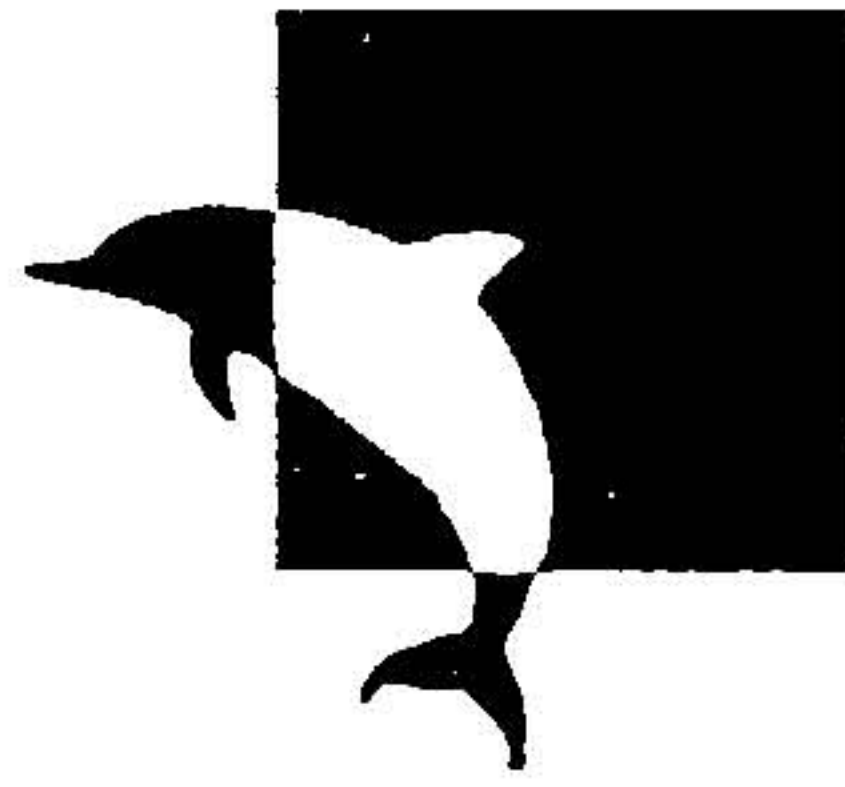




University
of Southampton

**FREQUENCY-DEPENDENT FOOD SELECTION BY THE
DOMESTIC CAT, *FELIS SILVESTRIS CATUS*.**

by

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Thesis submitted for the degree of Doctor of Philosophy

DEPARTMENT OF BIOLOGY

May 1994

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE
DEPARTMENT OF BIOLOGY

Doctor of Philosophy

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Preference for common food types ('apostatic selection') has been demonstrated in a wide variety of predators, and numerous mechanisms have been proposed to account for such selection. However, there are fewer examples of preferences for rare food types ('anti-apostatic selection'). In this study, frequency-dependent food preferences of farm, rescue shelter and cattery (laboratory) cats were examined using nutritionally defined artificial foods.

Initial experiments, designed to investigate the effect of spatial availability on selection, demonstrated that groups of farm and cattery cats tended to preferentially select the rare food types in 9:1 mixtures of two types of food pellet. Although simple mathematical models suggested that a component of this selection occurred purely as a result of variation between individual cats, further experiments on rescue shelter and cattery cats revealed that selection by individuals also tended to be anti-apostatic. Individual rescue shelter cats consistently showed stronger anti-apostatic selection than cattery cats. This result was attributed to differences between the foraging experiences of the two groups.

Experiments were also conducted on farm and cattery cats to examine the effect of temporal availability on food selection. Farm cats showed increased preferences for food types which had not been available to them for a defined period prior to preference testing, although this effect appeared to be dependent upon hunger levels and the temporal pattern of food availability. In comparable experiments, cattery cats showed only weak preferences for temporally rare food items. However, when foods were manipulated such that they were no longer nutritionally complete, these cats also displayed a clear preference for rare foods. These results are consistent with the hypothesis that anti-apostatic selection occurs when there are benefits to a mixed diet.

