stwt	385	-29	420	-14	145	-54	-96	378	-14
stav	678	-12	-42	-6	-37	-23	1230	-20	-6
crgo	-11	-5	-16	-2	-14	1160	-15	-8	-2

The p values for each of the transition pairs in this matrix are shown below, where * represents $p<0.05$, ** represents $p<0.01$ and *** represents $p<0.001$. NS represents transition pairs which are not significant.

	wawt	**waav**	**siwt**	**siav**	**crwt**	**crav**	**stwt**	**stav**	**crgo**
wawt	NS	NS	NS	NS	*	NS	***	NS	NS
waav	NS	NS	***	NS	NS	NS	***	***	NS
siwt	NS	NS	NS	***	NS	NS	NS	NS	NS
siav	NS	NS	***	NS	NS	NS	NS	NS	NS
crwt	NS	NS	NS	NS	NS	NS	NS	NS	NS
crav	NS	NS	NS	NS	***	NS	NS	NS	NS
stwt	***	NS	***	NS	NS	NS	NS	***	NS
stav	***	NS	NS	NS	NS	NS	***	NS	NS
crgo	NS	NS	NS	NS	NS	***	NS	NS	NS

behaviour patterns and the end of their performance. This may lead to erroneous measurement of frequencies of repeated behaviour patterns. It may be difficult to determine whether a repeated pattern is not just the continued performance of one pattern, and so should be noted as occurring once. Secondly, inclusion of auto-transitions may cause the matrix to be predisposed to only showing that certain patterns occur in repeated bouts. This may hide other, more interesting transitions. This occurs because the existence of high positive values in the diagonal of the matrix leads to an increase in negative values elsewhere in the matrix (Slater & Ollason 1972).

However, in play behaviour repetition of behaviour patterns is a prominent feature and may be important as an indicator of motivation. Therefore, the diagonals were maintained in the sequence analysis.

Once the significant behaviour transitions have been found a kinematic diagram can be created to illustrate them. A kinematic diagram is a simple flow diagram, which enables easy visualisation of sequences (see Chapter 2). The kinematic diagrams were used in the analysis described here as a method of grouping behaviour patterns into those which often occurred together, and to discern the following about the structure of play behaviour patterns:

1) Do particular behaviour patterns or behaviour pattern transitions typically occur at different levels of play motivation?

2) Are there particular behaviour patterns or behaviour pattern transitions which mark the termination of a play bout?

3) Are there any behaviour patterns or behaviour pattern transitions which act as turning points in play? These may be imagined to occur at the extremes of a particular level of play motivation. Their performance may lead to the performance of a behaviour pattern characteristic of a higher level of motivation, or motivation may remain at the same level.

6.2: METHOD

Based on Rasa's concepts, a sequence analysis of samples of cat play was undertaken with the aim of gaining similar information about the underlying motivation.

The object of this analysis was to look for significant temporal pairings of behaviour patterns, and, by building them into sequences, to find out if the occurrence of particular behaviour patterns or sequences of patterns may indicate motivation intensity. As mentioned above, Rasa found that the sequence structure of play changed in character as play progressed and as the motivation intensity changed. Changes in motivation could be predicted by changes in the character of play sequences. This may also be possible with domestic cat play.

Subjects and Toys

To collect data, nine cats were given one of the four most effective toys on four consecutive days, so that each cat had a different toy each day. (The data collected for each toy was massed for the analysis, thus the analysis reflects the behaviour of these specific cats, not cats in general). The four toys which elicited play most effectively were identified from the series of experiments described in Chapter 3. They were fakefur with legs, feathers, fakefur and real fur. Each cat was filmed playing with the toy until it stopped playing of its own accord, and ignored the toy. The filming was stopped when the cat had failed to contact the toy for 20 seconds. It can be difficult to determine whether an interval in behaviour performance represents an inter-bout or intra-bout pause, and it is usually necessary to define an arbitrary cut-off point. Twenty seconds seemed to be a long enough time interval to ensure that the play bout had actually finished. Cats which had not played with a toy for 20 seconds rarely started to play again after this interval. Data which had been collected in previous experiments in which cats were presented with the same toys (see the texture experiment in Chapter 3) using a similar protocol, was also used. This included data from six cats from the University colony (some of the same cats were used, also other cats which were not used in the previous experiments), 12 cats at WCPN, and 12 pet cats. A further three sessions per cat with the fur toy were recorded with the University cats. This data was combined with fur data from the first 4 days of filming and used to calculate probabilities for the transitions in different parts of the play session (Figures 6.8 & 6.9).

Data from the experiment to determine the effect of hunger on play (described in Chapter 4) were also used. In this experiment cats played with small and medium sized fakefur toys at three different hunger levels, measured as hours since the last meal. The levels were 0 hours, 5 hours and 16 hours. Data from the sessions with the small toy at 0 hours and 16 hours of hunger were analysed.

Sample sizes

Sequence analysis requires the collection of as large amount of data as possible. This is because to use the Chi-squared test it is necessary for the expected values to be over a certain minimum; according to Fagen & Young (1978), the minimum number of behaviour patterns required is $5R^2$, where R is the number of behaviour patterns in the repertoire. They suggest that $10R^2$ is a sufficient number of behaviour patterns. A small sample size would lead to a negative bias in the transition matrix. For this analysis the requirement for a repertoire of 25 behaviour patterns was 10 x 25 x 25 = 6250 patterns. In all the matrices discussed in this chapter the number of patterns varied from 768 to 11844 for the four toy types and the two levels of hunger. A smaller number of patterns than Fagen's suggested number, however, does not invalidate the use of sequence analysis, particularly for the purpose of this chapter, which is to enable simple description and visual comparison of play sequence structure with various toys. (The number of transitions which occurred in each matrix - including those which were not significant - is shown in Figures 6.3-6.12).

Data Analysis

Data collected from video with the Observer (version 3) was exported into MatMan (version 2.4). Sequence analysis was carried out on a number of data sets, so that the resulting kinematic diagrams could be compared. Play (from the four days of filming) with real fur was compared with play with fakefur with legs, feathers and fakefur. They were also compared with a sequence analysis of data from former experiments for a polythene covered toy. Polythene was found to elicit less play than other toys in Chapter 3.

The real fur data were used twice; once for the comparison of play with different toys (one session per cat), and again in the comparison of play in different parts of the play session (seven sessions per cat). In the latter, the shortest real fur play session was divided into thirds (giving 55 behaviour patterns each). The last 55 behaviour patterns and the penultimate 55 patterns were accordingly separated from all the other sessions with real fur. Analysis of these two parts of the play sessions enabled comparison of behaviour pattern transitions in the middle section of play, when motivation would be expected to be at its highest level, with those at the end of play sessions, when motivation would be expected to be dwindling.

Kinematic diagrams were used as a method of grouping behaviour patterns into those which often occurred together, and to discern trends in the structure of play behaviour. These diagrams cannot be compared statistically. Differences noted are merely those which appear from inspection of the diagrams (Figures 6.3 to 6.12). However, the transitions shown in the diagrams all occurred with a frequency which was statistically greater than if the behaviour patterns were performed independently of one another, so simple visual comparison has some validity. However, it must be expected that the number of significant transitions will increase as the total number of transitions analysed increases.

By examining the eight kinematic diagrams built up from all the sequence analyses, it was hoped that further qualitative differences between an intensive play response and a less intensive play response would be revealed. By doing this it may be possible to relate changes in play sequence characteristics to differences in external stimuli and to different levels of underlying motivation.

The data collected from the fur toy, the data collected when the cats were sixteen hours hungry, and the that from the middle of play sessions, would be expected to represent intensive play. Conversely, at a low level of hunger, with toys which were known to elicit only a weak response, and with data from the end of a play session, the play response would be expected to be less intensive. It was expected that the kinematic diagrams would reflect this difference.

6.3: RESULTS

Kinematic diagrams were drawn to enable a simple description of the sequences of play behaviour. A group of behaviour patterns which appeared to form the basic structure of play behaviour was determined, including 'hit', 'rear', 'grasp', clutch' and 'killbite'. These patterns appeared in a similar sequence in play with all toys, in all parts of the play session and at both levels of hunger. This basic structure could be split into four levels, shown in Figure 6.13, which seemed to correspond to the cats' play motivation level. This division of the play sequences and motivation was speculative, but it provided me with a convenient framework with which to describe the comparison of the different toy stimuli.

Separating the behaviours into levels enabled easy visualisation of the progression of the sequence of behaviours, and enabled the establishment of a basic structure of play. Within each level the transition pairs of patterns were mostly identical for every toy, and each level featured the same transition pairs. Some transitions appeared to be fixed in the play response at a particular level of motivation, and always occurred, in the same or similar order.

Between the levels in this basic sequence 'clutch' appeared to be an important determinant of

Figure 6.3 Kinematic diagram of behaviour pattern transitions with the fakefur with legs toy, (1087 transitions were analysed). The + and - signs indicate the start and finish of the play patterns with a finite duration i.e. 'clutch' and 'holdmouth'. Arrows indicate transitions significant at p<0.001.

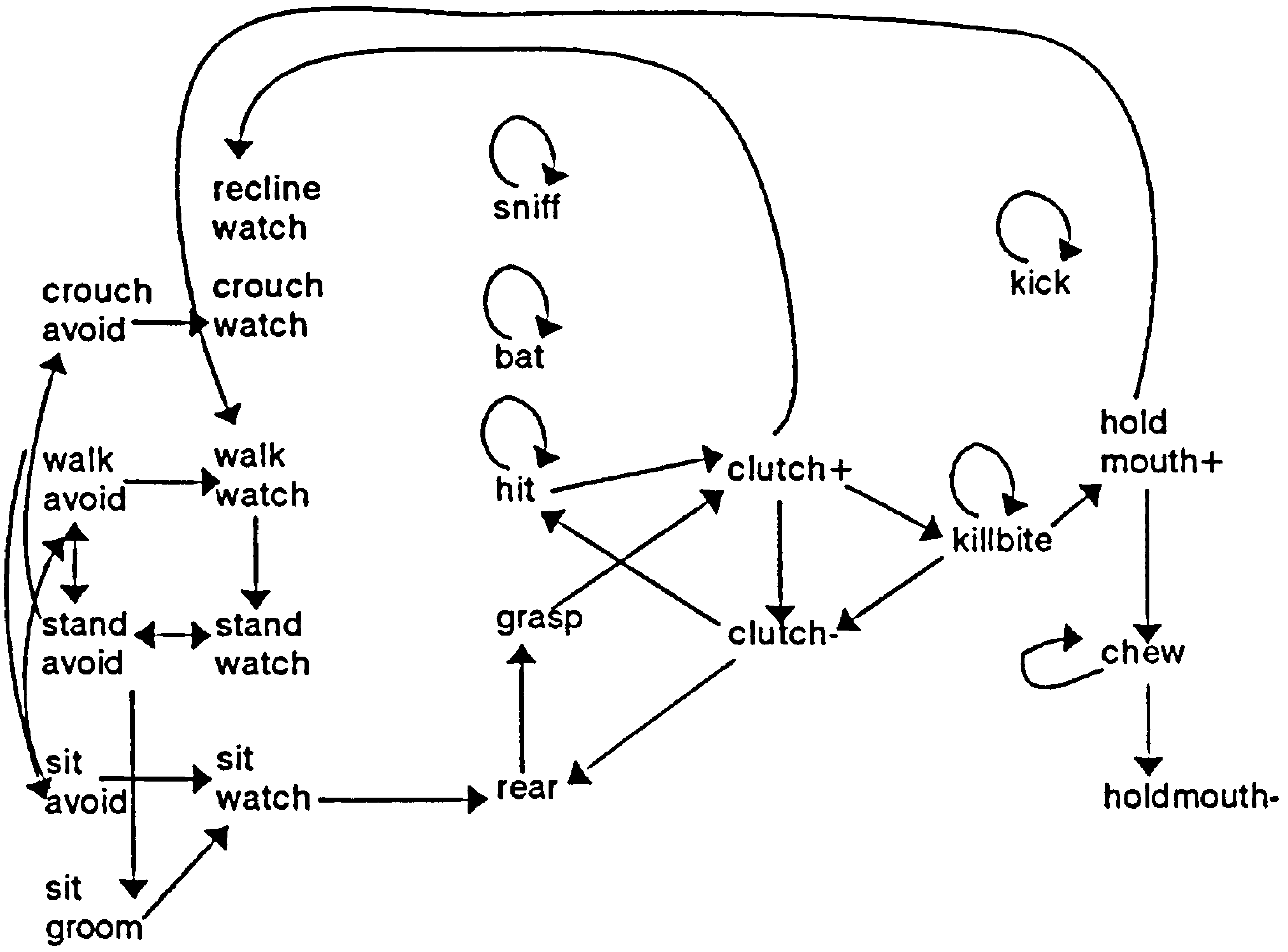


Figure 6.4 Kinematic diagram of behaviour pattern transitions with the feathered toy, (1012 transitions were analysed). Other details are as in Figure 6.3.

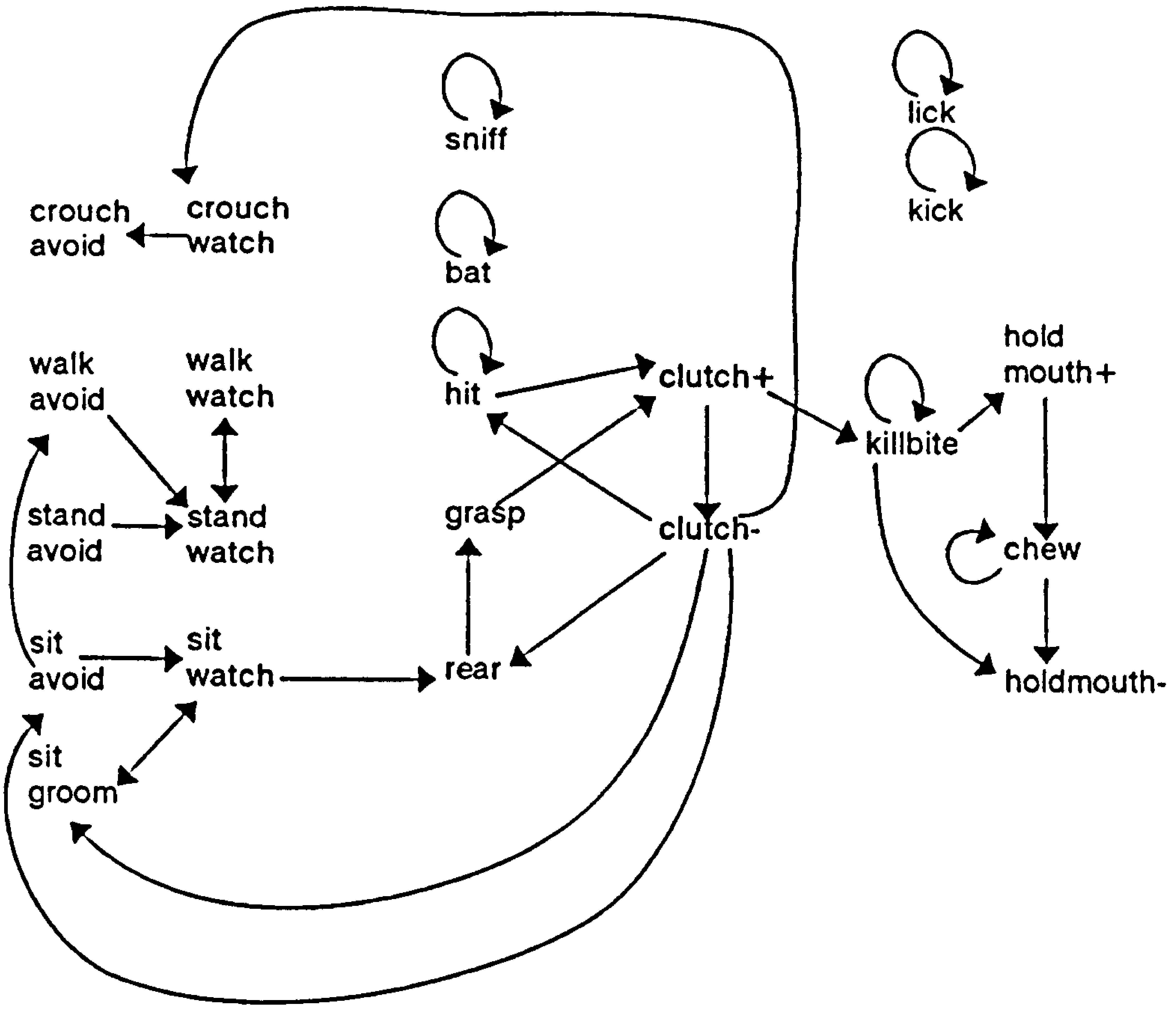


Figure 6.5 Kinematic diagram of transitions with fakefur, (768 transitions were analysed). Other details are as in Figure 6.3.

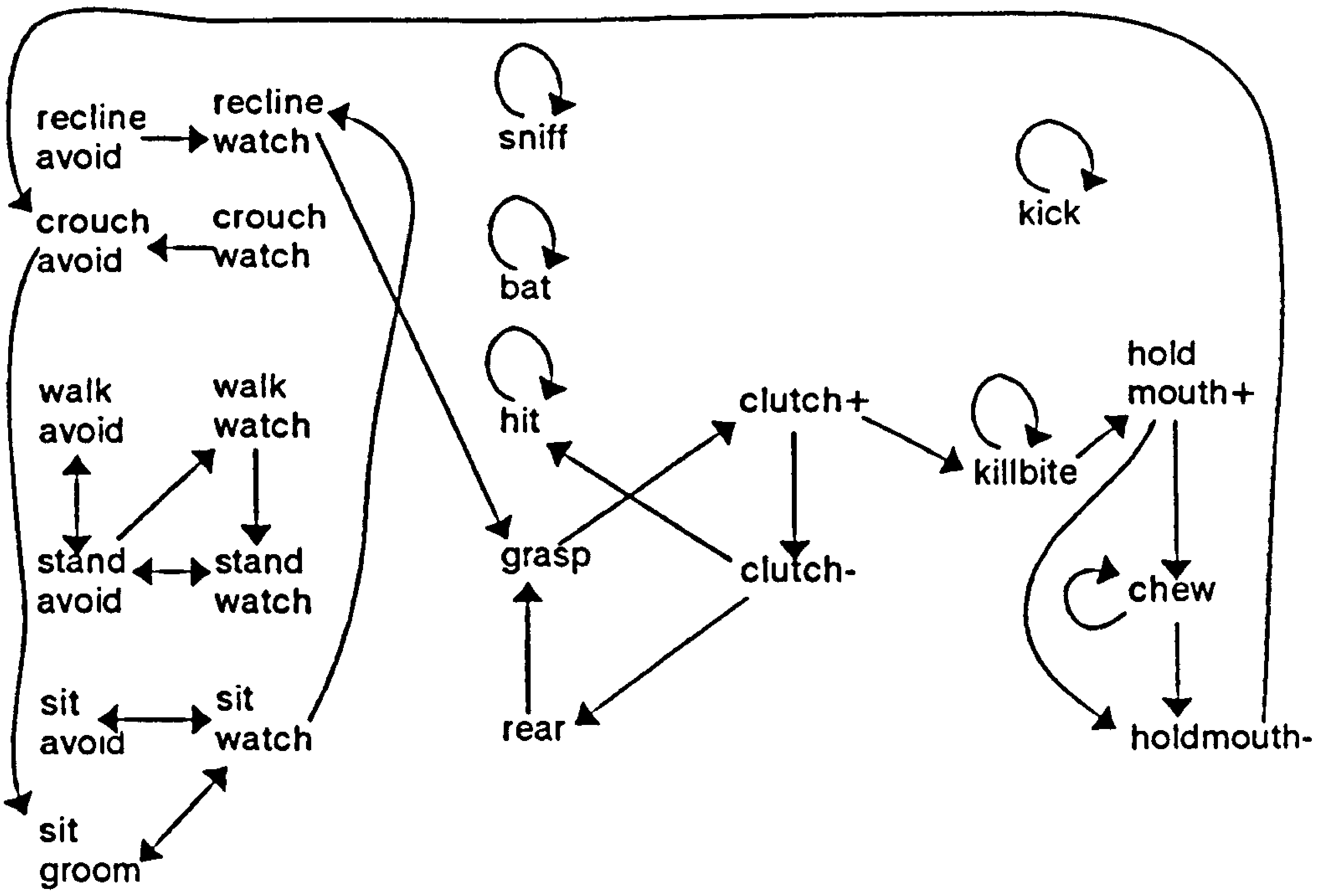


Figure 6.6 Kinematic diagram of behaviour pattern transitions with the real fur toy, (4048 transitions were analysed). Other details as in Figure 6.3.