These experiments may offer some insight into the success of the feral domestic cats in urban areas; although obligate carnivores, they appear to possess the behavioural flexibility to select a reasonably balanced diet from nutritionally variable resources such as pig swill or household waste.

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Introduction

The domestic cat, *Felis silvestris catus*, is by far the commonest and arguably the most remarkable of all 37 extant species of felid. During the past 3500 years, the domestic cat has successfully exploited a wide variety of urban and rural habitats over an enormous geographic range, largely by virtue of forging a close social bond with humans. In the past few decades, the commercial potential of the domestic cat as a companion animal has provided the impetus for a wealth of research addressing its nutritional requirements and food preferences. However, owing to the applied nature of much of this research, few studies have investigated the foraging decisions of urban domestic cats within an ecological context. The research presented in this thesis aims to go some way towards redressing this balance by considering the mechanisms and consequences of *frequency-dependent food selection* (FDS) by the domestic cat.

FDS occurs when the preference (selectivity) of a forager for a particular food type varies with the availability of that food relative to other food types in the environment. Such preference changes can be caused by a multitude of behavioural mechanisms (reviewed by Greenwood 1984). As a result, FDS is a taxonomically widespread phenomenon, having been demonstrated in many species of invertebrates (reviewed by Sherratt & Harvey 1993) and vertebrates (reviewed by Allen 1988a). This type of selection has primarily been of interest to population geneticists and ecologists because of its potential effect on the stability of prey populations (Murdoch & Oaten

1974, Hassell 1978) and the maintenance of morphs within populations. For example, FDS by visual predators has been proposed by several authors (Poulton 1884, Cain & Sheppard 1954, Clarke 1962) as a mechanism whereby colour pattern polymorphisms of prey species, such as that found in the land snail *Cepaea nemoralis*, are maintained.

To date, only one (unpublished) study has tested for FDS by the domestic cat (Miles 1989), although other researchers (Thorne 1982, Bradshaw et al., summarized in Bradshaw 1992) have obtained results which indirectly suggest that FDS might be commonplace. Owing to the paucity of published data, the main objective of this introductory chapter is to synthesize our current knowledge of both frequency-dependent selection and the general foraging behaviour of the domestic cat. Initially, I shall describe some of the essential biology of the domestic cat and identify and classify its food habits (this classification will be central to the entire thesis). I will then review the FDS literature. This will be a fairly general review, for two main reasons. Firstly, this study is necessarily exploratory in nature. It is therefore important to appreciate the variety of mechanisms which can cause frequency-dependent selection, as well as to be able to frame the study in the correct context. Indeed, the majority of this chapter will be concerned with the general mechanisms of frequency-dependent selection and, where relevant, I will attempt to identify those mechanisms which may be of particular relevance to the foraging behaviour of the domestic cat. Second, although devoid of references to cats, the FDS literature has addressed important theoretical and methodological considerations which *are* applicable to cats. In the final section of this chapter I shall, in the light of the information presented, state the aims of my research.

1.1. THE DOMESTIC CAT : AN INTRODUCTION.

1.1.1. A Brief History.

The domestic cat, *Felis silvestris catus* (Order: Carnivora, Suborder: Feliformia, Superfamily: Feloideaidea, Family: Felidae) (Wozencraft 1989) has only relatively recently been domesticated, the earliest records of its occurrence dating back to Egypt 3500 years ago. The actual mechanism of domestication is not clear since the cat "...is neither a man-made species...nor simply an animal made captive for utilitarian purposes.." (Bradshaw 1992, p.6). Possible mechanisms of domestication

have been discussed by Serpell (1988), Thorne (1992) and Bradshaw (1992).

The phylogeny of the domestic cat has also been the source of some controversy. Formerly classified as a single species (*Felis catus*) it is now considered to be a subspecies of *Felis silvestris*, along with the Scottish Wild Cat (*F.s.silvestris*) and the African Wild Cat (*F.s.lybica*). Current molecular evidence (Randi & Ragni 1991) suggests that *F.s.lybica* is the closest living ancestor of the domestic cat.