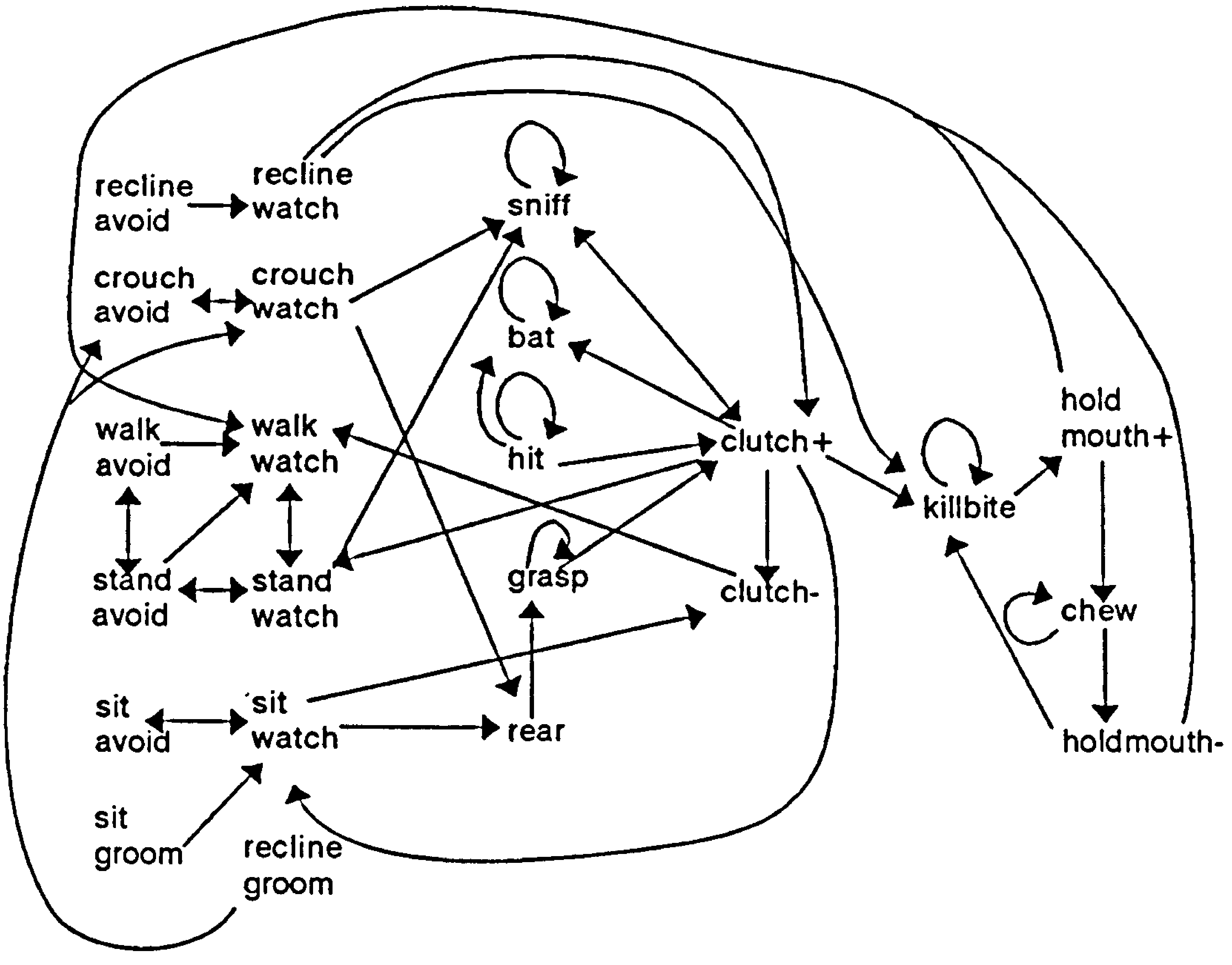
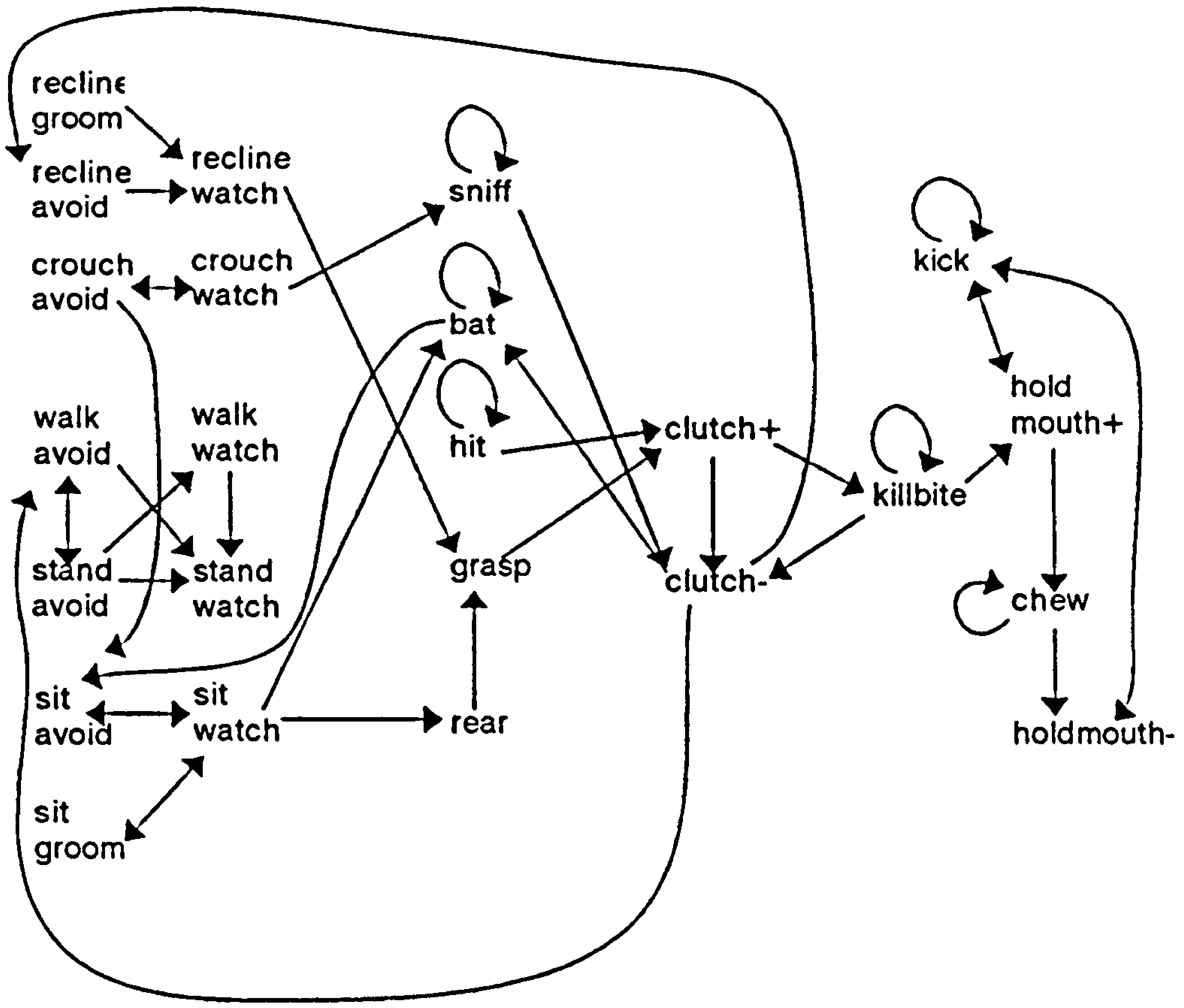


Figure 6.7 Kinematic diagram of transitions with the polythene toy, (1352 transitions were analysed). Other details as in Figure 6.3.



the character of each play bout. From 'clutch' the cat either released the toy and started again with initial, low level patterns, such as 'bat' and 'hit', or continued to escalate to higher level, close contact patterns, such as 'killbite','kick' and 'chew'.

Visual comparison of the diagrams revealed the following trends as characteristics of intensive play behaviour sequences, seen with the real fur toy (Figure 6.6), with the penultimate 55 patterns of play with real fur (Figure 6.8), and at sixteen hours of hunger (Figure 6.10):

1) A high level of general activity, with increased general movement around the experiment room.

2) Greater activity while playing, shown by high frequencies of play patterns and also numerous transitions from play patterns to a change in locomotion patterns and back to play patterns.

3) Increased repetition of small sequences of play patterns, so that a play bout was more likely to continue for a longer time.

4) Increased repetition of individual patterns, although repetition of individual patterns always occurs in play behaviour.

5) Increased elaboration from the central, basic structure of play shown in Figure 6.13.

6) Rapid and more frequent movement from low to high levels, and vice versa.

Trends which could be seen in the diagram's where less play had taken place, for example, at 0 hours of hunger (Figure 6.11), the fakefur with legs toy (Figure 6.3) and the fakefur toy (Figure 6.5) were as follows:

Figure 6.8. Kinematic diagram of the transitions during the penultimate 55 patterns with real fur,a subset of the transitions presented in Figure 6.1.2 (1984 transitions were analysed). Some transitions cannot occur, for example, it is impossible for 'recline groom' to precede 'rear', and play patterns cannot follow 'avoid' patterns, only 'watch' patterns. Other details as Figure 6.3.

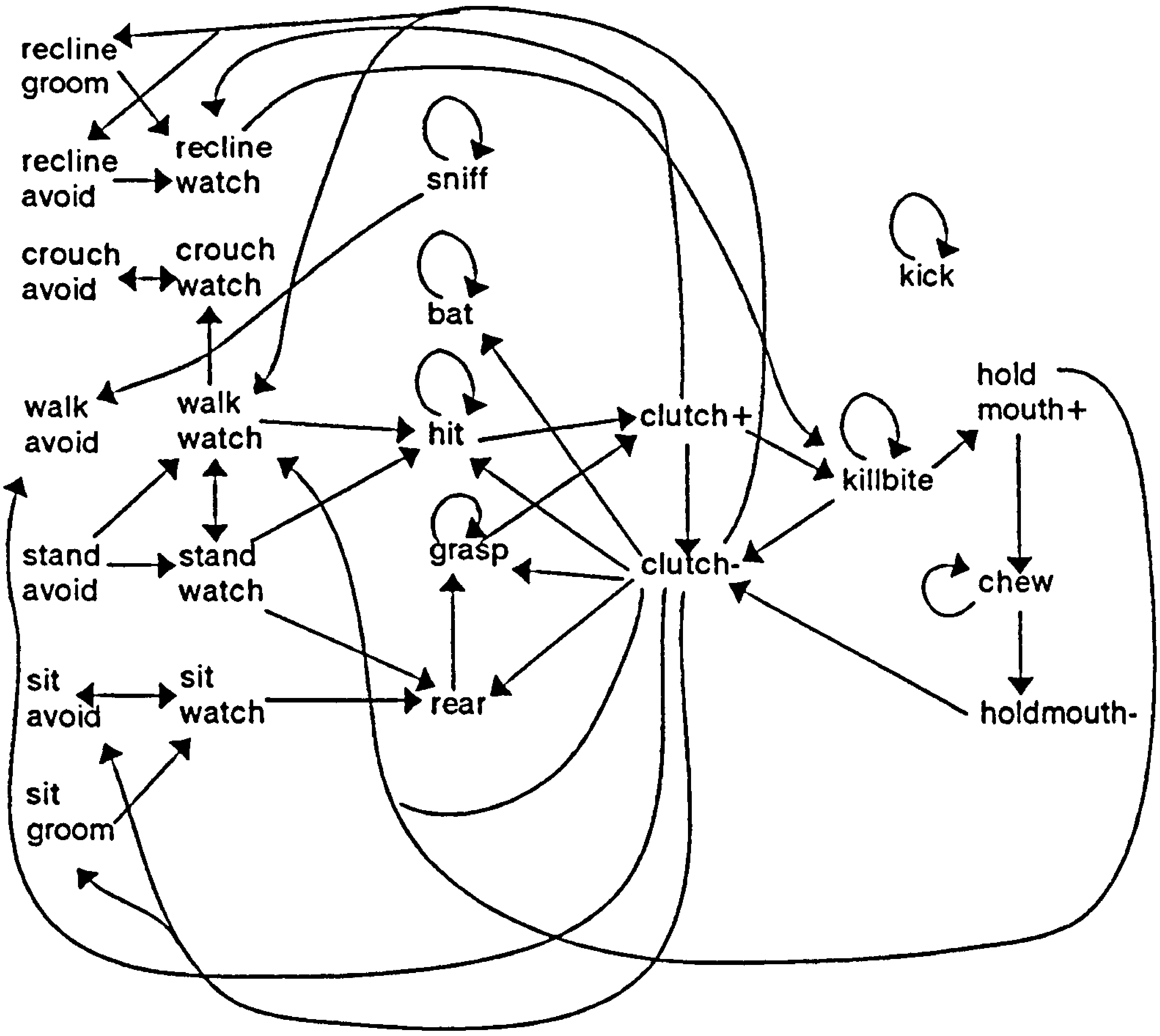


Figure 6.9 Kinematic diagram of the transitions during the last 55 patterns with real fur, a subset of the transitions in Figure 6.12 (1918 transitions were analysed). As in Figure 6.8 there are some transitions which cannot occur. Other details as Figure 6.3.

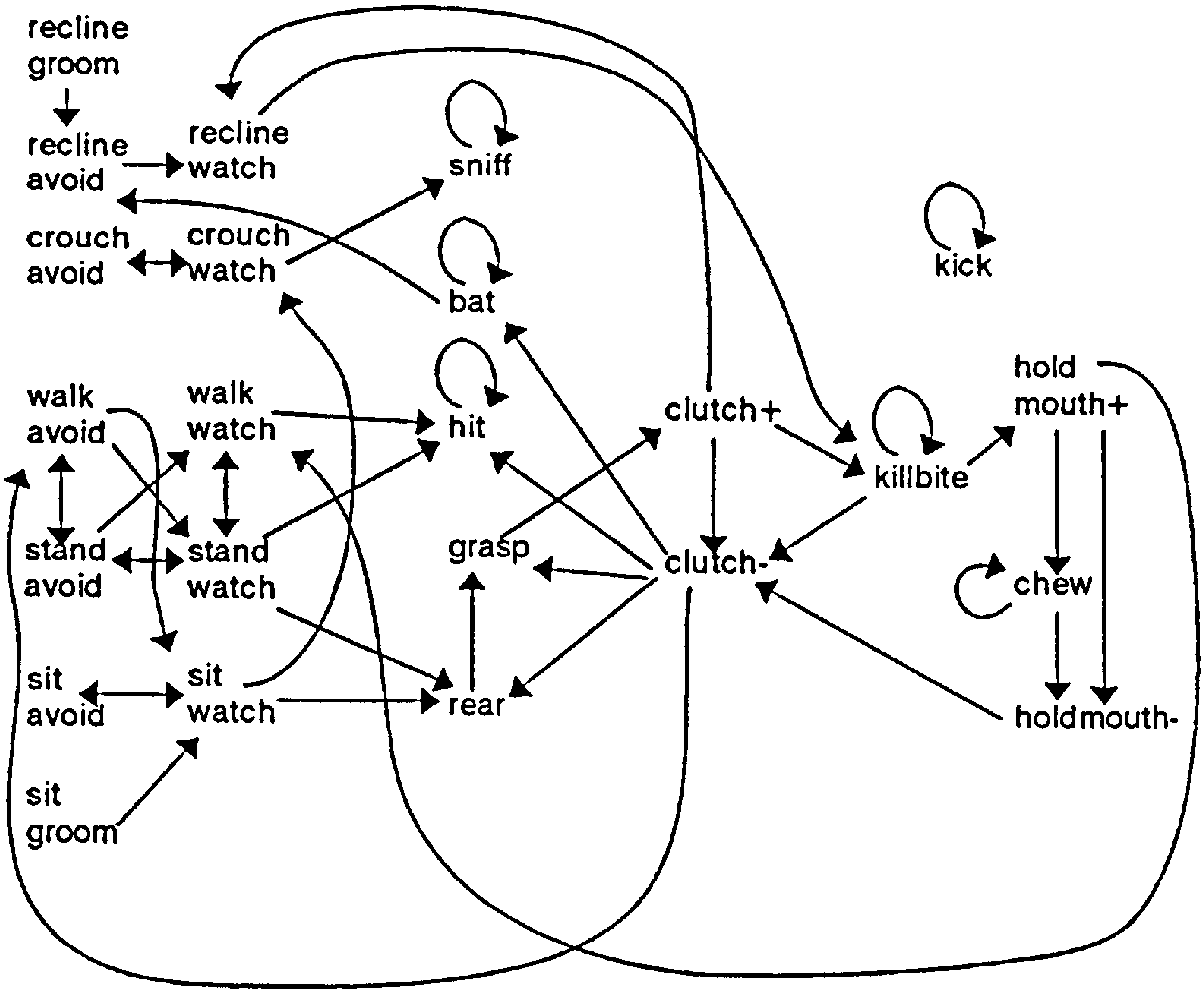


Figure 6.10 Kinematic diagram of transitions after sixteen hours of hunger, (1109 transitions were analysed). Other details as Figure 6.3.

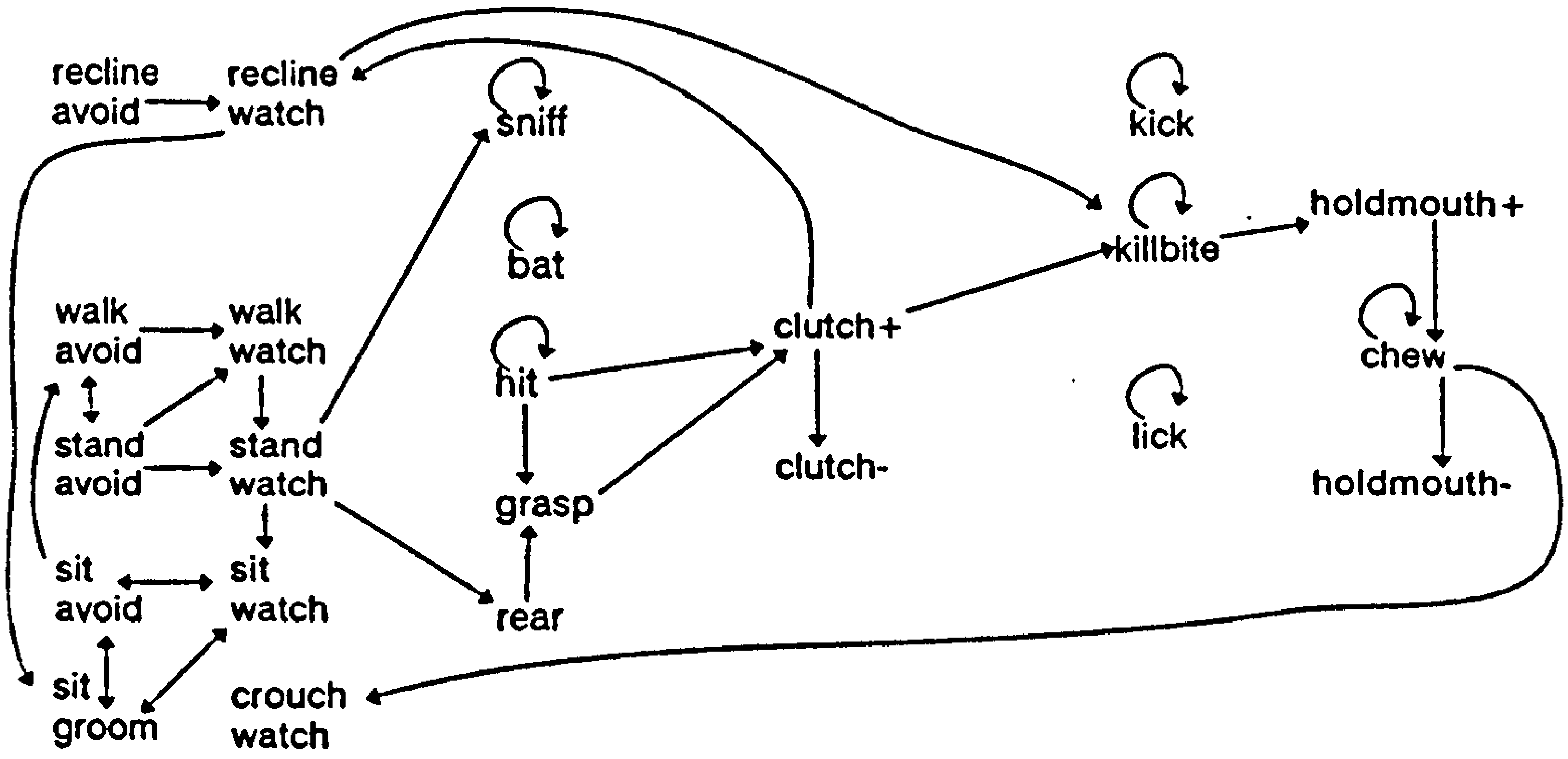


Figure 6.11 Kinematic diagram of transitions after zero hours of hunger, (1161 transitions were analysed). Other details as in Figure 6.3.

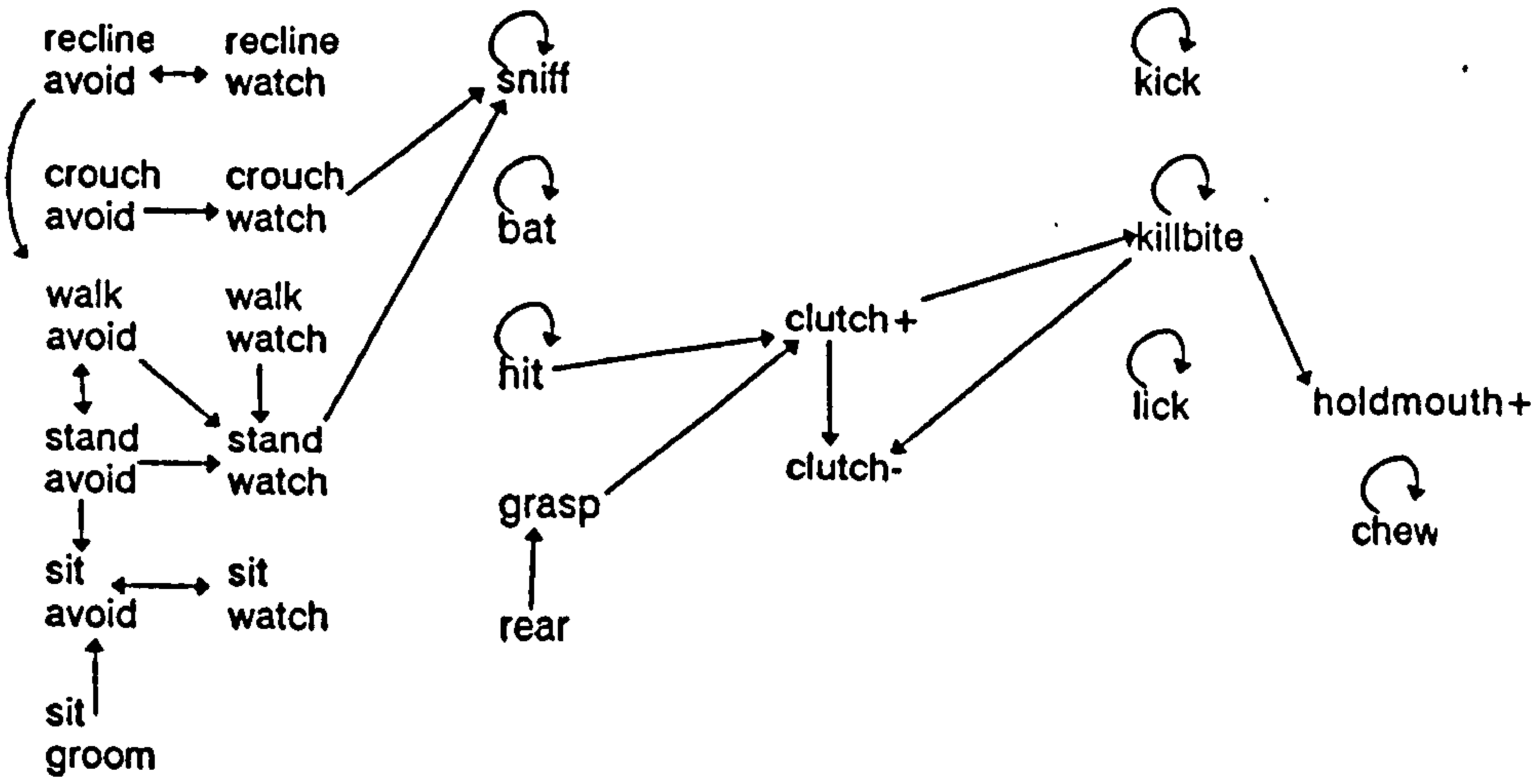


Figure 6.12 Kinematic diagram showing the probabilities (%) of row-wise transitions with the real fur toy, when a larger sample, of 16 cats, was used. Any transitions with no label have a probability of <10%. Where the transition is reversible probabilities are given for the left-to-right or above-to-below transitions.(11844 transitions were analysed). Other details as in Figure 6.3. Since there is a larger number of transitions, this diagram is not directly comparable with the others, and is included for the purposes of illustration only.