1.1.2. Food Habits.

The domestic cat, like all felids, is an obligate carnivore since it lacks the necessary metabolic pathways to utilize plant material efficiently. These metabolic peculiarities are discussed by MacDonald et al. (1984). Despite their precise dietary requirements, domestic cats thrive in both urban and rural environments by utilizing a variety of different sources of animal-based foods. These foods fall into three general categories: commercial cat foods, human household waste (table scraps) and live prey. Based on the relative proportions of these food classes in the diet, I shall classify the food habits of the domestic cat into three groups: companion cats, urban feral cats and rural feral cats. However, it must be stressed that these groupings are not well defined; they simply represent convenient points on a continuous spectrum of dietary composition.

1.1.2.1. Companion cats.

The diets of companion (pet) cats, especially in cities and towns, consist predominantly of commercial catfoods, although many individuals will scavenge for food and catch (but rarely eat) live prey (Churcher & Lawton 1987). Reviewing the literature on diet selection by domestic cats, Fitzgerald (1988) found that the diets of companion cats in Germany contained almost exclusively household food and virtually no natural prey items. In general, it can be argued that companion cats are not required to make important diet choice decisions since good quality commercial foods will meet all their nutritional demands.

1.1.2.2. Urban feral cats.

Urban feral cats are free-living individuals which largely scavenge for food around human settlements (usually towns and cities), although they are often provided with

commercial food by cat-lovers. In this group I also include farm cats, which usually obtain a large proportion of their diet by scavenging on farm scraps (e.g. pig swill), as well as often being provided with food by the farmer.

Urban feral cats are widely distributed in the British Isles. Bradshaw (1992) considers that there are between one and two million cats in the U.K. which "do not have specific owners, but rely on hunting, scavenging for waste food, and handouts from cat lovers". In a 1977 survey of 704 colonies containing an estimated 12,000 cats (Rees 1981), waste bins provided food in 66.4% of cases, while 91.9% were actively fed. Clearly, the food obtained from household waste is a vital part of the diet of the urban feral cat. Data about the actual diet composition is scarce, but that which has been published is presented in table 1.1. Many of the food types in table 1.1 are not nutritionally complete, or at least contain elements which are not complete. The dietary choices of urban feral cats are therefore likely to have important consequences, both for the fitness of unneutered individuals, and for the general health of neutered individuals.

1.1.2.3. Rural feral cats.

Some domestic cats have reverted to a completely rural, solitary existence. These cats feed almost exclusively on live prey, usually birds, rodents and lagomorphs. Fitzgerald (1988) has reviewed the large number of studies which have analyzed the composition of rural feral cat diets. In European rural feral cats, lagomorphs, mostly rabbits, form a major part of the diet, and are usually only surpassed in frequency by cricetid rodents, such as the common vole, *Microtus arvalis*. A detailed review of the food habits of rural feral cats is outside the scope of this thesis. The interested reader is therefore referred to Fitzgerald (1988) and Macdonald et al. (1987, page 57) for a fuller discussion.

LOCATION OF COLONY	FOOD AVAILABLE	SOURCE
Horsepath Piggery, Oxfordshire.	Meat joints, milk, household scraps, swill remains, live prey.	Kerby (1987)
Church Farm, Oxfordshire.	Household scraps, farm casualties, afterbirth, dried pig food, live prey.	Kerby (1987)
Knowle Hospital, Hampshire.	Commercial catfood, kitchen scraps.	Brown (1993)
Fitzroy Square, London.	Commercial catfood, household scraps.	Tabor (1981)
Barley Park Farm, Devon.	Powdered milk, live prey.	Macdonald (1981)
Portsmouth Dockyard, Hampshire.	Commercial catfood, milk, household scraps, fish.	Dards (1979, 1981)
Lower Lanherne, Cornwall.	Milk, table scraps, dry cattle pellets, live prey.	Panaman (1981)
Southern Wisconsin: various locations.	Live prey, offal, cheese, milk, potatoes, rice, apples.	Errington (1936)
Pennsylvania State: various locations.	Live prey and 30-80% "garbage" (table scraps, milk, offal and other refuse).	Eberhardt (1954)
Wichita Mountains Wildlife Refuge, Oklahoma.	Live prey, 16% "garbage" (potatoes, chicken skins, bread, eggs, bones).	McMurray & Sperry (1941)
Fort Sill Military Reservation, Oklahoma (residential area).	Live prey, 67% "garbage" (chicken and duck heads, cooked meats, vegetables, corn husks).	McMurray & Sperry (1941)
Baltimore, Maryland.	mainly garbage & table scraps, some live prey (mainly rats).	Jackson (1951)

Table 1.1 *The food of urban feral cats.*

1.1.3. The Domestic Cat as an Experimental Animal.

1.1.3.1. The effect of domestication on behaviour.

The domestication of the cat has led to the view among some biologists that they do not merit serious scientific study. Macdonald et al. (1987) and Macdonald (1991) suggest that the view that the behaviour of cats is "unnatural" is a fallacy. They argue that man's association with the domestic cat does not invalidate the search for an adaptive basis for its contemporary behaviour. There are two lines of reasoning behind this view. First, many cats have lived under conditions of semi-independence for hundreds of generations. Macdonald, et al. (1987) state that "...the ease with which individual cats drift back and forth along the continuum of dependence upon man, paralleling the ability of many carnivores to adapt to various habitats....suggests that they remain adapted to a variety of domestic and 'wild' circumstances." The second point is that even if the cat possesses some artificially selected traits (for example, social tolerance and coat colours), this simply means that "...the biologists' net must be cast further to identify the forces to which cat behaviour is adapted" (Macdonald 1991). However, caution must always be exercised when attempting to invoke adaptationist explanations for *any* animal (e.g. see Gould & Lewontin 1979). Although the domestic cat may not have changed inordinately in 3500 years, its habitat most certainly *has*, and this in itself might be enough to invalidate functional explanations of behaviour. This is a point to which I will return later in the chapter, and throughout the thesis.

1.1.3.2. The role of the domestic cat in studies of food selection

The potential role of the domestic cat in studies of food selection has been cogently summed up by Bradshaw (1991): "On the one hand, they are the only members of the Order Carnivora which are readily accessible for studies of food choice, which may then be extrapolated to their wild ancestral species. On the other, their adoption as pets in millions of homes worldwide has been paralleled by the growth of an increasingly sophisticated pet food industry, and concerted research into their nutritional needs". It must be stressed, though, that the view that the domestic cat can be considered as a model for the food selection behaviour of wild felids has by no means been vindicated. In addition to Bradshaw's view, it should be noted that the food selection of urban and rural feral cats is also of great interest in its own right because, as outlined above, diet choice decisions will have fitness consequences.

1.2. FREQUENCY-DEPENDENT FOOD SELECTION : SOME BASICS.

1.2.1. Terminology.

The terminology used to describe different forms of frequency-dependent selection is often rather confusing. This is because the literature is derived from several biological disciplines (population genetics, ecology, animal behaviour and psychology), each of which has adopted its own nomenclature. Fortunately, Allen (1989) has cleared up many of these misunderstandings.

Apostatic selection (Clarke 1962) is the term used by population geneticists to describe the tendency of predators to take an excess of a prey type when it is common relative to other prey types in the environment. Similarly, *switching* (Murdoch 1969) is used by ecologists to describe the choice of prey by the predator. Switching occurs when "...in response to varying relative abundances of its prey species, the predator increasingly allocates a disproportionately large fraction of attacks upon the prey that is becoming relatively more abundant" (Murdoch 1977). Switching therefore describes the same events as apostatic selection. Synonyms for apostatic selection and switching also include *matching selection* (Bond 1983), *apostasis* (Cook 1965), *reflexive selection* (Moment 1962, Owen & Whitely 1986, 1988, Allen 1988b) and *pro-apostatic selection* (Greenwood 1985).

Anti-apostatic selection (Greenwood 1985) and *counter switching* (Visser 1981) are the terms commonly used to describe the tendency of a predator to remove an excess of a prey type when it is rare. Other terms which have been used to describe this type of selection include *oddity selection* (Bond 1983, Ohguchi 1978, 1981) and *unifying selection* (Pielowski 1961, cited in Allen 1988a).