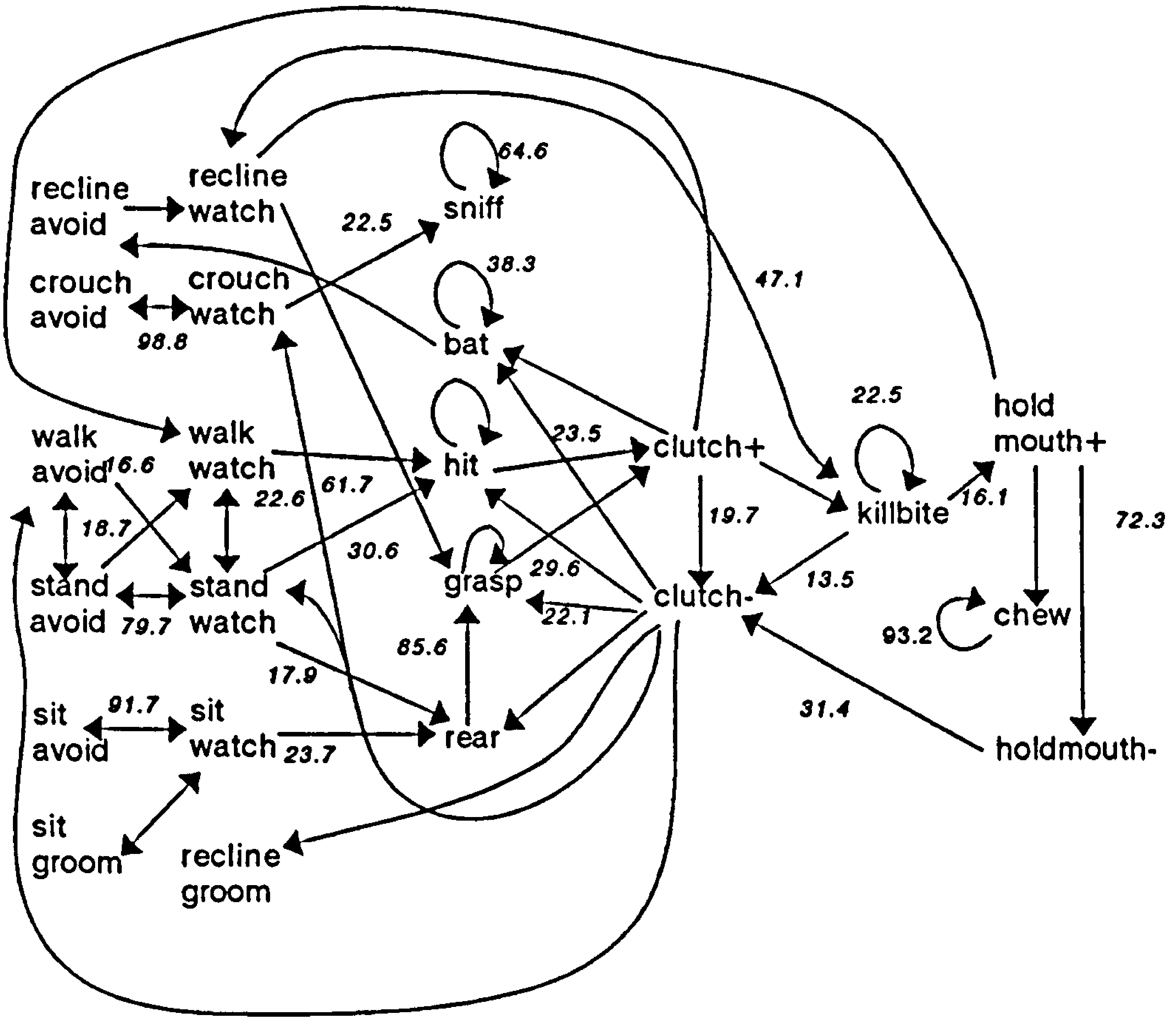
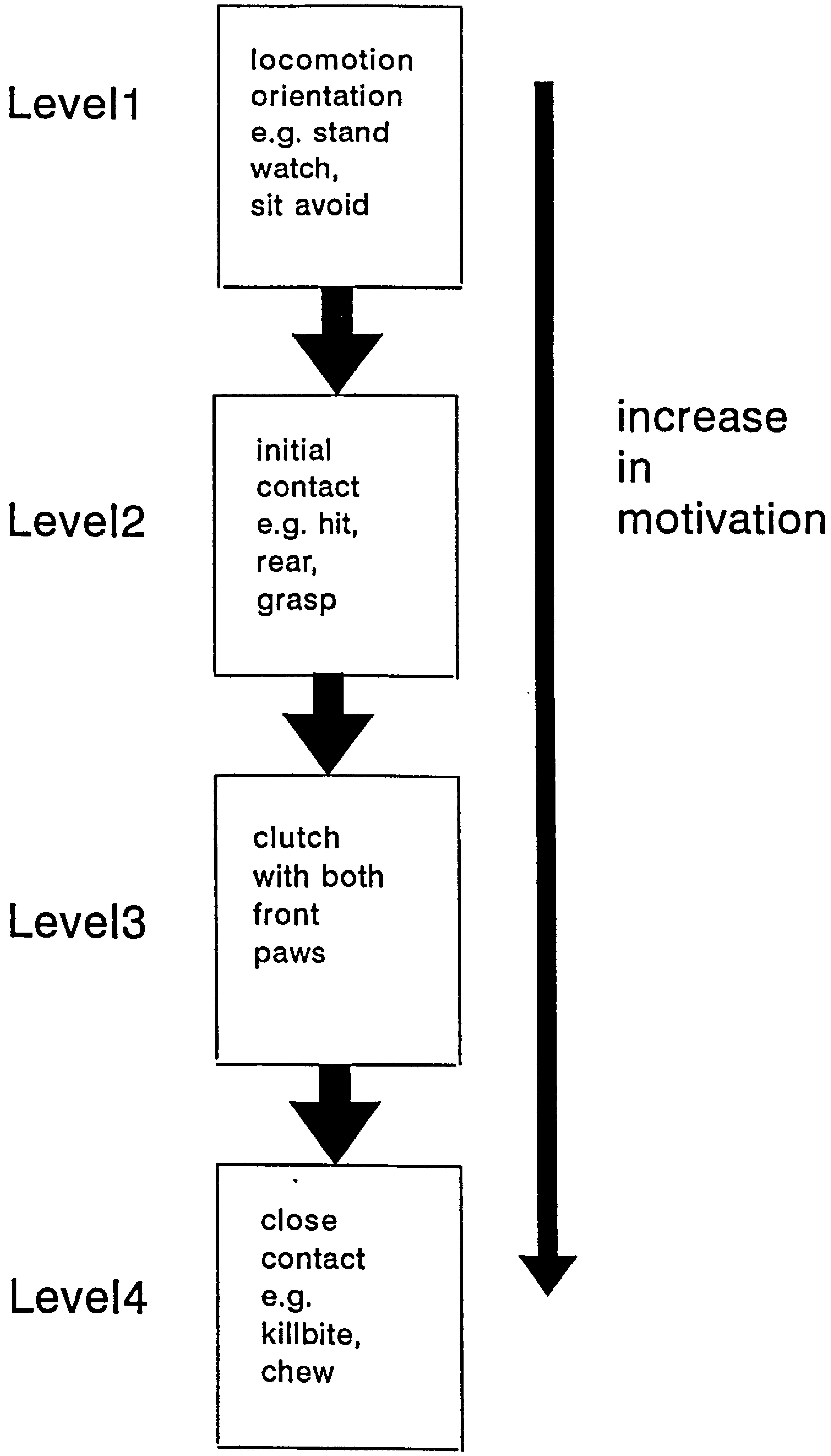


Figure 6.13. The suggested division of play behaviour into four levels corresponding to changes in motivation. Motivation increases from low level 1 to high level 4.



1) Greatly reduced elaboration upon the basic pattern, and less general activity.

2) Fewer transitions from the first level patterns up to higher level patterns. Escalation of play to involve close contact patterns occurred less frequently.

3) Less repetition of small sequences of play patterns, so that an individual play bout was often short.

4) Slightly less repetition of individual components.

Figure 6.12 shows the probabilities of significant transitions for the second analysis of four sessions per cat with real fur. This information is an accurate measure of how often the significant transitions actually occur. For example, repetition of patterns occurs frequently ('chew', 'sniff' and 'killbite' in Figure 6.12). When sequence analysis is used to provide information more important than simple description, these probabilities are of great importance.

6.4: DISCUSSION

There seemed to be a fairly predictable, basic play pattern, which appears to become more elaborated as the toy is more stimulating and the play response become more intensive. It was clear from the comparison of kinematic diagrams that a toy with which a cat was more playful caused a change in the quality of play. An unstimulating toy lead to a play sequence which deviated less from the basic pattern than a stimulating toy, and was generally less elaborate and more predictable. There was also an increase in general activity during the play session when the toy was stimulating.

The temporal proximity of behaviour patterns was held to indicate similarity in causation and in underlying motivation level. On this assumption the whole play response was divided into behaviour pattern transitions which characterised four different levels of motivation. The toys which elicited more play caused a higher level of motivation to be reached, and this was indicated by more frequent performance of behaviour patterns from the higher levels. Typically, behaviour patterns which indicated high motivation were those of close contact with the toy, such as biting and chewing. These behaviour patterns comprise level four in Figure 6.13. At lower levels of motivation, patterns with less close contact occurred, such as sniffing and batting. These behaviour patterns comprise level two in the diagram. There were also differences such as repetition of individual patterns and short sequences, and general elaboration of the basic response which indicated differences in motivation to play. Increasing elaboration and repetition, especially at level four, indicated high motivation and intensive play with an exciting toy. Less exciting toys were less likely to elicit a high frequency of level four patterns, less likely to elicit repetition of these patterns, and more likely to show behaviour patterns associated with lower levels of motivation.

Thus the kinematic diagrams indicated that play expression is more intense with toys of high sensory value. They also indicated that play quality altered throughout the play session. Compared with the penultimate third of the play session, the last third showed reductions in repetition and elaboration which may be consistent with the expected reduction in motivation to play as the cat is on the point of ending the play session.

The low motivation pattern of the last 55 behaviours of a play session led to a kinematic diagram with characteristics similar to those of the toys which elicit less, low intensity play than the fur toy. This strengthens the idea that low motivation causes little elaboration from a basic response. Increased motivation to play leads to elaboration upon this response, which was still visible, but was overlain by a greater complexity of transitions, so that any behaviour component could be followed by one of a variety of patterns, rather than always being followed by the same pattern, as in the basic response. This mechanism would allow for the development of individual idiosyncrasies in play style from the basic response, so that one cat may be more likely to show certain transitions rather than others.

The behaviour pattern which appeared to be most likely to indicate consummation and mark the end of the play session was 'clutch-'. As stated before, 'clutch' (+ and -) appeared to be important in determining the character of the sequence. From this pattern, the cat would either continue to attack the toy with level four close contact biting and kicking, or would drop back to lower, level two initial play behaviours. When a play sequence ended the last pattern to have occurred was often 'clutch-'.

It appeared that an exciting toy, such as real fur, and corresponding high motivation were necessary before the play response would continue beyond 'clutch+' to a pattern other than 'clutch-'.

6.5: CONCLUSION

It must be stressed that the use of sequence analysis was not of primary analytical importance to the aims of this study. This accounts for the brevity of the sequence analysis and for a certain lack of rigour in its undertaking. The sequence analysis was undertaken merely as a tool to enable visualisation of the play response with a number of toys. Rigorous analysis of the causation and motivation of play was carried out with different techniques described in the rest of this thesis. It is important to note that there were several flaws in this sequence analysis, which may preclude its validity.

Some potential errors concern methodology; several authors (for example, Slater & Ollason 1972) have suggested that massed data from many individuals should not be used for sequence analysis, since the existence of 'aberrant' individuals may alter the data, rendering the analysis unsuitable as a guide to population trends. However, it is difficult to accumulate so much data without massing data from many individuals. This is noted as only a minor problem by most authors, and an observer who is familiar with the varying behaviour traits of individuals within the sample can easily recognise results which stem from the strange behaviour of a particular individual.

Secondly most authors exclude auto-transitions from sequence analysis for the reasons already stated.

Finally there is a threat in sequence analysis of what Bakeman & Gottman (1986) termed a 'type 1 error', in which it is possible to claim more significantly occurring sequences than there actually are in a behaviour by over definition of behavioural patterns. As stated by Cane (1978),

'As ethologists improve the fineness of their discrimination the chance of summarizing their observations seems to become less and less'

A sequence analysis alone may be insufficient basis for hypotheses concerning the structure and causation of behaviour. There are a number of ways in which the analysis can be augmented.

Transitional probabilities can be calculated from the matrix of pattern frequencies and presented graphically in the form of state transition diagrams. These are the same as kinematic diagrams, but also include the probability of each transition occurring. Thus, significantly occurring transitions are shown along with information about how often they occur.

Sequence analysis enables the determination of first order transitions, that is transitions between two behaviour patterns. Having established these it would be useful to conduct an analysis which would detect any higher order dependencies in complex behavioural responses. As mentioned previously, this may be difficult as a result of the probabilistic relationship between patterns

Finally, Leonard (1984) has pointed out that a proper analysis of the sequence of behaviour should include temporal relationships between events, and should not just be a 'sequence record' of the pattern order. It is important to consider time in a sequence analysis, because without knowing the temporal relationships between patterns, establishment of a causal context for the performance of a behaviour is less accurate.

However, despite these criticisms and the possible incompleteness of the analysis, its use was successful in the aim of finding a method of visualising the play response and the relationship between behaviour pattern transitions and the underlying motivation.

7

MODIFICATION OF PLAY BEHAVIOUR WITH RESPONSE-REINFORCEMENT AND THE SOCIAL TRANSMISSION OF PLAY

7.1: INSTRUMENTAL CONDITIONING

The use of response-reinforcement frameworks in the study of behaviour is based upon the assumption that behaviour is shaped and maintained by its consequences (Skinner 1938). If an animal is not indifferent to the consequences of its behaviour; responses which have a consequence favourable to the animal are more likely to be repeated, and responses which have an unfavourable consequence are less likely to be repeated (Gross 1992). This understanding forms the basis of experimental work using response-reinforcement instrumental (or operant) conditioning as a method of investigating the maintenance of behaviour.

Animals are aware of certain cause and effect relationships in their environment, and it is because of this that it is possible to experimentally modify an animal's behaviour by teaching it new relationships between stimuli, behavioural responses and consequences, by selectively reinforcing particular responses that the animal makes.

This chapter describes the use of instrumental conditioning to modify the quantity and quality of cat object play, and to control and predict its performance. Instrumental conditioning is so named because the way in which animals operate in their environment is instrumental in bringing about certain consequences which determine the probability of that behaviour being repeated (Gross 1992). In instrumental conditioning rewards which are favourable to the animal can be used to positively reinforce (increase) the performance of a particular behaviour pattern. The behavioural response is known as a free-operant response. This refers to the fact that the response can occur at any time, and its operation brings about reinforcing consequences (Nevin 1973).

In order for this method of behaviour modification to be effective it is important to consider the nature of the reinforcer. Primary reinforcers, which are naturally reinforcing in themselves, are thus ideal for instrumental conditioning. Primary reinforcers include food, water and sex. In this chapter food rewards are used as reinforcers.

It is also important to consider the response selected for reinforcement. Animals are biologically predisposed to learn to perform actions and make responses which are of importance to their survival, and require little training to learn these responses. This phenomenon is termed 'preparedness' (Gross 1992). Actions which are irrelevant to the animals or are contra to their natural tendencies are not easily taught. The same applies equally to the stimulus used to elicit responses; unnatural stimuli to which the animal would not naturally respond are not usually effective.

There are a number of different schedules which can be used in instrumental conditioning experiments, according to when the animal receives reinforcement. These different schedules provide rules for selecting when the occurrence of a response is to be rewarded. The reinforcement can occur after a period of time has passed, irrespective of the behaviour of the animal at the time. This is an interval schedule, and can be fixed (fixed interval, FI), so that the interval between reinforcements is regular; or it can be variable (Variable Interval, VI), so that the length of time between reinforcements is varied. Alternatively, the reinforcement can occur according to the number of responses that have been made. The number of responses required before reinforcement is received can also be fixed (Fixed Ratio, FR), or variable (Variable Ratio, VR). These are the four basic types of reinforcement schedule used in instrumental conditioning, and each produces a characteristic pattern of response, and also extinction when the reinforcement is stopped.

Before these schedules are implemented it is usual to use a schedule of continuous reinforcement, in which every single desired response is rewarded. This enables the animal to learn a new response (Gross 1992).

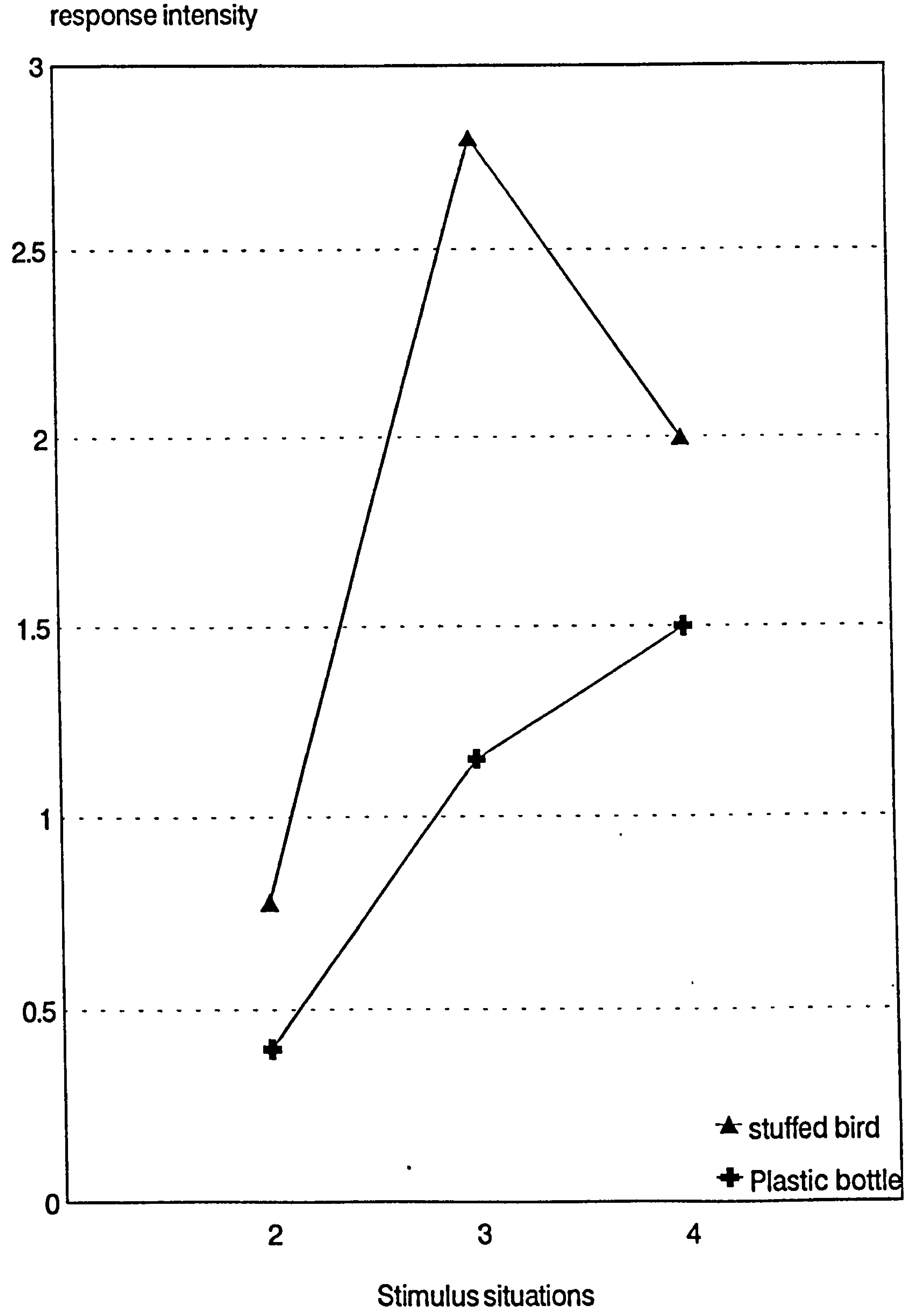
The actual reinforcement schedule used is generally a variation on these basic schedules, and is determined by the requirements of the particular experiment.

7.2: SOCIAL TRANSMISSION

In this chapter I also describe an exploratory experiment to determine whether modified play behaviour learnt as a result of instrumental conditioning could be learnt by other cats by social transmission (also called observational learning). In other words, will cats alter the way they play as a result of observing other cats? Social transmission does not require reinforcement, but occurs spontaneously without any effort on the part of the observer (Gross 1992). However, it can be difficult to determine whether the observer's behaviour shows any influence of learning. This depends upon the consequences of the behaviour. The behaviour of the 'teacher' or 'model' is most likely to be learnt if the consequence of the behaviour is favourable or valuable to the animal. Thus the 'preparedness' of the observing animal is again relevant.

It is possible to exploit this 'preparedness' in order to examine the constraints of learning in an animal; if an unnatural stimulus is presented or a novel behaviour observed it would be expected that the observation learning would be slower and incomplete. For example, if a 'model' is taught with instrumental conditioning to respond with a particular behaviour to a novel, ecologically irrelevant stimulus, it is unlikely that social transmission will be as effective as if the stimulus was a natural one. If a natural stimulus is presented or a commonly performed behaviour is observed, observational learning would be more rapid and complete. Experimental evidence to support this was shown in a study of the social transmission of avian

Figure 7.1. Comparison of the social transmission of mobbing of a stuffed bird and a plastic bottle by European blackbirds. Responses are of observing birds. (from Curio, Earnst & Vieth 1978).



2-pre-observation; 3-during observation period; 4-post-observation test mobbing of a novel stimulus, a plastic bottle (Curio et al 1978). Transmission of information about the plastic bottle was not as effective as for a more natural stimulus, a stuffed predator-sized bird. The difference in response to the two stimuli by the observer is shown in Figure 7.1.

Aims

Two experiments were performed with the overall aim of exploring the influence of positive reinforcement upon different cats' object play, one on the quantity of play and one on its quality. A further experiment was also designed to determine whether social transmission of play altered by instrumental conditioning could occur. These experiments provide an insight into the nature and extent of the control of play by its consequences, and may provide further insight into the motivation of play, and its role in the cats' behavioural repertoire.

7.3: POSITIVE REINFORCEMENT OF PLAY QUANTITY

A preliminary experiment to find out whether food reinforcement was effective indicated the need for a training period before the period of reinforcement, and also for a control for secondary reinforcement by the sound of a biscuit falling onto the floor. Secondary reinforcement occurs when a stimulus acquires its reinforcing properties through association with a primary reinforcer. The animal learns, through classical conditioning, to find the new stimulus reinforcing. Such a mechanism could occur if the cats do not eat the biscuits, but still show an increase in play duration. Dried kidney beans, which are of similar size, shape and colour to the biscuits, were used as the control treatment for the possibility of secondary reinforcement by the sound of the biscuit falling on the floor. If this does act as secondary reinforcement, it would be expected that the play of cats rewarded with beans would be affected in the same way as play reinforced with biscuits.

METHOD

The experiment was designed to determine whether play quantity could be altered by reinforcement with a food reward, and was planned as two parts. Dry food familiar to the cats was used as the reward. The biscuits used were IAMS dry cat food, (Leander International Pet Foods, Arden Grange, London Road, Arbourne, Hassocks, Sussex, BN6 9BJ). These biscuits are highly palatable to cats. Biscuits and beans reached the cats next to the toy via a length of plastic tubing through which the toy's string was threaded. It was important to ensure that the biscuit reinforcement appeared as close as possible to the toy, to ensure that the cats associated its appearance with the toy, rather than with the experimenter, the room, coming into the room, or interaction with the experimenter.

Part 1:

In this part of the experiment there were two treatments; the small, fakefur white toy with a FI food reinforcement of one 0.3g biscuit every 30 seconds; and the small, fakefur black toy with a FI 'false' food reinforcement of one dried kidney bean every 30 seconds.

Eight cats from the University colony were divided at random into two groups of four. One group received the white toy and biscuit treatment, the other received the black toy and bean treatment. Both groups underwent a training period of five days in which they received the toy but no reinforcement. Play duration during this period was measured with a stopwatch until no physical contact with the toy had been made for 20 seconds. The aim of the training period was to enable habituation to any irrelevant stimuli, such as the tube, so that all differences in play could be attributed to the reinforcement schedule. The cats were tested individually, on consecutive days, in the same experimental room as in all previous experiments. Trials were three minutes long.

The reinforcement schedule is shown in Table 7.1; The reinforcement schedule continued for

Table 7.1. *The experimental design for the positive reinforcement of play quantity, for parts 1 and 2*. The groups received the reinforcement for a day longer in Part 2, this was because it was necessary to continue reinforcement until any change in play had become stable. The extinction period was also longer (six days) in Part 2, for the same reason.

PART 1

Group 1	5 days of training	6 days of reinforcement with biscuits	3 days of extinction - nothing delivered
Group 2	5 days of training	6 days of reinforcement with beans	3 days of extinction - nothing delivered

PART 2

Group 1	5 days of training	7 days of reinforcement with biscuits	6 days of extinction - beans delivered
Group 2	5 days of training	7 days of reinforcement with beans	6 days of extinction - beans delivered

six days, by which time play duration in both groups appeared to have reached a plateau. In addition to play duration, the number of biscuits and beans received was also recorded. After six days of reinforcement no further biscuits or beans were given in order to bring about extinction of any differences in play. This extinction period lasted for three days.