In this thesis, I shall adopt the terms apostatic selection and anti-apostatic selection. There are two reasons for this. Firstly, the term "switching" has been mis-used in the available literature on felid foraging behaviour (e.g. Bergerud 1983, Kitchener 1991). In such cases, switching has generally been taken to mean a change in the major prey component of the predator's diet, without considering relative abundance (i.e. ignoring FDS). Second, the experiments presented in this report perhaps have more in common with those performed by population geneticists than those of ecologists. It is therefore more parsimonious to adopt the terms "apostatic selection" and "anti-apostatic selection".

1.2.2. The Evidence for Frequency-Dependent Selection by Vertebrates.

There is no doubt that FDS is an extremely widespread phenomenon. As I shall outline in sections 1.3 to 1.5, there exists such a multitude of behavioural mechanisms which can cause FDS that it is relatively rare to find experiments in which selection is frequency-*independent*. In this section, rather than attempt an exhaustive review of all evidence for FDS (which would be both too detailed and largely irrelevant), I shall simply attempt to (a) illustrate the experimental approaches and vertebrate subjects which have been used in studies of FDS, and (b) identify the experimental or natural conditions which influence the nature of FDS.

1.2.2.1. Testing for frequency-dependence.

The occurrence of FDS can only be demonstrated by quantifying the prey selectivity of the predator over a range of prey frequencies. Unfortunately, FDS is very difficult to demonstrate in natural ecosystems since field investigations require extremely accurate sampling of prey populations, precise observations or measurements of prey selection by the predator, and a long time span to allow prey frequencies to fluctuate naturally. The field data which is available, on lizards (Stamps et al. 1981, Perez-Mellado et al. 1991), sea otters (Ostfield 1982), roach (Townsend et al. 1986) and marten (Thompson & Colgan 1990), is therefore extremely valuable.

The logistic difficulties associated with field studies have dictated that most FDS studies have involved some form of experimental manipulation of predators and/or prey. These may range from near-natural experiments (e.g. Ringler 1985, Lundberg et al. 1990) to artificial laboratory situations (e.g. Reid & Shettleworth 1992). The majority of evidence for frequency-dependent selection, however, has come from "semi-artificial" experiments, in which wild predators (usually birds) are presented with artificial prey items (such as coloured pastry baits). These experiments attempt to model natural foraging situations, and have the advantage that artificial prey items can be easily manipulated.

Allen (1988a) identifies two types of experiment which can be used to demonstrate frequency-dependence: "training experiments" and "multi-frequency experiments". In training experiments, predators are trained on populations of a single prey type for a specified period, usually several days. At the end of this period, they are presented with equal numbers of the "familiar" prey type and an "unfamiliar" prey type, and the

relative predation on the two forms is observed. After a period of time, the training procedure is reversed. Preference for familiar (common) prey is indicative of apostatic selection. In multi-frequency experiments, dimorphic prey populations are presented to the predator(s) over a range of frequencies, and the numbers of each food type eaten are recorded. FDS occurs if there is an positive or negative association between prey frequency and prey preference. The merits of each of these methods will be discussed in chapter 2.

1.2.2.2. Evidence for apostatic selection.

Apostatic selection has been demonstrated in vertebrate predators using both training and multi-frequency experiments. The majority of studies have examined avian predators feeding on artificial prey. In these experiments, apostatic selection is usually detected at low prey densities, in which prey items are encountered *sequentially* (e.g. Allen & Clarke 1968, Allen 1972, 1976, Cook & Miller 1977, Cooper 1984ab, Fullick & Greenwood 1979, Manly et al. 1972, Raymond 1984, 1987, Tucker 1991, Willis et al. 1980). Multi-frequency experiments have also been used to demonstrate apostatic selection by fish (Popham 1943, Murdoch et al. 1975, Maskell et al. 1977, Hughes & Croy 1993).

Training experiments with vertebrate predators usually produce a training bias towards common forms (i.e. the food on which the predators have been trained is preferred over a novel food). Again, this has been demonstrated most frequently in birds (Allen & Clarke 1968, Allen 1973, 1974, 1984, Allen et al. 1988, Croze 1970, Harvey et al. 1975, Raymond 1984, 1987), although Soane & Clarke (1973) and Partridge (1981) have demonstrated a training bias towards common foods in rodents.