Part 2:

Two weeks after the completion of this experiment, the second part was undertaken. The two week break was deemed sufficient time for the effects of part 1 to have diminished. In part 2 the groups remained the same, but they received the other treatment; i.e. both groups had a training period of five days in which neither received reinforcement, then the group which received the white toy and biscuit reinforcement in the reward period of Part 1 received the black toy and beans, and vice versa. The method was unchanged during the training and reinforcement periods, but during the extinction period both groups received the bean reinforcement. The reason for this was that the group which had received the biscuit reinforcement had learnt to watch for a biscuit coming down the tube and also to listen for it falling on the floor. The beans were given to control for any reinforcement from the sight or sound of falling food. In part 1 of the experiment it was noted that the sight or sound of beans falling onto the floor did not reinforce play quantity (see Figure 7.2); their play response merely habituated. There was thus no change in the extinction period. It was, therefore, acceptable to continue giving beans in the extinction period in order to contrast the response of the other group which were also given beans in the extinction period.

Data from the two parts of the experiment were combined for analysis. Two types of analysis were performed:

1) Analysis was undertaken to determine whether play duration was significantly different between the two groups as a result of the different reinforcement schedules. This was done by comparing play duration for the two groups on the first four days of the extinction period. It was expected that the groups' play duration would be significantly different immediately after

the reinforcement period had ended, indicating that the reinforcement schedules had affected the play durations, but would become more similar as the effects of the reinforcement schedule diminished in the extinction period. At the point where the two groups have play durations which are not significantly different, extinction of the reinforced play response could be said to have occurred.

2) Play duration on the last two days of the training period and the last two days of the reinforcement period were compared to determine whether any changes in play behaviour had occurred as a result of the reinforcement schedule. If play duration had been reinforced it would be significantly different between the end of training and the end of reinforcement.

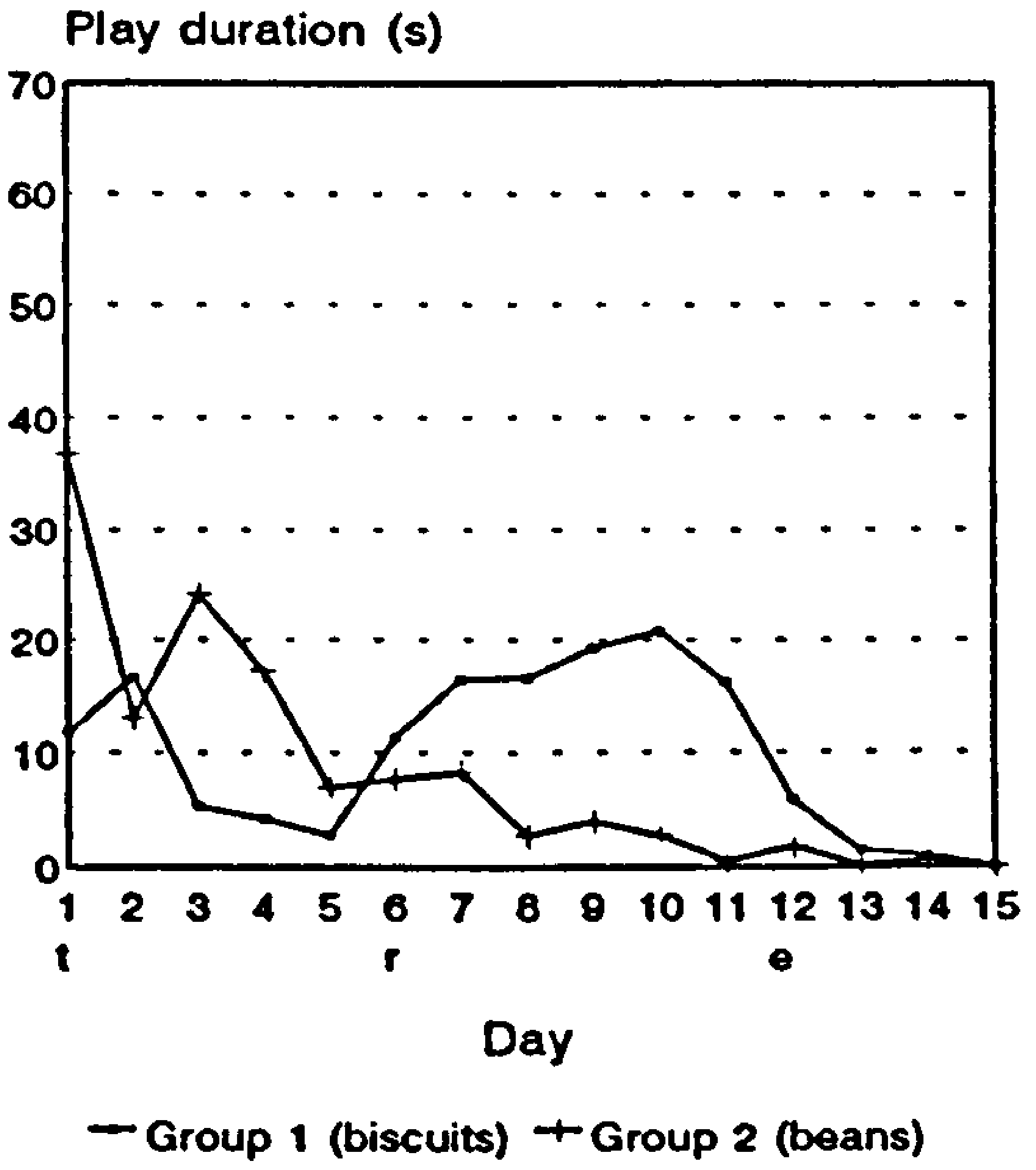
RESULTS

Data from the experiments is presented graphically in Figures 7.2 to 7.9 show the changes in play duration and the number of biscuits and beans received (before the 20 second cut-off point) for parts 1 and 2.

1) To test if the play durations of the two groups were different before and after the reinforcement period, two-way ANOVA was used to compare the last two days of training (days 4 and 5) with the last two days of reinforcement (days 10/11in Part 1 and 11/12 in Part 2). The factors were group and day, and the interaction term was group by day. The two parts of the experiment were analyzed separately.

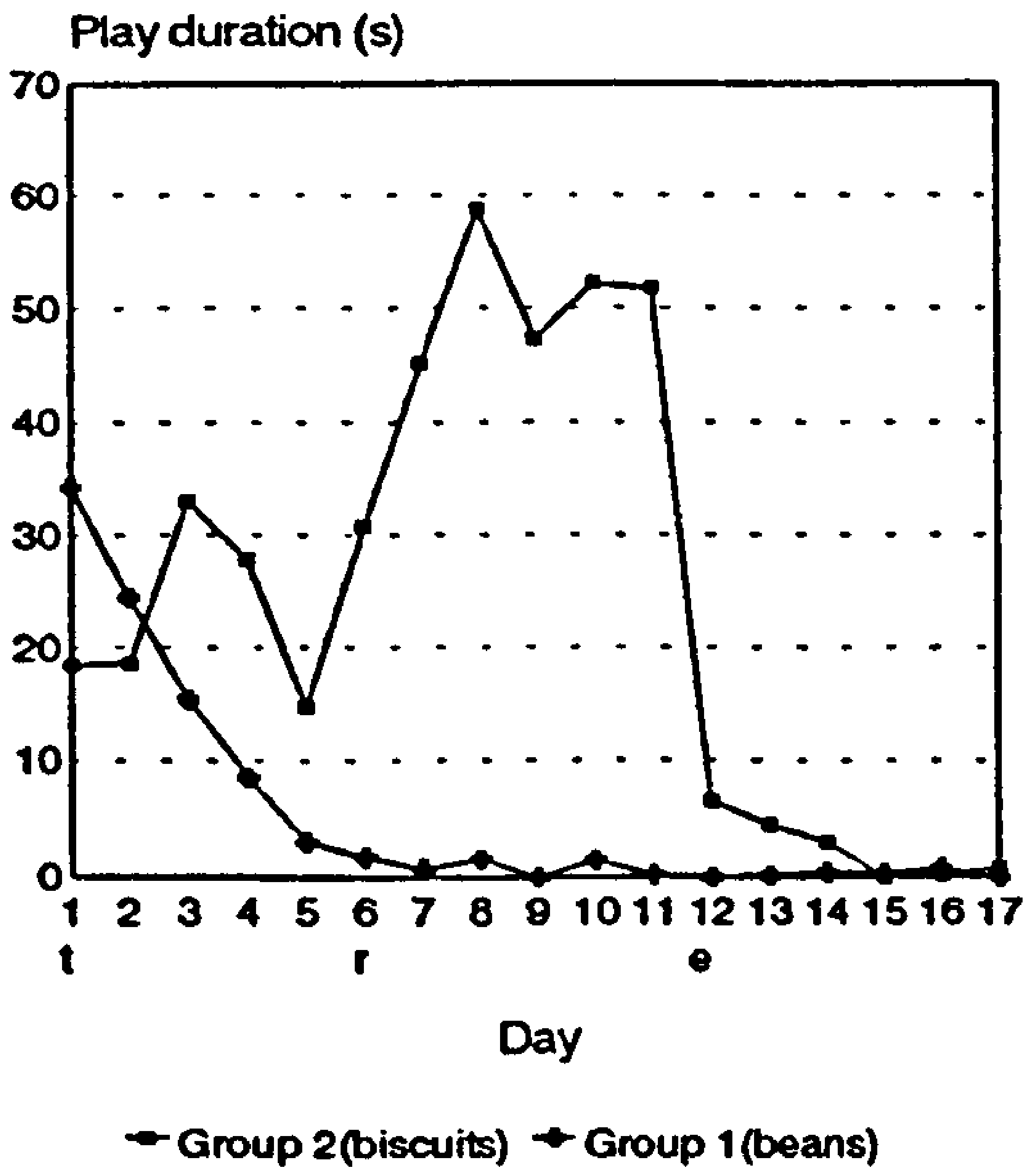
2) In the first part of the analysis, play duration was tested using two-way ANOVA to see if it was significantly different with reinforcement. The factors were the reinforcement group (beans or biscuits) and the experiment part (1 or 2), and the interaction term was the reinforcement group by the experiment part. The first four days of extinction were tested separately. On day one of the extinction period the play durations were significantly different at $p<0.05$ between the two groups. The means tables showed that the cats reinforced with biscuits had higher play duration than the cats reinforced with beans; the average play duration following biscuits was 2.44 seconds, compared with 0.46 seconds with beans. This indicated

Figure 7.2 The effects of food reinforcements on play duration in part 1 (extinction - no reward delivered).



t-start of training period; r-reinforcement; e-extinction

Figure 7.3 The effects of food reinforcement on play duration in part 2 (extinction - bean 'reward' delivered).



t-start of training period; r-reinforcement; e-extinction

Figure 7.4. The average play duration in the three periods of part 1.

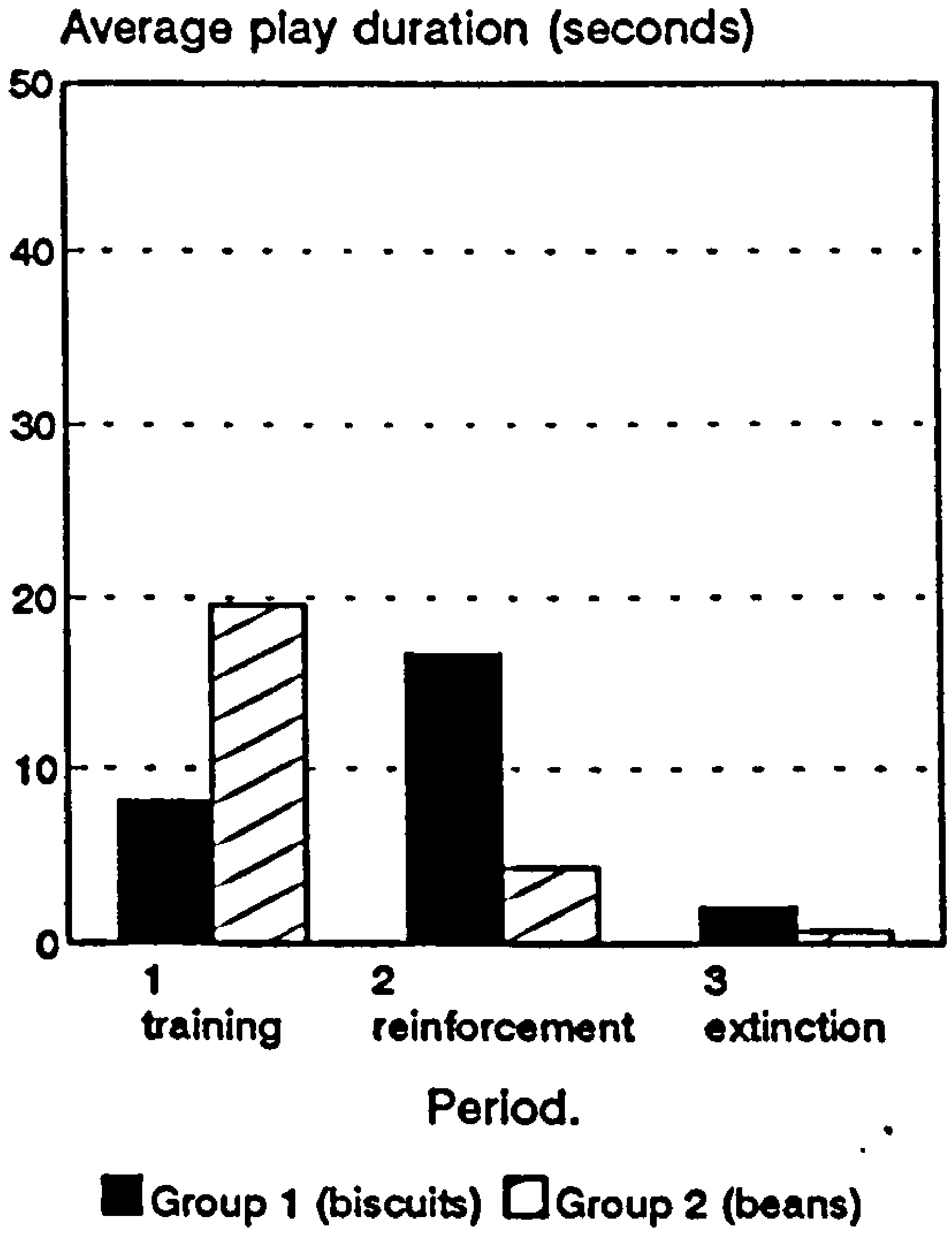


Figure 7.5. The average play duration in the three periods of part 2.

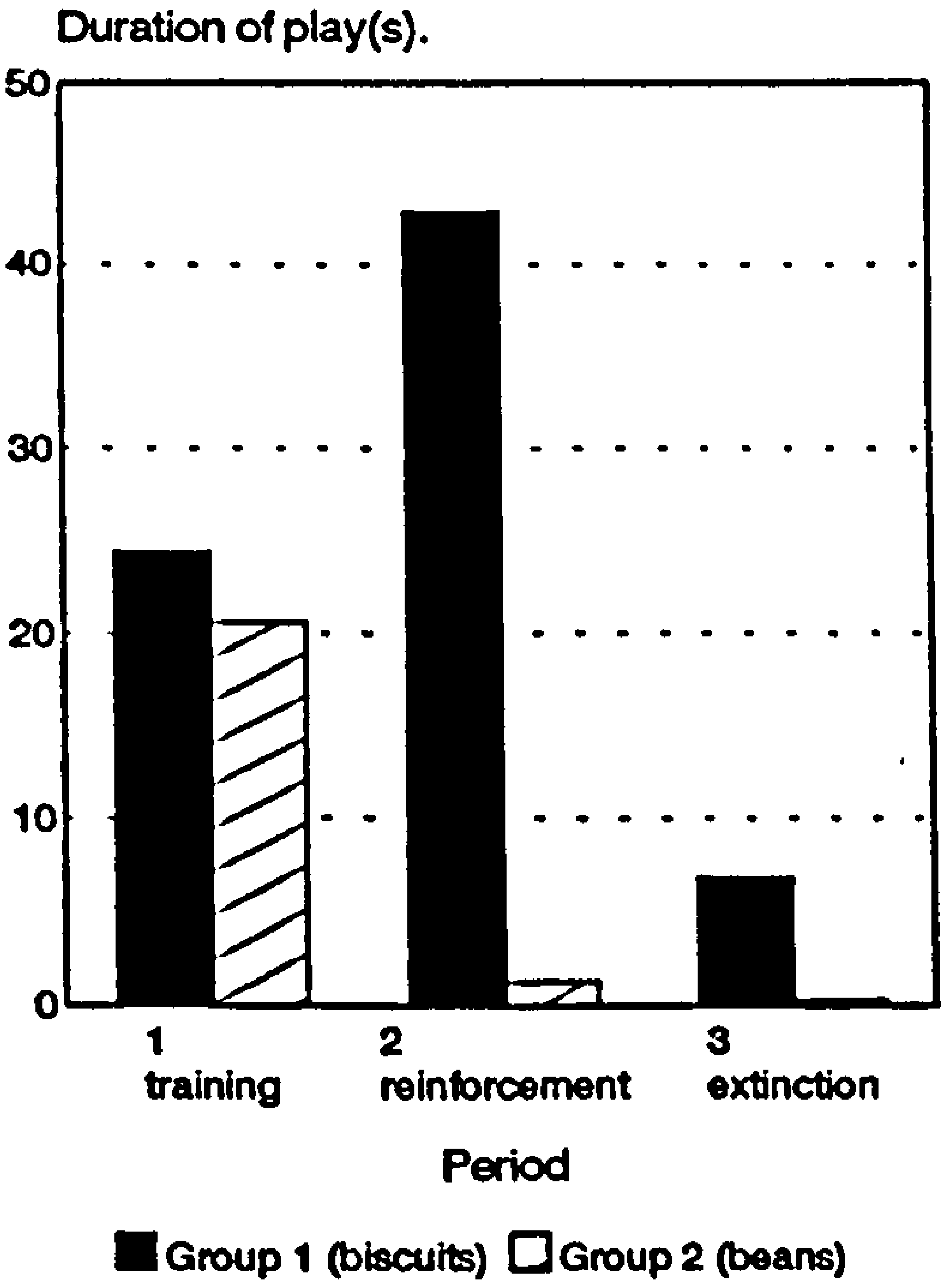


Figure 7.6 The number of beans received during the reward period of part 1.

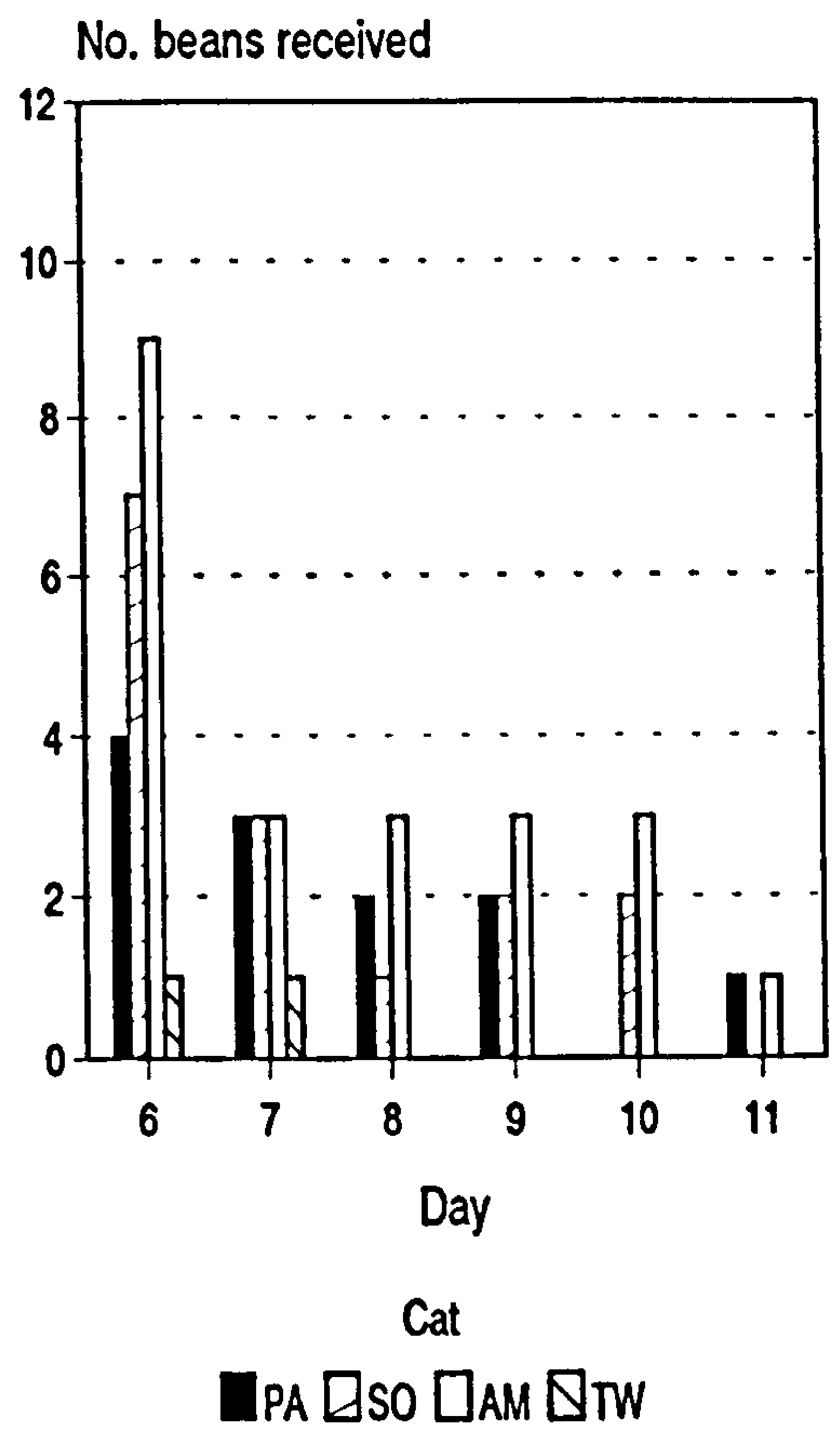


Figure 7.7 The number of beans received during the reward and extinction periods of part 2.

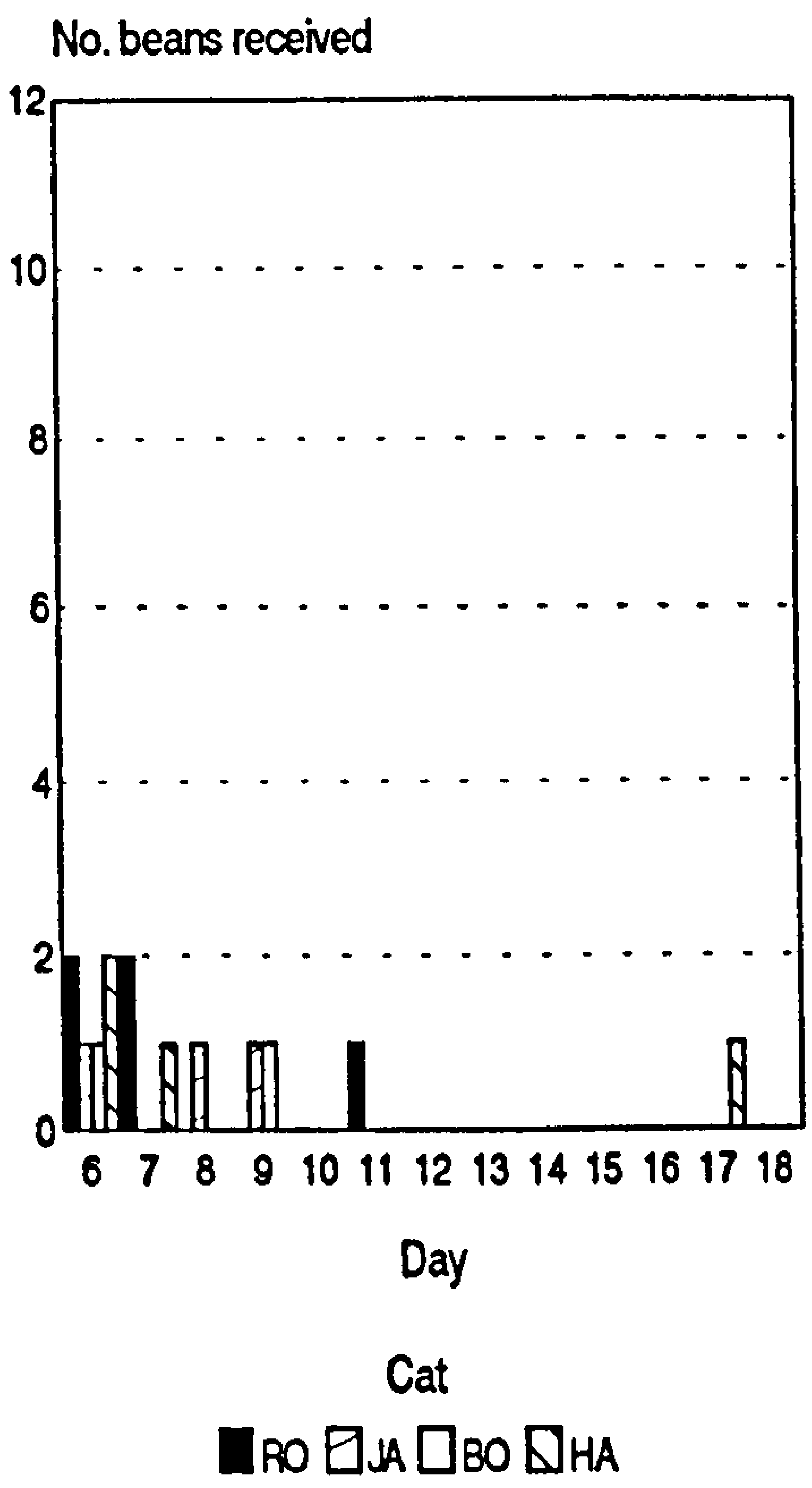


Figure 7.8 The number of biscuits eaten during the reward period of part 1.

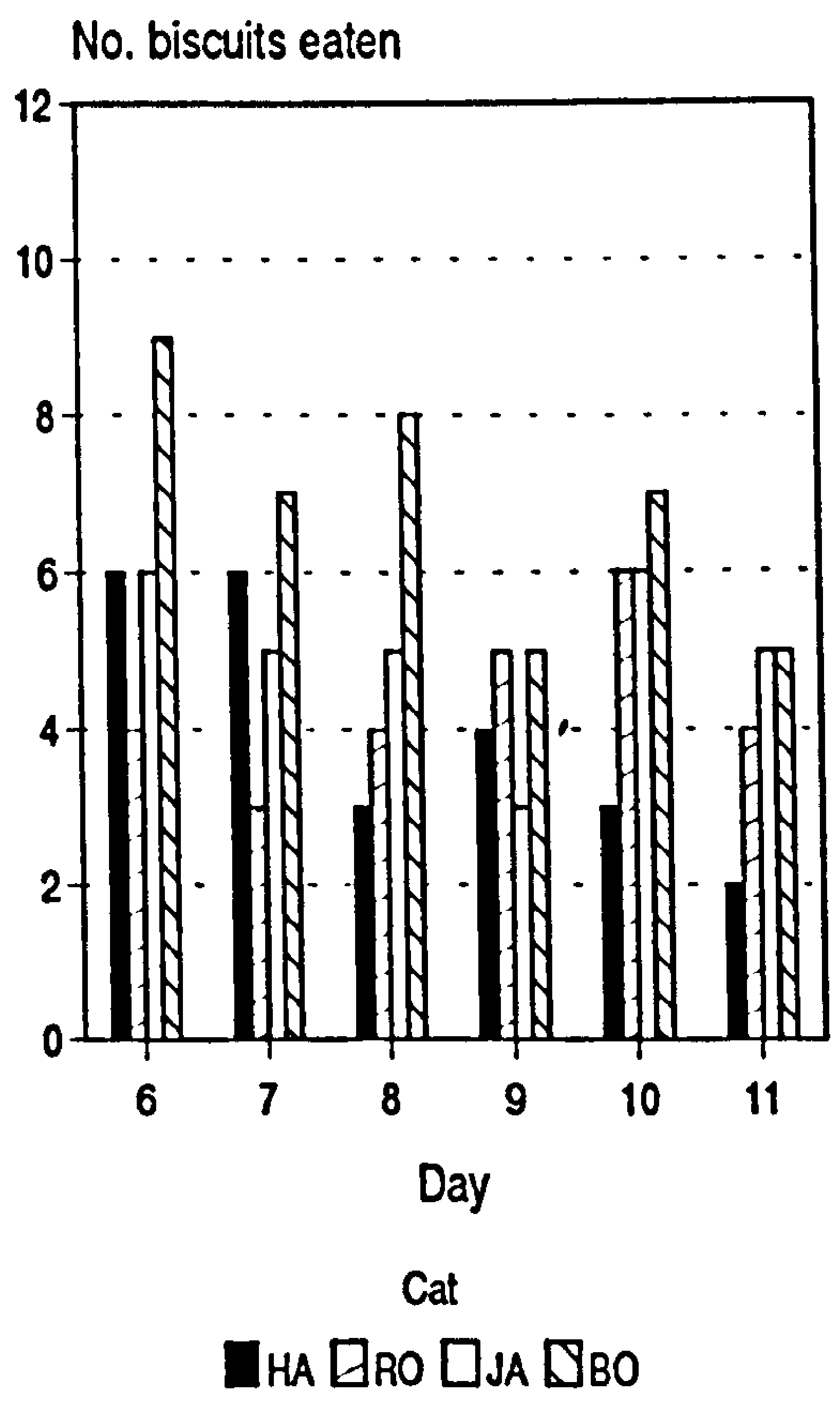
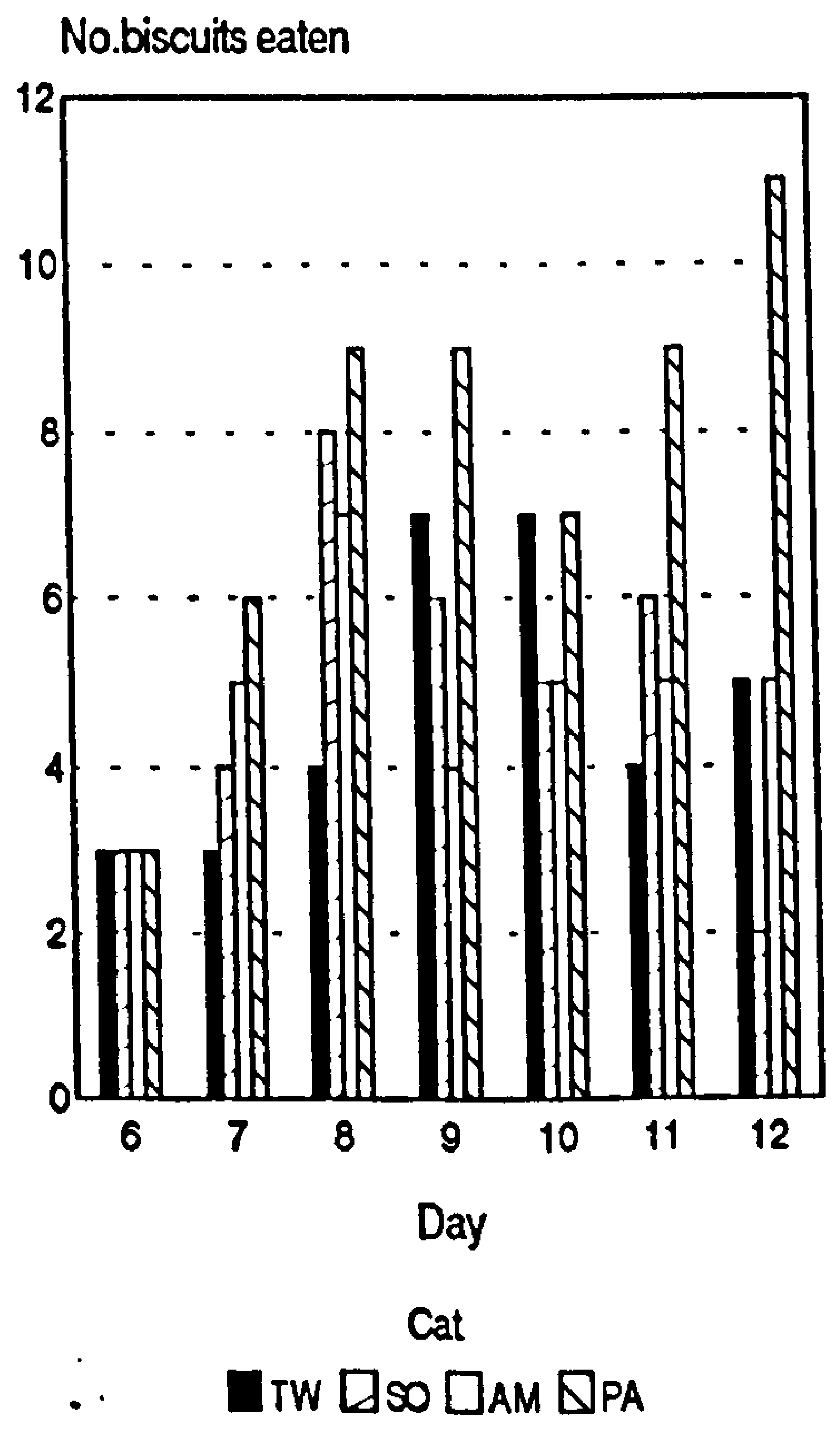


Figure 7.9 The number of biscuits eaten during the reward period of part 2.



that the effect of the biscuit reinforcement still existed on the first day of extinction. On the second, third and fourth days of extinction the play durations for the two groups were not significantly different. This indicated that extinction of the reinforced play response group had occurred.

In part 1 the play durations of the two groups comparing the training and reinforcement days (group by day interaction term) were significantly different at $p<0.005$, indicating that the play durations of the two groups were significantly different on these days. Group 1played slightly less than Group 2 prior to reinforcement, but for more than five times longer on the last two days of reinforcement (Figure 7.2).

In part 2 the play durations of the two groups on the same days were not significantly different (group by day interaction term, $p=0.08$), indicating that the two groups were not differently affected by their separate reinforcement schedules. During the last two training days, Group 2 played for approximately three times as long as Group 1, and although reinforcement with biscuits did increase the level of play in Group 2 (Figure 7.3), this appears to have been insufficient to generate a significant difference.

DISCUSSION

This experiment has shown that it is possible to alter play duration with food reinforcement. When part 1 and 2 were combined there was a significant difference between the food reinforced and bean reinforced groups on the first day of the extinction period. This indicated that the reinforcement schedules had affected play. Biscuit reinforcement was associated with higher play duration than bean reinforcement. The beans given to the white/biscuit group in part 2 had no effect on the pattern of extinction, see Figure 7.3.

The effects of the reinforcement schedule disappeared rapidly so that play durations of the two groups were not significantly different by day two of the extinction period. The rapid extinction of a FI schedule reinforced response was expected.

Overall, the results were rendered inconclusive because of two problems. Firstly, the sample size was too small, with only four cats in each group, to allow for noise from individual variation. Finally, the groups were not balanced, so that differences between the groups could not be clearly attributed to the experimental protocol, because one group of cats played more than the other with both the biscuits reinforcement and the beans reinforcement.

7.4: POSITIVE REINFORCEMENT OF PLAY QUALITY

An experiment was designed with the aim of altering the quality of play behaviour by selective reinforcement of a particular behaviour pattern with a food reward. The behaviour pattern chosen for reinforcement was contact with one or the other of the front paws. The aim of reinforcing this behaviour pattern in a group of cats was to increase its frequency of performance.

METHOD

Initially nine cats from the University colony (seven that had taken part in the previous experiment) were trained to play with a small real fur toy (with an attached tube later used for food rewards), for five days. (Only nine cats in the colony were suitable for the experiment, that is made more than one paw contact over the five days of training). The frequency of paw contact per cat on each day was recorded. After the five day training period the cats were divided into two groups. They were ranked according to their overall score of paw contacts over the five days. One group comprised the cats ranking 1, 2, 3, 4 and 9 (rank 9 being the cat which had the lowest score), and the other group comprised cats ranking 5,6, 7 and 8. The two groups were deliberately kept unbalanced; the cats lowest ranking cats were assigned to the biscuit reinforcement group to ensure a more obvious response.

Group 1, the higher ranking group, was then put on a FI reinforcement schedule of 30 seconds. IAMS dry cat food biscuits were used as the food reward.

Group 2, the lower ranking group, was put on a modified continuous reinforcement schedule, in which they were reinforced only when using a front paw to contact the toy. Each bout of paw contacts was reinforced with a single biscuit. However, a minimum of 15 seconds had to pass between reinforcements, and it was ensured that overall the cats received the same number of biscuits as the FI group.

Each cat was tested for three minutes per day, thus receiving a maximum of six biscuits per day, and experiment days were consecutive. The cats remained on these schedules until there was a relatively consistent change in the frequency of paw contacts for a large number of days (14 days). This was determined by referring to a graph of the daily average paw contacts of both groups.

Once this had occurred the reinforcement schedules were stopped, and an extinction period followed in which the experimental procedure remained the same but the cats received no biscuit reinforcements.

Similar tests as in the quantity reinforcement experiment were used. The number of paw contacts from different days for both groups were compared using two-way ANOVA, in which group and day were factors, and group by day was the interaction term:

1) The last two days of training were compared with the last two days of reinforcement for both groups. This would determine whether the reinforcement schedule had affected the play response.

2) The last two days of reinforcement were compared with the last two days of extinction for both groups. This would also determine whether the reinforcement schedules had affected play.

3) The differences in average frequency of paw contacts of Group 2 between the last two days

of reinforcement and the last two days of extinction were tested separately.

It was expected that Group 2 would show an increase in frequency of paw contacts during the reward period. This should then decline in the extinction period. It was also expected that Group 1 would show a smaller change in frequency of paw contacts throughout the experiment in all three periods (training, reinforcement extinction) since paw contact had not specifically been reinforced.

RESULTS

ANOVA results were as follows;

1) The last two days of training (days 4 and 5) and the last two days of reinforcement (days 18 and 19) were significantly different at $p<0.01$, between groups(group by day interaction). More paw contacts were performed by Group 1 during training, but Group 2 were performing more paw contacts by the latter part of the reward period (Figure 7.10). The reduction in paw contacts in Group 1 during reinforcement may have been a result of some cats learning that rewards were delivered whether they played or not.

2) The last two days of reinforcement and the last two days of extinction were significantly different at $p<0.0001$ comparing the two groups (group by day interaction term). This appears to be largely caused by the continued moderate level of play by Group 1 during extinction, although this was not as high as during training (Figure 7.10). Group 2 showed the expected decline in number of paw contacts during extinction (Figure 7.10), and was therefore tested separately.

3) In Group 2, the frequency of paw contacts was significantly different with day (when the last two days of reinforcement and the last two days of extinction were compared), at $p<0.0005$; and was significantly different with cat at $p<0.0001$. The average frequency of paw contacts for Group 2 was greater on the last two days of reinforcement (59.5 and 55), compared with the last two days of extinction (17 and 16.25).

Figure 7.10 The changes in frequency of paw contact resulting from food reinforcement. t-start of training; r-reinforcement period; e-extinction.

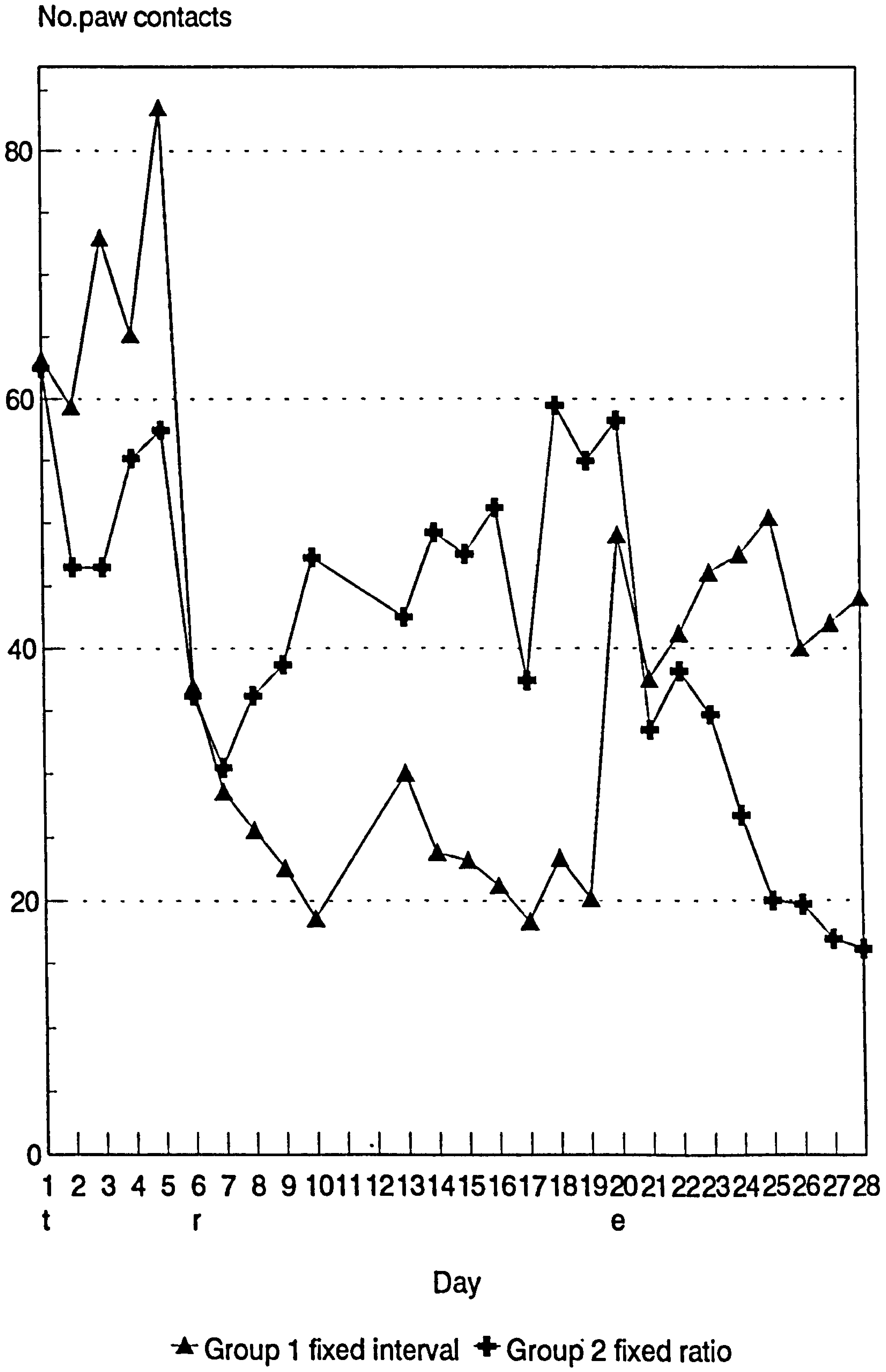
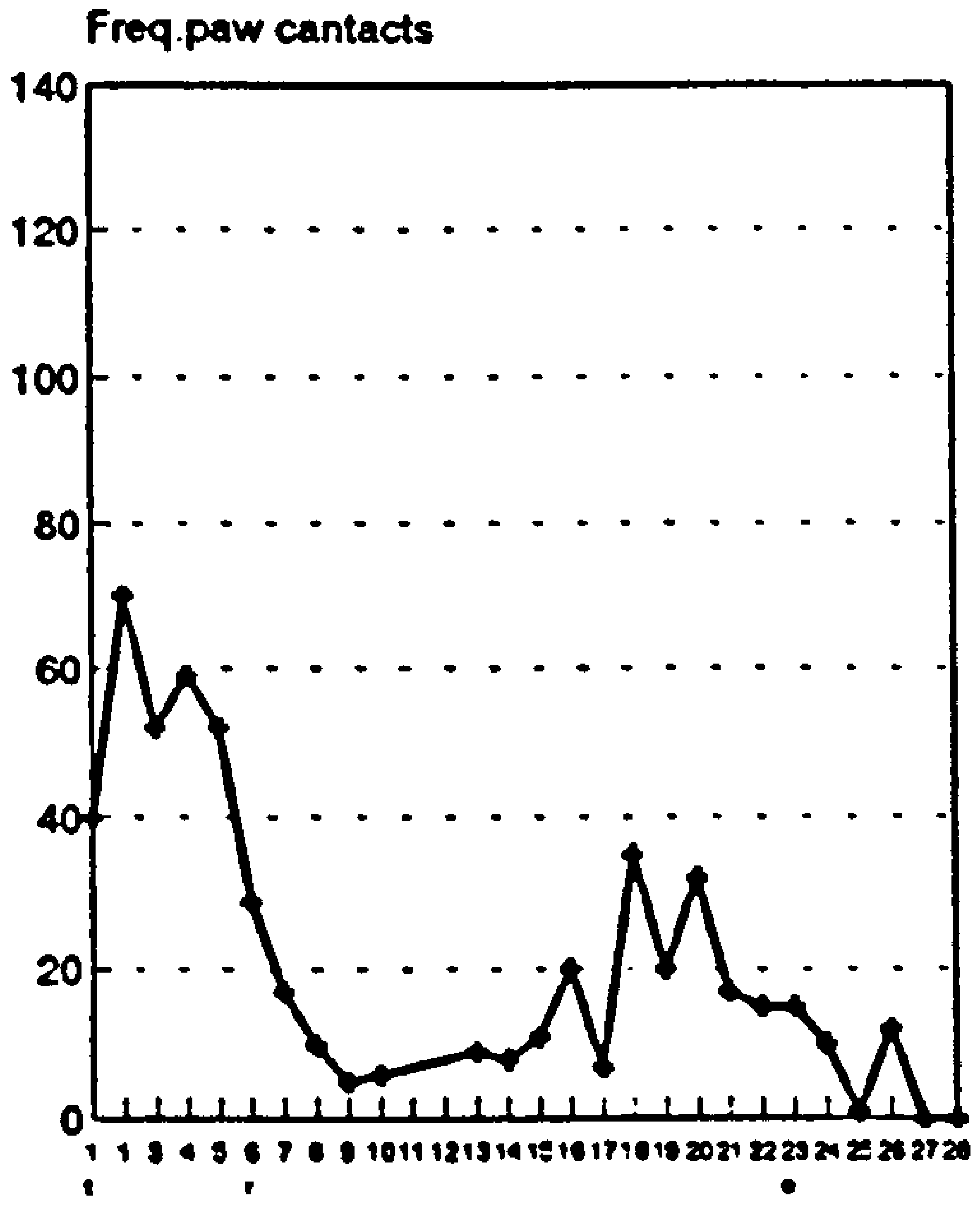
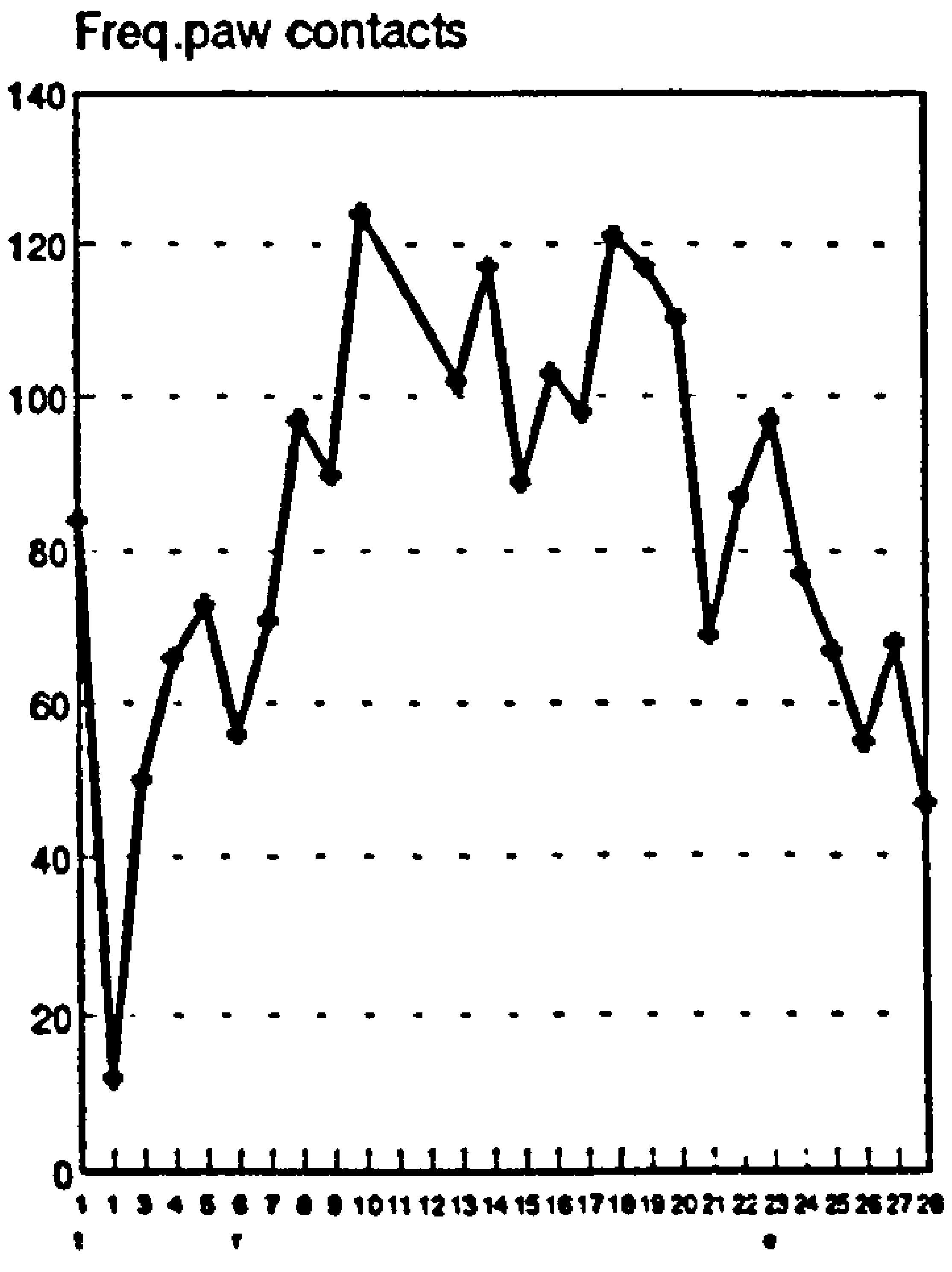


Figure 7.11 The change in frequency of paw contacts under the FR schedule, for cat SP.