There is no direct evidence for FDS by any species of felid in the wild. Although rural feral cats (Liberg 1984, Fitzgerald 1988) and lynxes (Bergerud 1983) are known to be flexible in their prey choices, FDS has not been directly investigated. What little indirect evidence there is suggests that wild felids do not show any frequency-dependent preferences; Brand et al. (1976) found that lynxes exhibit a type I functional response to snow shoe hares, which implies opportunistic predation. Fitzgerald (1988) has also suggested that rural feral cats are opportunistic predators.

1.2.2.3. Evidence for anti-apostatic selection.

There are relatively few accounts of anti-apostatic selection by vertebrates. Whether this reflects the true behaviour of foragers or merely a lack of investigation is not entirely clear. However, there are excellent field data which provide evidence for anti-apostatic selection in natural populations. Perez-Mellado et al. (1991) examined the gut contents of the lizard *Lacerta monticola* over a six-month period and sampled the availability of its insect prey during this time using pitfall and sticky traps. Anti-apostatic selection was shown for three of the four major prey taxa of the lizard. Stamps et al. (1981) produced similar results in a field study of *Anolis aeneus*. Anti-apostatic selection has also been demonstrated in semi-artificial multi-frequency experiments when prey are at high densities (several thousand prey per m²). Allen & Clarke (1968), Horsley et al. (1979) Allen & Anderson (1984) and Wilson et al. (1990) have all demonstrated anti-apostatic selection by avian predators feeding on high-density prey. Similar results have been obtained for mice (Greenwood et al. 1984ab) and fish (Landeau & Terborgh 1986, Ohguchi 1978, 1981).

In general, training experiments have rarely resulted in preferences for the "unfamiliar" food type. However, Thorne (1982) has demonstrated that domestic cats show a decline in preference for a maintenance diet relative to a novel diet. Bradshaw et al. (summarized in Bradshaw 1992) also showed that feral and house cats preferred foods which were dissimilar to their usual diets.

1.3. BEHAVIOURAL MECHANISMS OF FREQUENCY-DEPENDENT SELECTION : I. PROXIMATE CAUSATION.

In this section, I consider the proximate mechanisms which can cause FDS. These mechanisms are, necessarily, described in a fairly broad context since virtually nothing is known about FDS by the domestic cat. In addition, it must be stressed that the mechanisms outlined here are restricted to those in which FDS arises primarily as a result of the behaviour of the predator, rather than as a result of predator-avoidance behaviour by the prey (e.g. communal defence, ability to find refuges; see Greenwood 1984).

1.3.1. Sensory and Perceptual Mechanisms.

1.3.1.1. Visual perception and attention.

The vast majority of FDS experiments have studied visual predators (Allen 1989). The perception of prey by the predator is influenced by the density of the prey, and this can lead to frequency-dependent biases in selectivity.

(a) Search image formation.

Apostatic selection by visual predators appears to be stronger when prey are cryptic (Cooper 1984, Tucker & Allen 1988), possibly because predators form "search images" for common, cryptic prey types (Allen 1989). Lawrence & Allen (1983) define a search image as "a perceptual change in the ability of a predator to detect familiar, cryptic prey". While there is much evidence purporting to support the search image hypothesis (e.g. Dawkins 1971ab, Lawrence 1985ab, Pietrewicz & Kamil 1979, Gendron 1986), Guilford & Dawkins (1987) have argued that this evidence could be equally well explained by a reduction in the search rate of the predator. To date, and perhaps surprisingly, it has not proved possible to distinguish between these two hypotheses experimentally.

(b) Confusion & perceptual contrast.

The search image hypothesis predicts only apostatic selection. However, there is a proximate mechanism based on visual perception which predicts anti-apostatic selection. I shall refer to this as the "visual contrast hypothesis". When prey occur at very high densities (such that the substrate is virtually obscured), it is possible that the rare forms become conspicuous in a "sea" of common forms (Greenwood 1984). As a result, the predator tends to focus on these rare prey types. Indeed, increased predation on odd or conspicuous prey in large uniform prey groups has been well documented in vertebrates (Mueller 1968, 1971, 1975, Ohguchi 1978, 1981, Landeau & Terborgh 1986) and, as we have seen, anti-apostatic selection tends to occur at high densities of prey. The confusion effect may be enhanced by prey movement; Wilson et al. (1990) showed that the anti-apostatic selection by wild birds on densely aggregated prey was greater when the maggots were moving (at 25-33°C) than when they were virtually stationary (at less than 3°C).