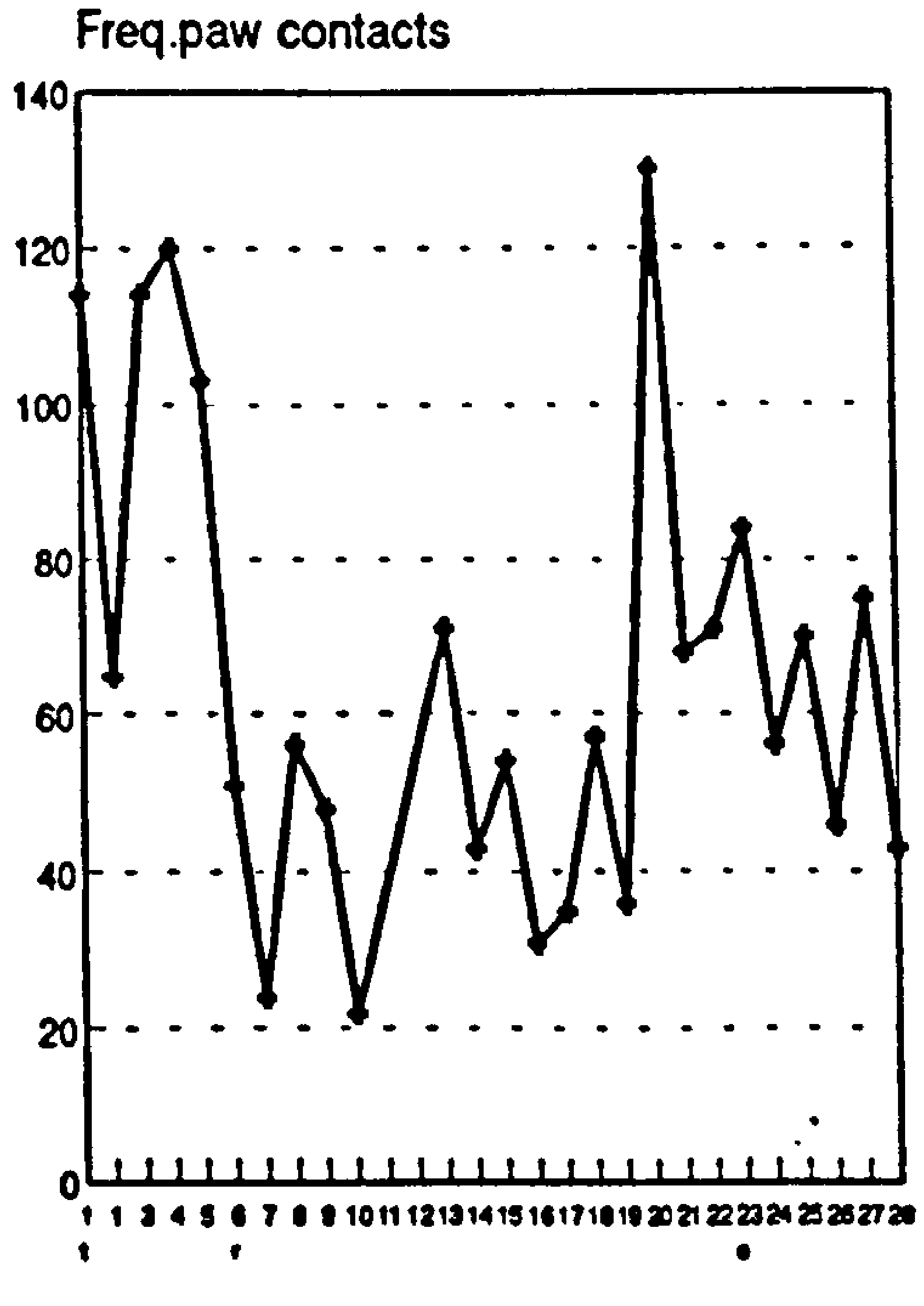
t-start of training period; r-reinforcement; e-extinction

Figure 7.12 The change in frequency of paw contacts under the FR schedule, for cat HA.



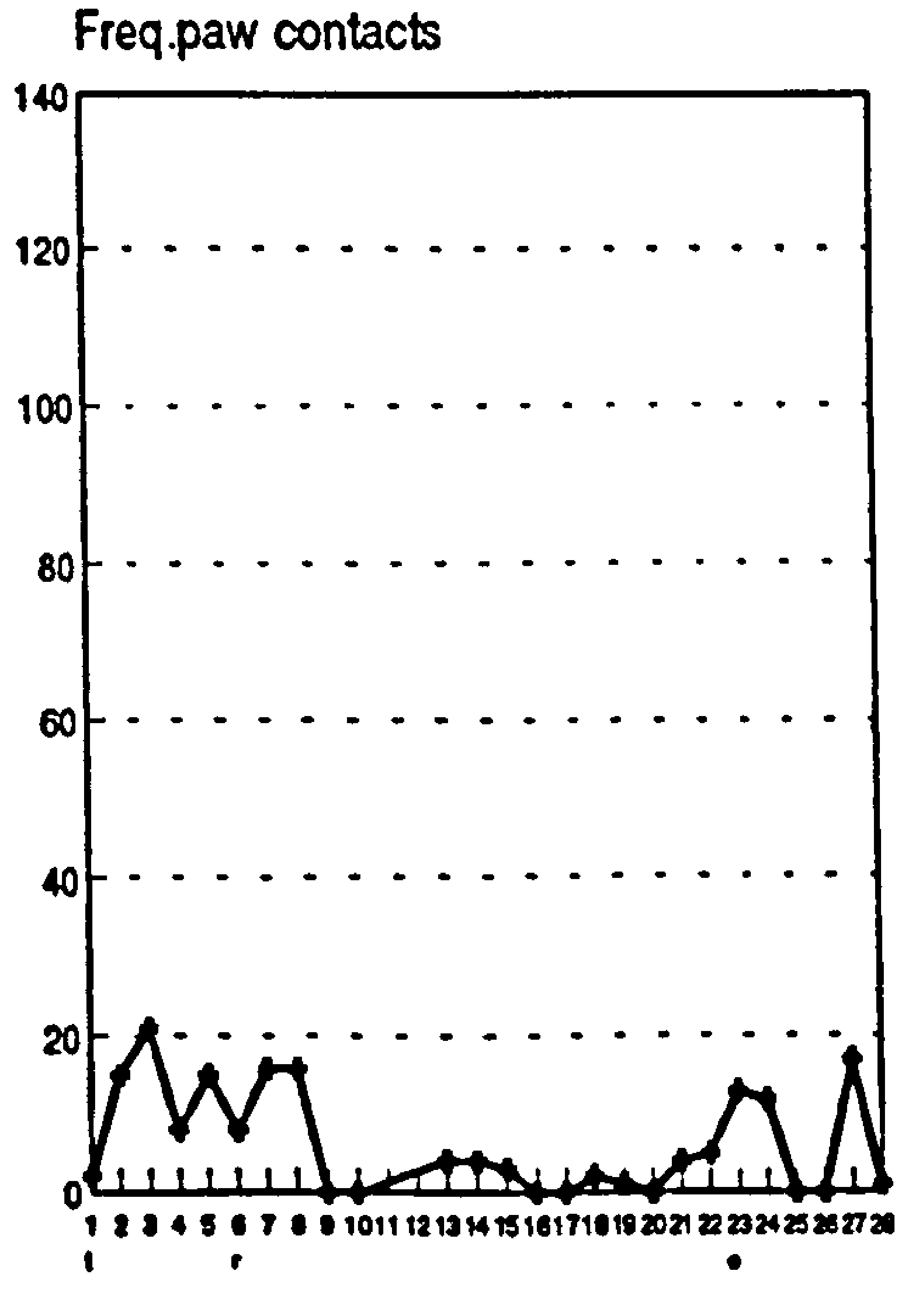
t-start of training period; r-reinforcement; e-extinction

Figure 7.13 The changes in frequency of paw contacts under the FI schedule, for cat AM.



t-start of training period; r-reinforement; e-extinction

Figure 7.14 The change in frequency of paw contacts under the FI schedule, for cat BO.



t-start of training period; r-reinforcement; e-extinction

DISCUSSION

Both reinforcement schedules had an effect on the frequency of paw contacts made in the three periods of experimentation. With both schedules there was a decrease in frequency at the end of the training period, probably a result of habituation, followed in Group 2 (paw contact rewarded) by an increase throughout the reinforcement period, and finally a steady decline in response through the extinction period. Thus fixed ratio food reinforcement caused an increase in the frequency of paw contact. The fixed interval reward (Group 1) caused an overall decline in paw contact (and play in general).

There was a large amount of cat -to- cat variation in the experiment. Examples of individual responses to the experiment protocol are shown in Figures 7.11 to 7.14. From these graphs it is clear that the average responses of the groups are not particularly reliable. There were enormous fluctuations in the frequency of paw contacts for each cat; the only cats which showed a stable response were those that performed very low frequency paw contacts (see Figure 7.14). The extent of individual variation makes the results inconclusive.

Clearer effects of the FR schedule may have been hindered by the fact that the behaviour response required for reinforcement was not an instinctive response: a cat would not normally expect to receive food merely by hitting at an object. If the object was a prey animal further predatory behaviour patterns would be required before food could be obtained. Thus, reinforcement of an inappropriate behaviour pattern may have reduced the effect of the schedule.

Overall, the results of this experiment are relatively inconclusive, although, as in the previous experiments, it is clear that cat play behaviour can be modified by selective positive reinforcement.

7.5: SOCIAL TRANSMISSION OF PLAY BEHAVIOUR

There were two aims in this experiment which was based upon work on the cultural (social) transmission of avian mobbing in European blackbirds *Tardus merula*. In a series of experiments blackbirds learned to mob a novel object (a plastic bottle) through a reinforcement schedule, observer birds watching the first birds response to the bottle learnt to respond to the bottle with similar intensity mobbing. This social transmission of modified behaviour was effective along a chain of at least six birds (Curio 1978, Curio et al 1978, Vieth et al 1980).

This experiment was designed to explore whether a similar phenomenon of social transmission could be duplicated with cat play behaviour. The protocol requires two achievements; the first aim was to reinforce play in a group of cats with a novel toy which would not normally elicit intense play. When play intensity had increased as a result of reinforcement, other cats watched the first group as they played with the toy. The aim was that the observer cats should learn to play with the novel toy, with which they would not normally play, as a result of social transmission.

METHOD

To establish baseline play performances of each cat, 34 cats from the WCPN colony were presented with the real deer fur toy for a three minute session. The total time for which each cat was in physical contact with the toy was measured. These times were then used to rank the cats and to balance them into five matched groups, four containing seven cats, and a fifth with six cats. On the second, third and fourth days the cats were trained with one of two toys, the real fur toy, or the novel toy, also for three minutes. The novel toy was covered in polythene, a texture shown to elicit low level play and avoidance, and was 30x9x10 cm (cat size). This large size had also been shown to elicit low level play and avoidance (see Chapter 3). The real fur toy (7x5x1 cm) had elicited high-intensity play in previous trials (see Chapters 3 and 5).

Table 7.2. *The experimental design for the study of the social transmission of reinforcement-modified play behaviour.* Where, C-control group, no change to protocol throughout experiment; TR-training with novel toy; TR*training with real fur toy; R-reinforcement; NR-no reinforcement; W-watch teacher group; T-test day; EX-extinction period.

Group /day	1	2	3	4	5	6	7	8	9	10	11	12
1 real fur control	C	C	C	C	C	C	C	C	C	C	C	C
2 teacher reward	TR *	TR *	TR *	TR *	R	R	R	R	R	R	EX	EX
3 teacher no reward	TR *	TR *	TR *	TR *	NR	NR	NR	NR	NR	NR	EX	EX
4 watch group 2	TR	TR	TR	TR	W	W	W	W	W	W	T	T
5 watch group 3	TR	TR	TR	TR	W	W	W	W	W	W	T	T

Two groups, which would be the 'observers', were trained with the novel toy, while the other three were trained with the real fur toy (see Table 7.2). One of the three groups receiving real fur acted as a control for the rest of the experiment, and received the real fur toy every day for three minutes each. The other two groups which received the real fur toy during the training period received this toy only for the training period, before continuing the experiment on reinforcement schedules with the novel toy. Real fur was used in their training period to enable comparison with the control group and with the two 'observer' groups (trained with the novel toy).

Throughout the three days of training the number of 'killbites' performed by each cat was recorded. 'Killbite' is a behaviour pattern which occurs relatively infrequently, making any change in performance frequency easier to identify. It is also an unambiguous behaviour pattern, easily reinforced by the experimenter.

At the end of the training period the reinforcement period began. During this period one group which had been trained with the real fur toy started to receive the novel toy, and was reinforced with a biscuit reward (Whiskas cocktail, Pedigree Petfoods, Melton Mowbray, Leics, LE13 OBR) whenever 'killbite' was performed (a continuous reinforcement). When bouts of 'killbites' were performed the cat was reinforced once for the whole bout, since reinforcement of every 'killbite' was impossible in practice, since biscuits could not be given quickly enough to match the speed of biting.

A second group of cats which had received the real fur toy during the training period, also changed to the novel toy, but did not receive reinforcement. These two groups formed the 'teacher' groups.

The remaining two groups which had been trained with the novel toy became observers. During the reinforcement period these cats were placed, individually, in a room adjoining the experimental room, of which they had a clear view through a wall glazed for the entire upper part. One group of observers watched the unreinforced 'teacher', the other watched the reinforced 'teacher' group. Each observer watched a different cat from the relevant 'teacher' group each day. One observer group contained only six cats (all other groups contained seven); thus on each day of the reinforcement period only six of the seven cats in the teacher group were watched by another cat. The group which received real deer fur continued on the same protocol, and was not watched by any cats.

The reinforcement period continued for six days until there had been a levelling in the 'killbite' frequency of the cats being reinforced. The experiment was continued for two further days on which the observer cats again received the novel toy, and the frequency of 'killbites' they performed was recorded.

Extinction of the reinforced 'teacher' groups' response took only two days to almost disappear, hence the short extinction period. These treatments are summarized in Table 7.2.

On completion of the experiment a number of statistical tests were carried out to determine whether the reinforcement of 'killbites' had affected the level of their performance, and to determine whether the performance of 'killbites' by the observer groups had been affected by watching the 'teacher' groups during the reinforcement period:

1) The last two days of the training period were compared with the last two days of the reinforcement period for group 2 (reinforced 'teacher' group), and then for group 3 (unreinforced 'teacher' group). This would determine whether the reinforcement schedules had any affect on the 'killbite' frequency.
2) The last two days of the reinforcement period were compared with the two days of extinction for group 2 and for group 3. This would also indicate whether the reinforcement schedules had any affect upon 'killbite' frequency.
3) The data from groups 2 and 3 from the last two days of training, the last two days of reinforcement, and the two days of extinction were compared. This would indicate whether

there was a difference in the average group responses throughout the experiment.

4) Group 4 and 5 data were compared for the two test days (11 and 12). This statistic would determine whether there was a difference in response between the two groups as a result of watching the play behaviour of the two 'teacher' groups, assuming that the two 'teacher' groups had themselves been affected by the reinforcement schedules. All tests were performed with two-way ANOVA; factors were group and day, and the interaction term was group by day.

RESULTS

The change in frequencies of 'killbite' were recorded for all groups throughout the whole experiment and data for individual cats are shown in Figures 7.15 to 7.19. Figure 7.20 shows the average changes for all five groups throughout the experiment. These figures indicate a number of trends:

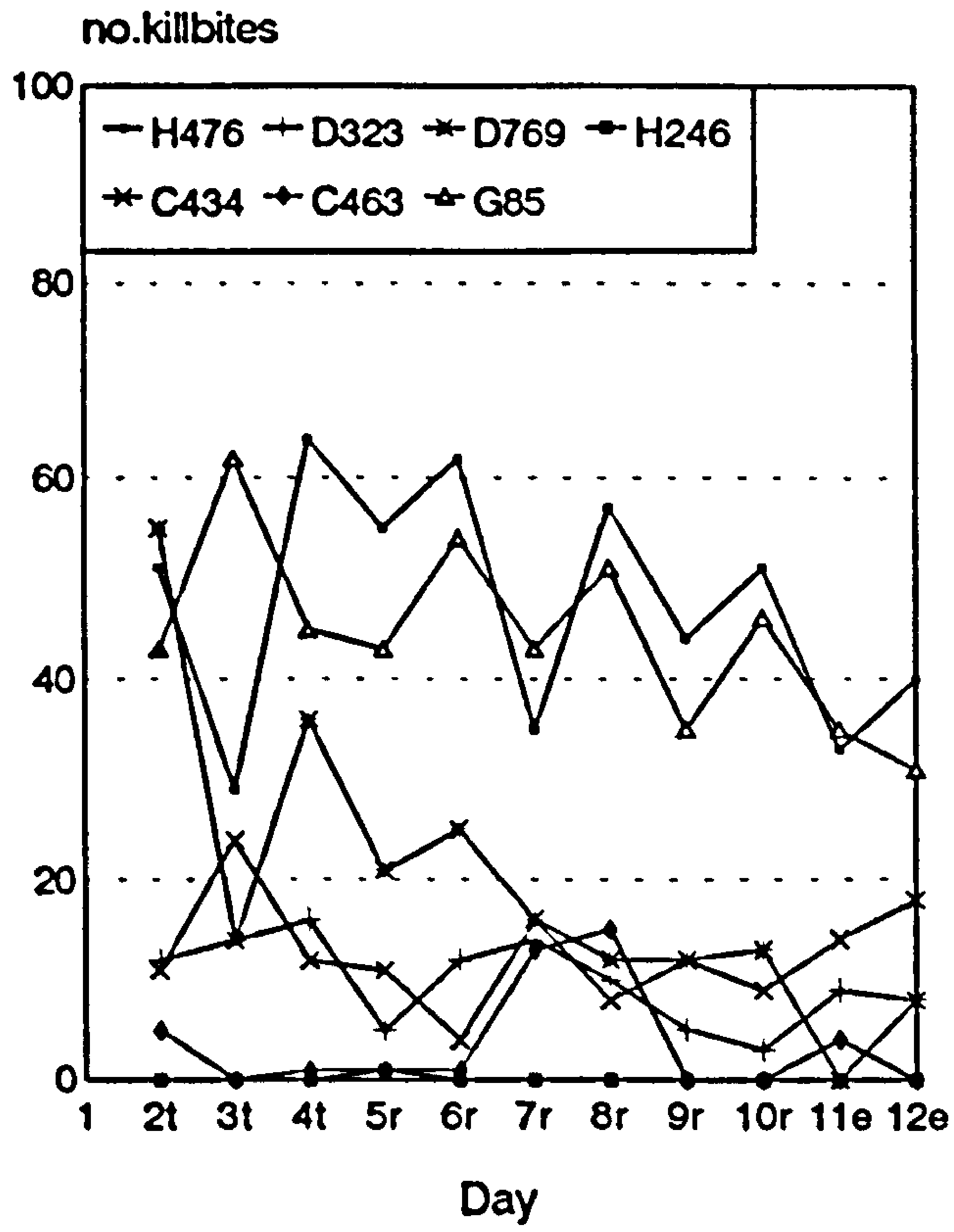
1) The frequency of 'killbites' performed by the real fur control group remains largely unchanged throughout the 12 days of experiment, although there was a slight decline. This was the expected trend for this group. Real fur has been shown (see Chapters 3 and 5) to elicit high intensity play, and very little habituation, either within one play session or over the long term.

2) The frequency of 'killbites' remained stable, if not high, for group 2 which received food reinforcement for biting the novel toy. A decline in frequency of 'killbites' from the training period when the real fur toy was presented was expected, since the novel toy was designed to elicit low intensity play.

3) Group 3, which received no reinforcement, showed a rapid decline in 'killbite' frequency, after initial higher response to the real fur toy. This was also expected. By day seven of the experiment, all cats were performing less than ten 'killbites' each.