It is not known whether visual contrast or search images are important factors in determining food selection by the domestic cat. However, since cats do not feed on

visually cryptic prey, instead relying on movement for visual detection of prey (Turner & Meister 1988), the search image hypothesis is not likely to be applicable. Although cats also have poor eyesight at less than 10-20cm (Bradshaw 1992), it is conceivable that, when food items are at high density, visual contrast may have an effect on food selection. Other sensory modalities, such as olfaction, may be more important, though.

1.3.1.2. Olfactory mechanisms.

Many predators, particularly mammals, utilize olfactory cues in prey detection. Such cues have been referred to as "chemical search images" (Melcer & Chiszar 1989) or "olfactory search images" (Nams 1991), but this term is not particularly helpful since too little is known about the nature of olfactory prey detection to use the term "search image" accurately. Soane & Clarke (1973) trained mice on artificial flour and lard baits flavoured either vanilla or peppermint (the two flavours produced virtually identical bait colour). The mice showed a significant preference for the familiar flavour when presented with a choice of familiar and unfamiliar baits. Soane & Clarke concluded that predators hunting by smell can develop preferences for familiar types of prey, leading to apostatic selection.

Greenwood et al. (1984ab) have shown that mice select anti-apostatically when presented with rat cake crumbs of differing flavour and colour in mixed frequency experiments. Visual cues were found to be unimportant in determining preference. Instead, olfactory cues were probably responsible for the observed selection. Greenwood et al. (1984a) suggested that the odour of the rare food type contrasted with that of the common form, thus facilitating predation on the rare form. I shall refer to this as the "olfactory contrast hypothesis". This is analogous to the visual contrast hypothesis.

Little is known of how perception of odours by cats is related to food choice (Bradshaw 1990b), although Rofe & Anderson (1970) consider it to be the predominant component in the cats' total flavour experience. Mugford (1977) demonstrated the importance of odour in food choice by showing that food-derived odours could initiate and sustain the consumption of a diet (stale chow) which would not otherwise be eaten. Despite the lack of detailed understanding, it appears that olfactory cues are likely to be of great importance in the food selection behaviour of domestic cats. This is likely to be especially true in scavenging urban feral cats,

whose food may provide no auditory and little visual stimuli (unlike live prey).

1.3.2. Dietary Effects.

The intrinsic properties (e.g. nutrient composition, palatability) of food items can influence the diet choice decisions of foragers in ways that can cause FDS.

Following Bradshaw (1991), it is convenient to consider these effects under the headings of "flavour experience" and "nutrient experience".

1.3.2.1. Flavour experience.

(a) Palatability.

Natural selection has favoured the evolution of unpalatability (distastefulness) in many prey species. When food types are unpalatable, it is predicted that selection will be anti-apostatic since foragers are more likely to learn to avoid common unpalatable prey (Mallet & Barton 1989, Greenwood et al. 1981, 1988). However, if a food type is extremely unpalatable (i.e. gives a very strong negative reinforcement) only one encounter might be necessary for the forager to learn to avoid it completely.

(b) Preference for novel flavours.

Experiments with visual predators (see section 1.2.2.2.) have generally resulted in apostatic selection. However, studies of mammalian food selection within a nutritional context have revealed increased preferences for novel food flavours in rats (Morrison 1974), dogs (Griffin et al. 1984) and domestic cats (Mugford 1977, Hegsted et al. 1956, Thorne 1982). Although the mechanisms underlying these preferences are not well understood, studies in human nutrition have suggested two mechanisms which might also be applicable to foraging animals. In humans, the palatability of a particular food declines as it is eaten (due to the sensory characteristics of the food), thus increasing the preference for alternative food types. This is *sensory-specific satiety* (Rolls 1986). Sensory-specific satiety is a short-term effect, the initial decline in palatability in humans beginning at around two minutes after the start of a meal (Rolls 1986). It is conceivable that a similar mechanism could explain the preferences for novel foods in non-human animals listed above. This would be predicted to cause anti-apostatic selection; the palatability of rare foods may decline more slowly than common foods, and this would be manifested as an increase in preference for the rare food.