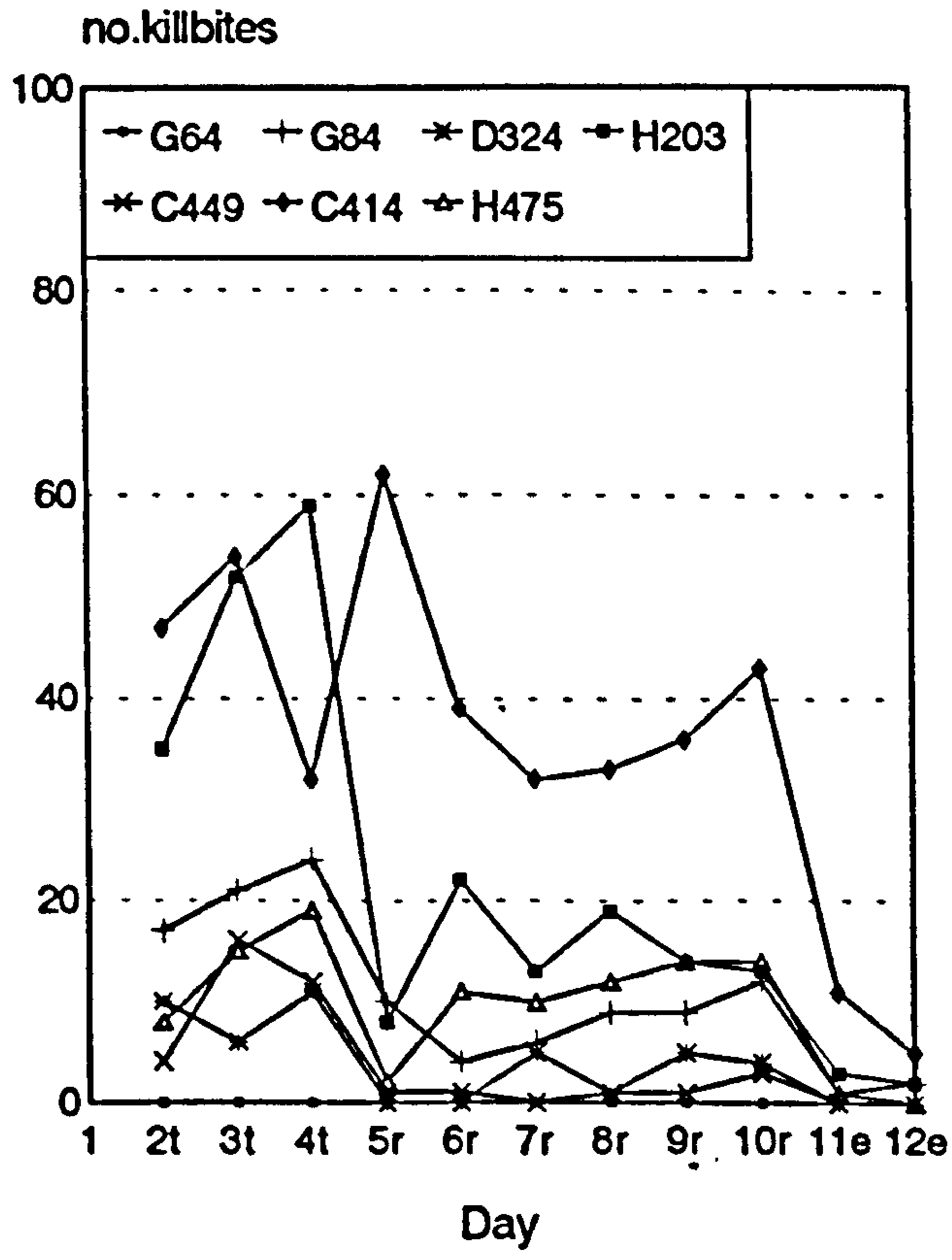
4) Group 4, which watched 'teacher' group 2 (food reinforcement group) showed a higher frequency of 'killbites' on test days 11 and 12 than group 5, which watched 'teacher' group 3 (no reinforcement).

Figure 7.15 The frequency of killbites in group 1, the real fur toy control group.



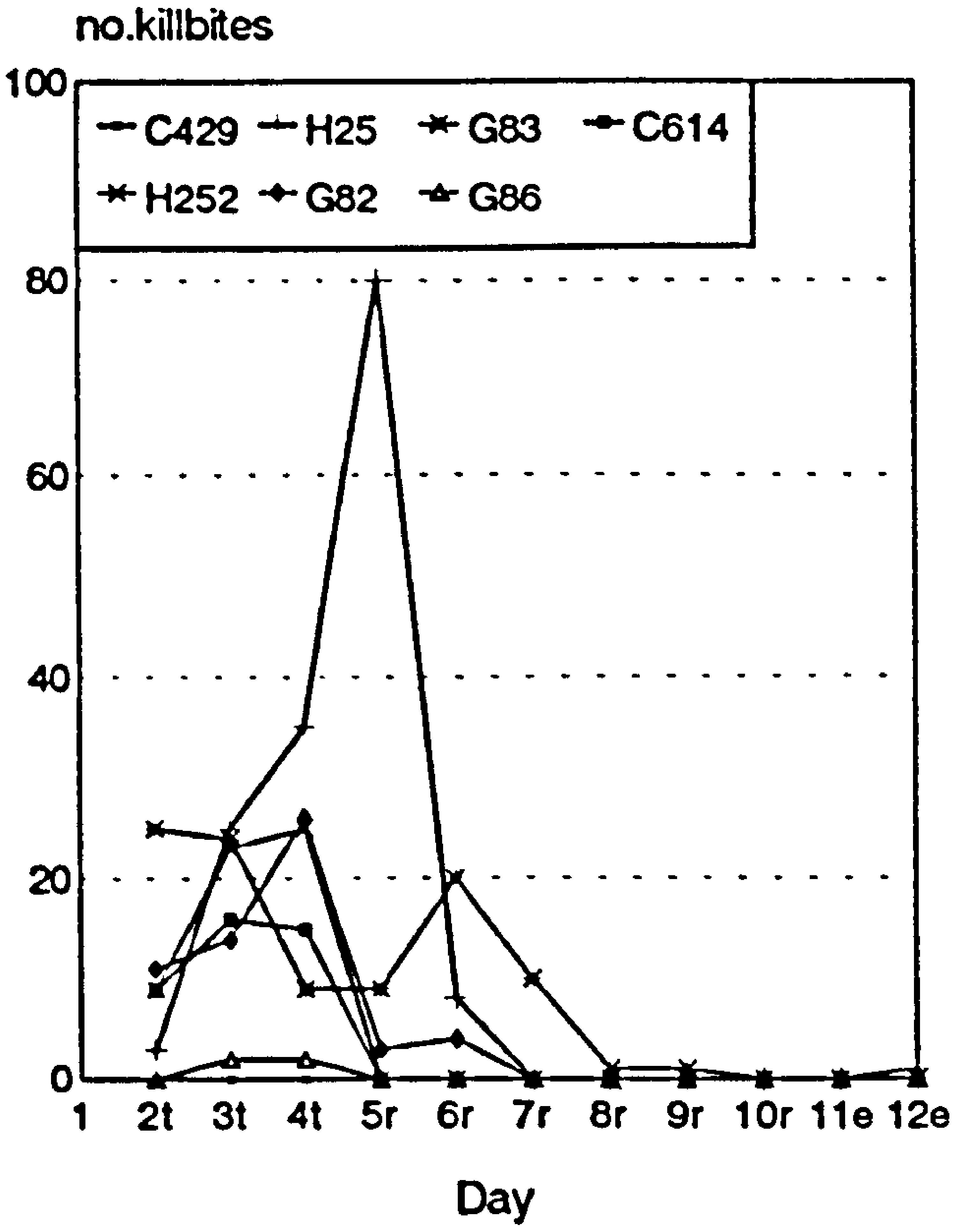
t-training period; r-reinforcement; e-extinction

Figure 7.16 The frequency of killbites in group 2, the reinforced 'teacher' group.



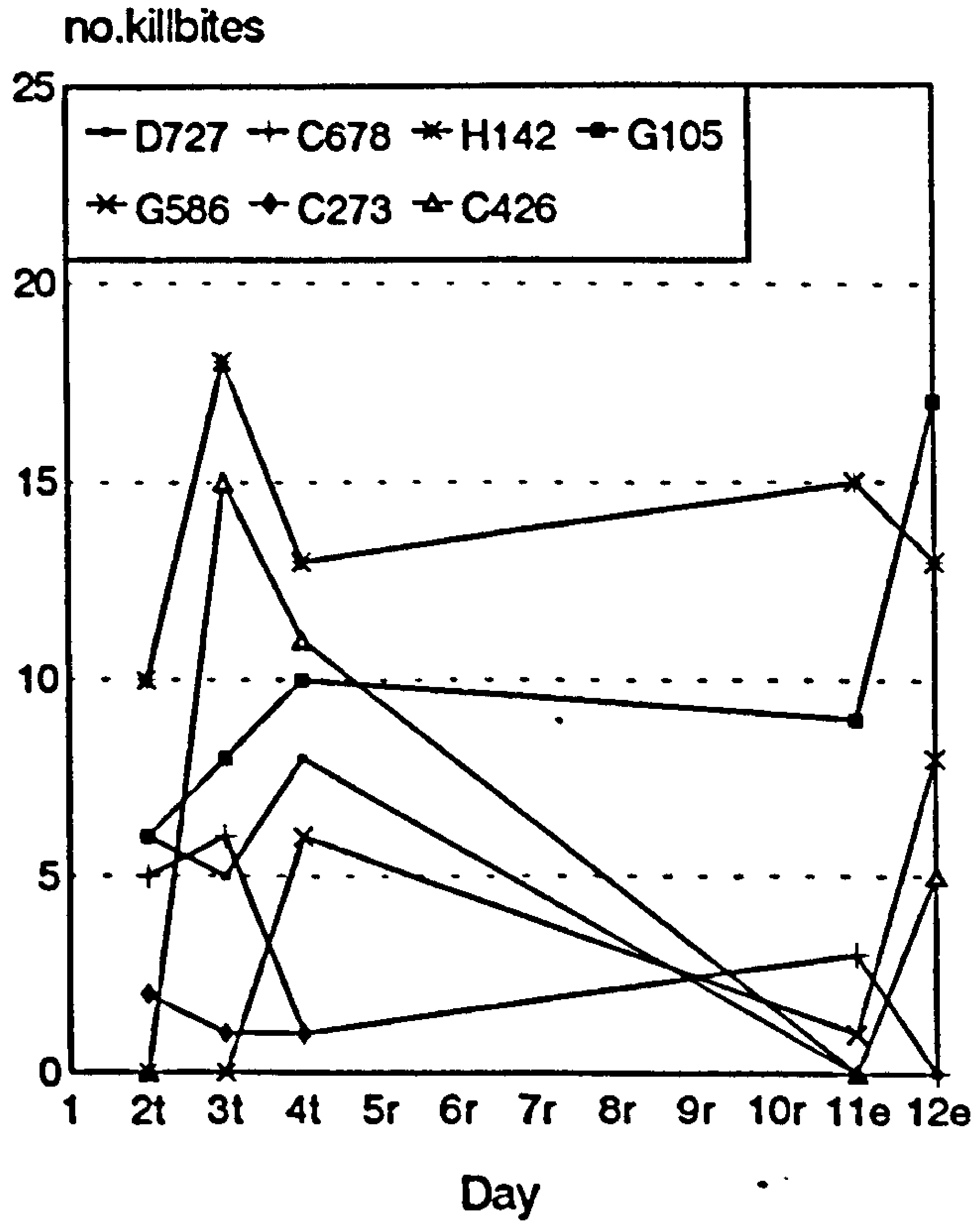
t-training period; r-reinforcement; e-extinction

Figure 7.17 The frequency of killbites in group 3, the unreinforced 'teacher' group.



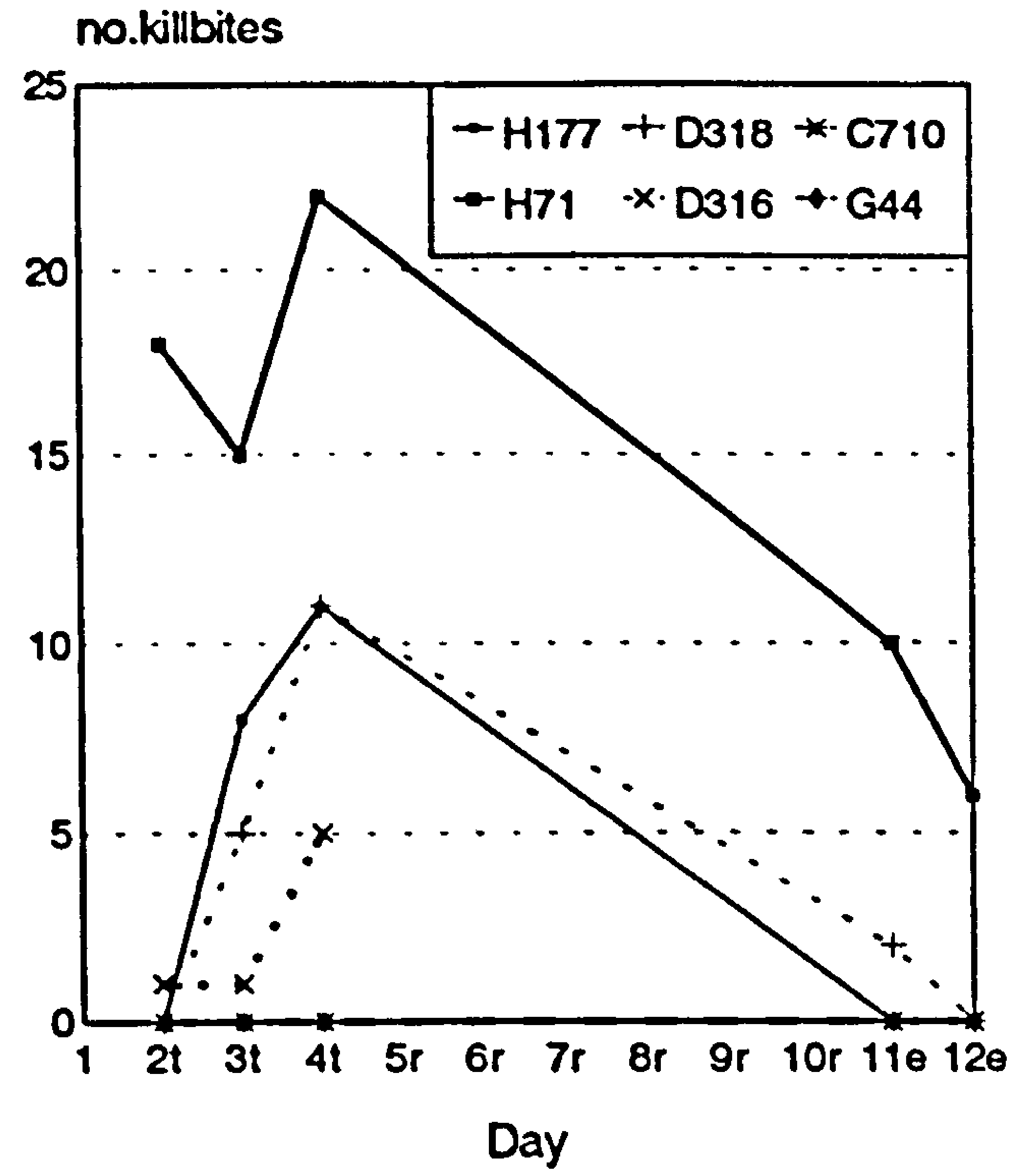
t-training; r-reinforcement; e-extinction

Figure 7.18 The frequency of killbites in group 4, the group observing group 2 (reinforced teacher group).



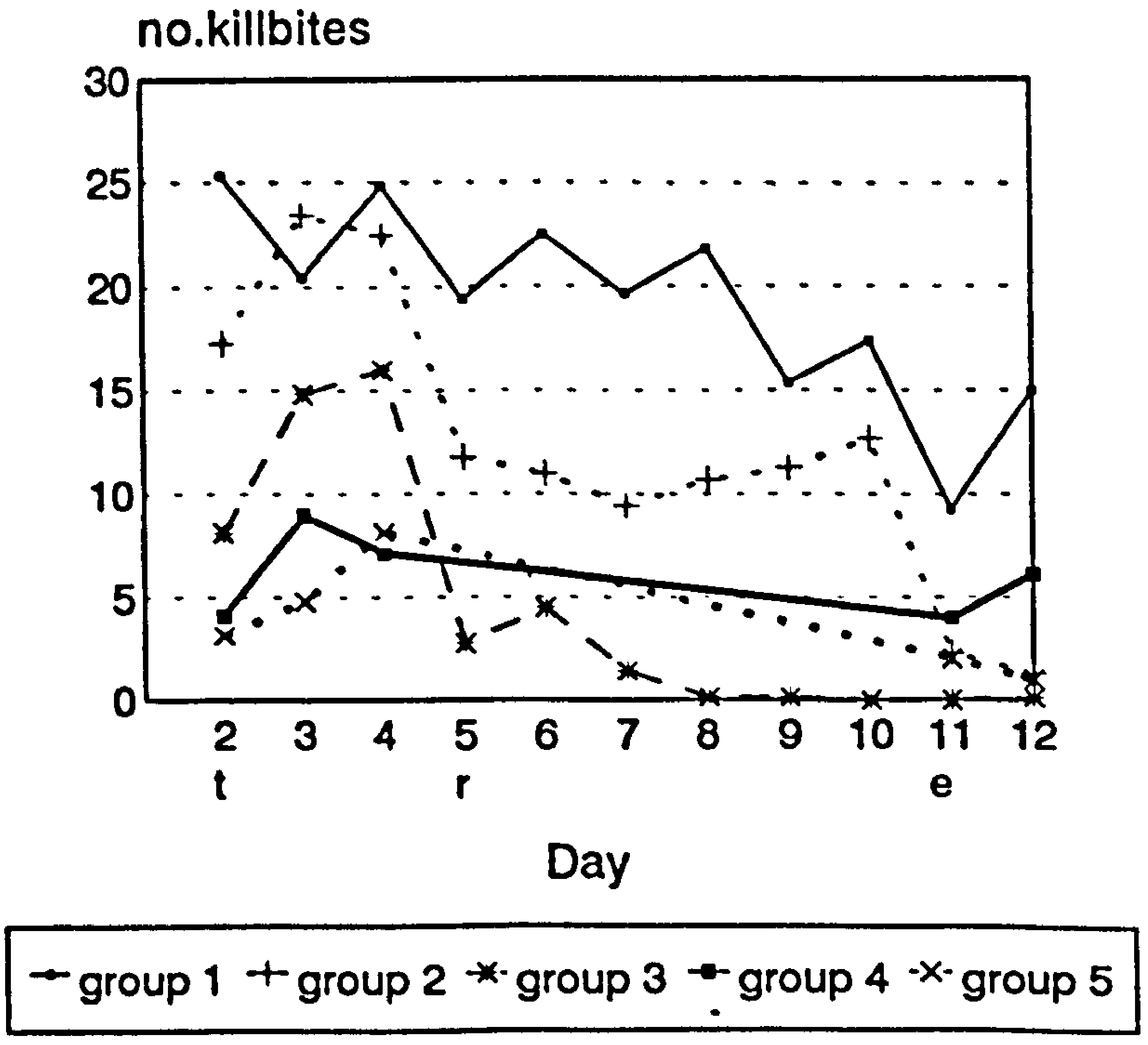
t-training; r-reinforcement; e-extinction
cat C273 was moved on day 4 of the experiment

Figure 7.19 The frequency of killbites in group 5, the group observing group 3 (unreinforced teacher group).



t-training; r-reinforcement; e-extinction
cat D316 was moved on day 4 of the experiment

Figure 7.20 The average number of killbites per group throughout the social transmission experiment.
t-training period; r-reinforcement; e-extinction



group 1-fur control' group 2-reinforced teacher;
group 3-unreinforced teacher;
group 4-observer of group 2; group 5-observer of group 3.

The statistical tests provide more reliable information, however:

1) 'Killbite' frequencies in the last two days of training and the last two days of reinforcement for group 2 (reinforced 'teacher' group), and group 3 (unreinforced 'teacher' group) were both significantly different, at $p<0.05$ and $p<0.0001$ respectively. The frequencies were both lower in the reinforcement period, much lower in the case of group 3.

2) The frequency of 'killbite' was significantly different on the last two days of reinforcement and the two days of extinction for group 2, at $p<0.005$. The frequencies were lower in the extinction period. In group 3 there was no significant difference between the frequencies in the last two days of reinforcement and in the extinction period.

3) Of the comparisons of group 2 and 3 data, there was a significant difference between frequencies of 'killbites' on the last two days of reinforcement ($p<0.05$), but no significant differences between the 2 groups on the last two days of training or the two extinction days.

4) Finally, there was no significant difference between the 'killbite' frequencies on the two test days (11 and 12) for groups 4 and 5, the observer groups.

DISCUSSION

These tests uphold most of the trends deciphered from Figures 7.15 to 7.20. Tests 1) and 2) indicate that the frequency of 'killbites' declined in both 'teacher' groups. This was expected, since both groups received real fur in the training period, and the novel toy was chosen for its poor play stimuli. Even though play with the novel toy was reinforced the frequency of 'killbites' was lower than with real fur. This provides an insight into the extent of the effect which food reinforcement can have on response to a stimulus which is very different to toys which elicit intense play. This may be a result of the limit set by the cats' 'preparedness' to modify their behaviour; the large, polythene covered toy is a highly unnatural toy, and learning to play with it was expected to be limited as a result.

However, the food reinforcement received by group 2 did significantly increase the frequency of 'killbites'; the frequencies were higher in the reinforcement period than in the extinction period, indicating that the cats increased 'killbites' in response to a food reward. When no food reward was received the cats in group 3 showed no change in 'killbite' frequency.

The difference in 'killbite' frequency between groups 2 and 3 on the last two days of reinforcement also indicates that the food reward was reinforcing play, since group 2 performed higher frequencies of 'killbite' than group 3. That there was no difference between these two groups on the last two days of training was expected, since both were receiving the real fur toy and were balanced groups. The lack of difference between these two groups during the extinction phase is harder to interpret; it would be expected that they should be different, since the food reward received by group 2 had increased 'killbite' frequencies, and this difference should continue into the early part of the extinction period. However, this discrepancy may be explained by the fact that a reinforced response to an unnatural stimuli such as the novel toy may be expected to be extinguished extremely rapidly once reinforcement had been discontinued. This may account for the lack of significant difference between these two groups.

The final test indicated that there was no difference between the two observer groups on the test days. Since one group had been watching the reinforced 'teacher' group, which showed higher 'killbite' frequencies than the unreinforced 'teacher' group, it can only be concluded that there was no social transmission of the different play behaviour.

However, it is possible that social transmission could have taken place; a behavioural modification which has been learnt by observation is generally only performed by the observer if the (favourable) consequences of performing the behaviour are available. In the two test days group 4, which observed the reinforced 'teacher' group, did not receive any reinforcement when presented with the novel toy. Without the favourable consequence which it had been observing throughout the reinforcement period, the observer cats did not perform the newly learnt behaviour. For this reason the results of this experiment do not prove definitely whether social transmission had occurred or not. Had the novel toy been presented with the favourable consequence (biscuits) which the observer cats had learnt were associated with it, there may have been a difference in their response on the test days.

7.6: CONCLUSION

These three experiments have provided an indication of the flexibility of the cats' play repertoire. It has been shown that cats will respond to food reinforcement by altering both play quantity and quality as required. It was possible to increase play duration in the first experiment, and to increase the frequency of paw contacts in the second experiment, by appropriate reinforcement with a food reward. In the third experiment it was possible to reinforce an increase in the frequency of biting of a novel toy which had very low sensory value, a toy which would normally receive a very low frequency of biting. These changes in play occurred rapidly, suggesting that play can be easily modified in response to feedback and reinforcement received when play is performed.

There are some important factors which should be taken into consideration when attempting to explain the problems of these experimental protocols. Some problems were a result of protocol faults, such as small sample sizes, and difficulty establishing controls. Also, the performance of an animal on any reinforcement schedule is affected by its motivation. In general, reinforcers are most effective when the animal is under deprivation conditions (Nevin 1973), such as hunger, which serve to increase the animals motivation to perform the behaviour required. Deprivation appears to alter (shorten) the time not spent performing the reinforced behaviour, rather than increase the frequency of performance of the behaviour. It is thus possible that depriving the cats of food for several hours before the experiment might have increased their motivation to perform the reinforced behaviour patterns. However, all cats used were tested shortly after their morning meal, and were thus less motivated to respond to food reinforcement. (However, the reinforcer used was highly palatable; when deprivation is used the reinforcer is usually normal food of only moderate palatability).

Insufficient motivation may have been a problem in the social transmission experiment; it may have been that merely watching the 'teacher' cats through glass provided incomplete information for the observer cats, and that they were unable to learn fully the favourable consequences (receiving a biscuit) of playing with the novel toy. Again motivation to perform the learnt behaviour must be sufficiently high in the observer cats, and this may have increased by previous deprivation.

The extent to which modification of play can occur must also depend upon the cats' behavioural flexibility. The response-reinforcement design used in these experiments does not account for factors such as behavioural flexibility and 'intelligence' of the cats (Bindra 1978). This is because motivation is not considered in the response-reinforcement framework. However, for the exploratory purposes of this chapter these weaknesses are not of great importance.

8

DISCUSSION

The main hypothesis of this study is that object play in adult domestic cats, including non-hunting adults, is related to predatory behaviour. This hypothesis was initially based upon the observation that object play and predation are structurally similar (Egan 1971, Russell 1990). In this study I have shown that adult object play is also similar to predation in its external and internal causation, the latter including its motivation and the influence of hunger.

In order to substantiate the hypothesis presented here, it has been necessary to draw parallels between the known properties of predation, its structure, causes and motivation, and object play by adult cats. Since this study has focussed upon play behaviour alone, for ethical reasons, comparison was made with published accounts of predation. Thus, in order to discuss the findings of this study with respect to predation, it is necessary to briefly recap the relevant features of predatory behaviour.

8.1: PREDATION

The importance of a predator's environment and life experience upon its predatory behaviour also has parallels in the study of play behaviour. Understanding the nature of predatory behaviour, whether it is a consummatory behaviour, what motivates it and what factors end its performance is also germane when considering play behaviour. The experiments described in this thesis in chapters 3 to 7 mainly address similar questions. One of the most relevant areas of research for the conclusions of this study is the influence of hunger on the expression of predation.

The influence of hunger

Much early research focusing upon the influence of hunger on predation was concerned with determining whether the killing instinct was part of the same motivational system as hunger and feeding, so that they were effectively the same class of behaviour. Experimentation was mostly neurobiological, involving the search for neural structures and correlates with behaviour observed.

In a review of research findings up to 1975, Polsky (1975) examined a large amount of experimental work, some of which provided evidence for the hypothesis that hunger (and feeding on prey) has no influence upon predation, and some which provides evidence for an association between the two.

Polsky documented strong arguments to support the hypothesis that hunger has no influence upon the expression of predatory behaviour. Electrical stimulation of the so-called attack site in a cat's hypothalamus was shown to elicit attack on a prey animal (rat) despite the fact that the cat was feeding, and had been deprived of food prior to its meal (Flynn 1970). Behavioural observations support this; cats deprived of food for 48 hours before being fed with their preferred food still interrupted feeding in order to attack a rat (Adamec 1976). Both types of experiment corroborate the hypothesis that predatory behaviour and feeding are separate behavioural systems which are under separate control, and are expressed in response to particular, distinct stimuli. The control sites of attack/predation and feeding were found at different locations in the brain, suggesting a physical as well as a control separation of both behaviours.

Phenomena such as surplus killing also point to a disassociation of hunger and predation, since despite not being hungry (or being hungry only initially) some predators (including cats) may kill numerous prey, without stopping to feed. In this situation predation occurs independently of the hunger of the animal; hunger does not cause predatory behaviour, and satiation does not stop predatory behaviour.

However, there is also evidence for an interaction between hunger and predation. In experiments in which naïve non-killer animals are subjects, hunger is often found to influence predatory behaviour. However, the influence recorded by Polsky (1975) is indirect; hunger is said to 'potentiate the induction of killing in the naïve subject'. For a naïve animal which is exposed to prey, dead or alive, and fed dead prey when juvenile, hunger often induces predatory behaviour (Paul & Posner 1973).

The influence of hunger also appears to be variable between and within species, and appears to be highly context-specific. Polsky concluded that hunger influences and potentiates predatory behaviour in naïve rats and hamsters *Mesocricetus auratus.* Biben (1979) found that the probability of a kill could be predicted according to hunger and prey vulnerability in domestic cats. This finding contrasts with that of Kuo (1930), who found that hunger condition had no effect on rat-killing in kittens.

Overall, the relationship between hunger and predation remains unresolved, and there is no general theory which can be applied to all predators, other than that predatory behaviour appears to take precedence over feeding (Polsky 1975, Adamec 1976). The influence of hunger is equivocal, and affected by species, and by the age and experience of the individual animal. Most authors conclude that while hunger and predation may not interact at the control or motivational level, they are still mutually interactive (Adamec 1976).

The ontogeny of predatory behaviour

It is generally agreed that an individual's adult predatory behaviour is directed and modified by its exposure when juvenile to prey, both dead, alive, and as food, and by other factors such as observational learning from adults (Kuo 1930), and the individual's developing 'personality', whether defensive or aggressively biased (Adamec 1983).

From neurobiological experiments it is known that the basic features of predatory behaviour develop without any influence from experience. Predatory attack can be elicited by electrical hypothalamic stimulation in cats which have been raised in isolation and with no exposure to prey (Flynn 1967). Newly born predators which have not had any experience of prey respond instinctively to certain key prey characteristics, such as size (Curio 1976), and may even be born with innate prey preferences (Burghardt 1970).

However, as stated by Kuo (1930);

'In behaviour, nature is what can be built in and not what is supposed to unfold from within.'

This statement suggests that an animal's behaviour is determined by its experiences throughout life. In particular, prey preferences are formed by a young animal's early experience with prey, and the young animal's eventual predatory 'style' is influenced by its early experience and especially by observational learning from its mother's behaviour. However, the extent to which such experience and learning influence the animal's behaviour probably has more of a modifying role, rather than a strongly determining role (Adamec 1980).

The object play of juvenile carnivores is thought to be a method of practicing and refining predatory skills for later, adult use (Leyhausen 1979, Sen Gupta 1988). This hypothesis is based on the structural similarity of kitten object play patterns and adult predatory patterns. However, it has never been proven that juvenile object play results in an adult with superior predatory skills, or that a lack of juvenile object play results in an adult with inferior, undeveloped predatory skills (Caro 1980).

Appetitive or consummatory?

It was traditionally assumed that the consummation of predation was eating the captured prey. The capture of food was supposed to be the function of predatory behaviour. However, in the light of studies of the relationship between hunger, feeding and predation, this can no longer be assumed (Polsky 1975). Hunger is not the chief determinant of predation, and the whole feeding system appears to be physically and motivationally separate (but interactive) from the predatory system.

If predation was necessarily appetitive for feeding behaviour, problems would arise when the predator received food without having performed predatory behaviour (for example, scavenging for carrion). Animals could be expected to ignore this food if there was no opportunity for the performance of the appetitive behaviour (Paul & Posner 1973). Food presented to a predator should also prevent predatory behaviour, but this does not occur in many cases (Polsky 1975).

Predation does have appetitive characteristics, despite the often made proposition that killing the prey is the both end-point and function. Killing the prey often does not mark the end of predation; felids commonly continue predatory behaviour with prey they have just killed (Leyhausen 1979). This suggests that the death of the prey is not consummatory. Various authors have termed this continued predation play, though this appears to be a purely subjective distinction based on the observer knowing that the prey is dead, that the functional goal of predation has therefore been obtained, and so predation should be complete. Despite this criticism, it seems likely that predation is appetitive to killing (Russell 1990), and that there is no pre-determined consummatory point or pattern which causes predation to stop. The circumstances of each performance of predation will determine the duration and end-point in each case. Thus, the expression of predatory behaviour is highly flexible, and cannot be as easily characterised as once thought.

8.2: ADULT OBJECT PLAY

This understanding of the structure, motivation and ontogeny of predation forms the basis of the hypothesis that adult object play is closely related to predation. The experiments described in this study have revealed some characteristics of adult object play in cats which are similar to those of predation, as described in 8.1. This in turn suggests that there must be a reason for this association other than pure coincidence.

Is the structure of object play more variable than predation?

One of the reasons for the definition of object play as being distinct from predatory behaviour, which it resembles, is that despite involving the same behaviour patterns, the structure overall is more variable. All types of play are said to be recognisable according to a number of structural differences from the behaviour they resemble. These include the unnecessary or uneconomical repetition and exaggeration of behaviour patterns; incomplete and inhibited behaviour patterns; a lack of order of the behaviour patterns; the inclusion of behaviour patterns from more than one type of behaviour; and detachment from any specific stimuli (Symons 1978). On these grounds play is defined as a separate behavioural category, invoking a distinct motivation and causal stimuli conditions.

However, there is evidence that some of these characteristics do not apply to adult object play, and that the predatory behaviour which adult object play resembles also possesses some of the features which are said to define play.

The following results obtained in this study have shown that adult cat object play does not conform to the definition of play as a separate behaviour.

In the sequence analysis of object play in Chapter 6, repetition of behaviour patterns was found. However, this is also true of predatory behaviour, in which patterns such as 'killbite', 'chew', 'kick', 'hit' and 'clutch' are repeated many times (Biben 1979). Repetition of the same behaviour patterns occurred in object play. The repetition was also found to occur with toys of high sensory value such as real fur and feathers. The stimuli with high sensory value for play correspond to those expected from prey animals, such as real fur, feathers and small size. The extent of repetition of patterns was also found to be variable, depending upon the sensory value of the toy. Toys with lower sensory value elicited less repetition of close contact, 'killing' patterns, but some repetition of minimal contact 'preliminary' patterns was exhibited. This has been observed in cats with prey; cats which are presented with suitable prey show a tendency to dispense with preliminary patterns, and show repetition of close contact patterns. Conversely, cats presented with prey which is large or intimidating, show an increased repetition of preliminary patterns which do not involve close contact, such as 'hit' (Biben 1979).

There does not appear to be any exaggeration or inhibition of play patterns within adult object play. It is commonly suggested that the 'killbite' in particular does not occur or is inhibited in object play, this being the proposed consummatory behaviour pattern in predation (Egan 1971, Martin 1984). However, sequence analysis shows that the killbite does occur, as well as the evidence regularly provided by toys which are destroyed by biting and ripping with the teeth during play bouts by juvenile ferrets (Russell 1990). Destruction of toys was also common in my own observations of play in cats throughout this study. A lack of exaggeration has been observed in other types of play. Hill and Bekoff (1977) compared three behaviour patterns which occurred in both play-fighting and true fighting in eastern coyotes *Canis latrans*. They noted that for one pattern, 'scruff bite', there was no significant difference in duration of performance (their selected measure of exaggeration) between play-fighting and fighting. The other two patterns, 'stand over' and 'general bite', were actually less exaggerated in play-fighting than in true fighting. In the sequence analysis of adult cat object play in Chapter 6, repetition of particular behaviour patterns was found, but there was no suggestion of exaggeration of patterns. The general impression is that it is not an exaggerated, and that play patterns are performed in the same manner and for the same duration as in predatory behaviour. However, this study was not aimed at producing supporting experimental evidence. It would have been necessary to compare the performance of play patterns with those of predatory behaviour to determine whether the play patterns are exaggerated.

The claim for the incompleteness of adult object play is that the 'killbite' does not occur. As noted above, the sequence analysis of play has revealed that the 'killbite' does occur in adult object play, and is as strong as in predation, as are other patterns such as 'kick' which are also responsible for the destruction of toys.

Sequence analysis also revealed that adult cat object play possesses a structure which can be easily described. A central, basic structure was defined and related to changes in the motivation of the cat. Patterns were identified which were used to characterise low motivation and high motivation, and the pattern 'clutch' was identified as a point in the performance of a play bout from which play could either escalate to close contact, high motivation patterns, or could revert to low motivation, low contact patterns. Overall, the structure was defined as being predictable at a basic level, with repetition and elaboration of particular patterns being determined by the sensory value of the toy, and factors such as the motivation of the cat and the cat's individual play 'style'.

That adult cat object play may include behaviour patterns from more than one type of behaviour is not supported by observations made in the course of this study. All behaviour patterns recorded were clearly analogous with predatory behaviour patterns (see Appendix for ethogram). All behaviour patterns were unambiguous, and no patterns from other behavioural systems were ever noted, except when the cats were avoiding or ignoring the toy. In this circumstance behaviour patterns such as 'groom' and 'avoid' were recorded.

The inclusion of behaviour patterns from more than one behavioural system is more characteristic of social play, which often involves patterns taken from more than one behaviour, such as aggression, copulation and prey capture, especially when performed by juveniles (Muller-Schwarze 1968, 1971).

Finally, in the experiments described in Chapter 3, adult cat object play has been shown to occur as a result of some of the same external stimuli as predatory behaviour. Toys which elicit intensive play were shown to be those which possessed characteristics reminiscent of real prey, such as real fur, small size and movement. Conversely, toys which did not elicit intensive play, and which were mostly ignored or avoided, were those with stimulus characteristics dissimilar to real prey, such as a polythene covering, no movement, an alien or novel odour or sound, and large size.

What is the influence of hunger?

The influence of hunger on adult object play was examined in Chapter 4. All cats used in the experiment were inexperienced hunters, with no previous exposure to rodent prey, only to unobtainable birds sighted from their enclosed yard. Experience of predation would only have been with insects. Interpretation of the results obtained was carried out using the relevant literature as reference and for comparison of play with predation. This was necessary, since (as already mentioned) no experiments with predation of live prey could be carried out during this study.

In Chapter 4 food deprivation was found to increase play intensity, and to change play quality. The frequency and duration of play patterns was greater with increased time since the last meal. Exploration (as shown by performance of 'sniff') of a medium sized toy increased with hunger. With a small toy, close contact behaviour patterns such as 'killbite' increased with hunger, while exploratory behaviour patterns decreased with hunger, as play was physically closer to the toy. This change in play with increased hunger was also illustrated with sequence analysis in Chapter 6. The cats did not increase the frequency of close contact behaviour patterns with the medium sized toy. This was interpreted as being the result of an inability to overcome fear of the larger toy, despite increased hunger.

Hunger was insufficient motivation in this situation.

It has been suggested that hunger may produce a 'general arousal' which may account for the increased play behaviour and decline in fear when the cats were hungry (Hepper, pers.comm). While increased general arousal may explain the effects of hunger on the small toy (increased play and general activity), it cannot explain the specific increase of exploratory sniffing of the medium toy. In this case hunger can only have affected a specific motivation, causing the cat to show more exploration and interest in the toy, without a simultaneous increase in general activity or 'arousal'.

It may not be straightforward to relate the influence of hunger on object play to that on predation in general, since the influence of hunger on predation is modified by species, age and predatory experience. However, the influence of hunger upon cat predation has been studied, both in kittens and adults. Kuo (1930) found that hunger had no effect upon the expression or emergence of predatory behaviour in kittens which were first presented with rats and mice from six days of age. Adamec (1980) found that hunger affects predation in inexperienced juvenile cats which were between six months and one year old; specifically hunger intensified biting and facilitated pawing attack. He also found that defensive behaviour toward the prey was attenuated by hunger. Finally, Biben (1979) found that hunger increased the likelihood of killing prey in adult cats that were experienced hunters.

Thus, the effect of hunger on object play described in Chapter 4 was similar to that found by Adamec and Biben on predation in young and adult cats. This suggests that motivation of the two behaviours is similarly affected by hunger, that is, it is increased. Adult object play and predation may share their motivational basis. This would explain why there are also corresponding qualitative changes, in the frequency of biting, and in exploratory behaviour, with increased hunger in both object play and predation.

Is object play appetitive?

Part of the findings of Chapter 5 concerned the nature of object play. Object play lacks an obvious goal, end-point or circumstance. This leads to the assumption that it is an appetitive behaviour, these being some of the features of an appetitive behaviour (Wood-Gush & Vestergaard 1991, 1993). One of the aims of the experiments in Chapter 5 was to determine how the performance of an object play bout was stopped, there being no consummatory end-point either in terms of a goal or consequence or an obvious qualitative change in the behaviour which might indicate that it is about to end. The motivation of object play was found to remain at an unchanging level throughout a play bout, but the play was stopped by habituation to unchanging stimuli.

Sequence analysis of different sections of play bouts (middle and end third), did not reveal any qualitative differences in the structure of object play which could indicate that the play bout was about to end. Although it was possible to describe the motivation level of the cat according to the behaviour patterns it performed, no changes in frequency of pattern performance could be used to predict the end of a play bout. In particular, the 'killbite' did not appear to have a consummatory role since it occurred throughout play bouts. It was therefore concluded that object play is an appetitive behaviour.

Why should adult object play be solely appetitive? It is possible to speculate that adult object play is appetitive for reasons that assume a close motivational and structural relationship with predation. This was discussed in detail in Chapter 5. A motivational system was suggested which could be applied both to predation and object play. The general response to any object which a cat encounters is to habituate rapidly to it. This is halted if the object possesses any features determined by two mechanisms, one responsible for stimulus quality selection and another which monitors changeability of the object. Selected stimuli prevent the cat from habituating to the object and enable further exploration of the object. However, changeability is also required to prevent habituation to the object and to allow play or predation to continue. Only if the object possesses the correct stimuli and is constantly changing will habituation be prevented, and play or predation continue.

Stimuli which elicit play were determined in Chapter 3, and were found to be similar to those which are known to elicit predation. However, in Chapter 5 habituation occurred to these stimuli unless they were regularly changed. The two characteristics of stimuli quality and changeability interact to determine the play or predation response.

This system enables appetitive exploration of any object which has the correct stimulus characteristics and changeability, and prevents unnecessary attempts to play or hunt unsuitable objects, that is those which do not possess the correct characteristics.

What role does object play have in the adult cat's behavioural repertoire?

The aim of this discussion has been to demonstrate that adult object play in domestic cats which are inexperienced hunters is closely related to predatory behaviour. This is based upon the comparison of work in this study and the work of other authors to understand the control of predation. Comparison has shown that these two types of behaviour are very similar in structure, are elicited by the same external stimuli, are both primarily appetitive behaviours and are affected in a similar way by food deprivation. These findings uphold the hypothesis that adult object play and predation in cats are controlled in the same way and share the same motivational basis.

The findings of this study suggest either that the usual defining characteristics of play as a distinct behavioural category are erroneous, or that adult object 'play' behaviour is not play, and is not distinct from predation.

To determine the role of object play in the behavioural repertoire of adult cats it is necessary to consider the following;

1) In kitten behaviour object play is most easily explained as practice for predation (West 1977).

2) Adult cats which have learnt predation through kitten object play, and which have become experienced hunters have no need to practice predation with object play, but continue with predation (Loizos 1966, West 1977, Biben 1979). (Hunting cats 'play' with prey as well as inanimate objects, but this behaviour is beyond the scope of this study).

Adult non-hunting cats must therefore either be still practicing predation as kittens do, or are performing predatory behaviour and effectively hunting their toys. That adult object play is similar to predation in the ways described above suggests that the latter hypothesis is more likely. Despite the absence of the death of a prey animal, object play may correspond to the appetitive parts of predation, attacking, injuring and immobilising the prey (Russell 1990).

8.3: THE MODIFICATION OF ADULT OBJECT PLAY

While the main aim of the study was to examine the control of object play and relate it to predation, the final part of the study was not concerned with testing this hypothesis. The experiments described in Chapter 7 were concerned with exploring whether it is possible to alter a cat's play structure using positive reinforcement. They were also aimed at determining if it is possible to alter the cats' response to external stimuli so that they would respond with play to stimuli which do not normally elicit play.

Although smallness of sample meant that statistical analysis was dominated by individual differences, it was clear that it is possible to modify the quantity and quality of object play using food rewards to positively reinforce the required changes. The control and motivation of object play can thus be affected by positive reinforcement with food rewards. Cats learnt to associate food rewards with the performance of a particular behaviour pattern and increased the frequency of the chosen pattern in order to obtain more food rewards.

It was also possible to alter the cats' response to an object which was of low sensory value, a cat-sized, polythene covered toy. Positive reinforcement of 'killbites' with food rewards resulted in an increase in biting on a toy which combined two stimuli which had been shown to elicit more avoidance than play and very low frequency biting (see Chapter 3). That the cats were able to alter their play response to this toy, and to increase the frequency of biting, indicates that the play response is flexible and can be altered by experience. This may indicate that links between play and feeding can be established easily, as would be expected of predation and feeding. The cat is modifying its 'technique' in both cases according to whether food results. However, it must be an appropriate reward for responding to a particular stimulus: certain responses cannot be learnt despite a food reward for performing the response. For example, cats are unable to learn to run towards a sound stimulus for a food reward delivered in a different place, since this is inappropriate reinforcement of the response to the sound (Davey 1989). That food is an appropriate reward for an increase or change in play (as it would be expected to be for an increase or change in predation), suggests that play and predation are closely related.

Although attempts to illustrate social transmission of play changed by positive reinforcement were unsuccessful, this experiment was affected by the use of an imperfectly designed protocol, so it cannot be concluded that social transmission of object play does not occur.

8.4: CONCLUSION: DEFINITION OF ADULT OBJECT PLAY IN DOMESTIC CATS

It has been argued that adult object play in domestic cats is closely related to predation, and various experimental evidence has been provided which supports this hypothesis. The definition of play (object, social or solitary locomotory) has always been inexact (Fagen 1981). However, it may be possible to classify adult object play in non-hunting domestic cats with predatory behaviour. The two share external and internal causation and are structurally similar.

Therefore it may not be necessary to determine or ascribe any effects, role or motivation of adult object play as distinct from those of predation, since this play may be part of the same behavioural system, with predation being called predation because it involves prey, and play being called play because it does not.

It is possible to speculate that adult object play in non-hunting domestic cats is an artefact of domestication and dependence upon human owners for the provision of food. Such play may not be observed as frequently, or be elicited as readily in feral domestic cats, or in wild *Felis* species, for whom the hunting of prey is essential for survival. However, it is possible for a non-hunting, human-owned cat to survive and reproduce successfully without ever having hunted live prey, only ever having hunted objects and toys. Thus, adult object play may have become a distinctive part of domestic cat's behaviour because of reduced opportunities for hunting. This may be a result of lack of hunting experience in an individual cat's lifetime and/or genetic changes in the central organisation of hunting behaviour, brought about by domestication. Hunting may only be classified as play as a result of anthropomorphism by owners; behaviour which does not result in the death of a small animal is termed play, while behaviour with similar external and internal causation which results in the death of a small animal is termed predation.

APPENDIX

DESCRIPTION OF BEHAVIOUR PATTERNS

Play behaviour patterns

***sniff**, the cat sniffs the object.

***bat**, the cat gently touches the object with one front paw, with the claws retracted.

***hit**, the cat touches the object with one front paw, claws extended, with more force than above. The object may be thrown aside.

***rear**, the cat stands up on it's hind legs in order to reach the object.

***grasp**, the cat uses both front paws to take hold of the object. The claws may be either retracted or extended.

***clutch**, the object is held close to the body with one or both front paws.

***kick**, the cat rakes and kicks the object with it's hind legs, while lying on one side, clutching and\or holding the object in it's mouth.

***killbite**, the cat delivers a strong bite to the object.

***holdmouth**, the object is held firmly and retained in the mouth, for a greater duration than is necessary for a single bite.

***chew**, the cat holds the object in it's mouth and chews it with rapidly repeated bites. The bites are smaller (that is, the mouth is not opened as wide as in a killbite), less forceful than a killbite.

***lick,** the cat licks the object.

Non-play behaviour patterns

***walk**

***run**

***stand**

***sit**

***crouch,** similar to sitting position, but the front legs are also bent.

***recline,** the cat lies on the floor, on it's side, front or back.

***watch,** the cat pays close attention to the object, tracking it's movement. The eyes are wide open and ears are directed at the object.

***avoid,** the cat ignores the object, paying no attention to it.

***groom,** the cat either licks it's fur or licks it's paw and wipes it over its head, ignoring the toy.

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