Siegel & Pilgrim (1958) proposed a long-term effect, *monotony*, whereby repeated consumption of a particular food over a period of days or weeks results in lowered acceptance. Monotony is not the same phenomenon as sensory-specific satiety (Rolls 1986). Rather, it is due to *cognitive* satiety - the forager learns that it has consumed a great deal of a particular food type. Monotony could be an important long-term effect in frequency-dependent selection; rare forms might be taken more frequently than expected to reduce monotony, and this would lead to anti-apostatic selection.

(c) Rejection of novel flavours: neophobia.

Food neophobia, the rejection of novel flavours, can result in increased preference for familiar foods. However, it is unlikely to be a major factor in influencing frequency-dependent selection since it is a transient phenomenon, only occurring when a new food type is introduced. Bradshaw (1986) reports that simply exposing cats to an unfamiliar food decreases their neophobia towards that food.

1.3.2.2. Nutrient experience.

Food preferences can be influenced greatly by the nutritional composition of available foods. Richter (1943), in a classic study of diet selection by rats, proposed that foragers possess "specific hungers" for essential nutrients which allow them to select a balanced, mixed diet. Specific hungers for salt and water are known to exist in rats, and metabolic and physiological effects undoubtedly influence preference to some extent (Castonguay 1983). However, current evidence suggests that nutrient-based food preferences occur as a result of foragers learning to avoid less nutritious foods rather than possessing specific hungers for nutrients which are absent from the diet (Rozin 1976). In extreme cases, where a food type may contain toxins, a classic flavour aversion may occur (i.e. a forager learns the association between the flavour of the food and its deleterious nutritional qualities; see Davey 1989, Rogers & Blundell 1991).

The nutritional composition of the diet may also influence the composition of the gut flora. This, in turn, might cause the forager to select only familiar food items since any change in preference (i.e. selecting a novel food) might lead to digestive problems. Partridge (1981) and Partridge & Green (1985) suggested that such a mechanism might account for the increase in preference shown by mice and voles for foods which they had been maintained on for 40 days.

1.4. BEHAVIOURAL MECHANISMS OF FREQUENCY-DEPENDENT SELECTION : II. ULTIMATE CAUSATION.

The majority of proximate mechanisms outlined in section 1.3. can be explained in terms of their ultimate causation, or function. In this section, I shall demonstrate how models which assume that animals forage optimally also make predictions about frequency-dependent selection, and I shall outline how assumptions about the optimization currency influence these predictions.

1.4.1. Optimal Foraging Theory.

Optimal Foraging Theory (OFT), pioneered by MacArthur and Pianka (1966), rests on the (controversial) assumption that natural selection has favoured the evolution of animals which tend to forage in a way which maximizes some *a priori* foraging currency (e.g. maximization of energy intake rate, minimization of foraging time, optimization of specific nutrient requirements), given certain, specified, constraints. Although the assumption that animals forage optimally is fundamentally flawed (see Gould & Lewontin 1977, Futuyma 1986 pp. 254-257, Pierce & Ollason 1987, Rapport 1991), OFT is heuristically valuable and still represents the most practical framework in which to contemplate questions about foraging behaviour¹. I do not intend to discuss OFT in general terms since many reviews have been published (notably Stephens & Krebs 1986). Instead, I shall simply consider how FDS may be explained in terms of OFT.

1.4.2. Predictions of FDS Based on Maximization of Energy Intake.

Most conventional models of optimal foraging maximize the net rate of energy gain while foraging (Stephens & Krebs 1986), and it is these models which have generally been interpreted in terms of frequency-dependence. Hubbard et al. (1982) provide the most explicit theoretical demonstration of the equivalence of FDS and OFT. They showed that by combining Charnov's (1976) classic optimal diet model with Roger's (1972) random predator equation, apostatic selection is predicted.

Visser (1981) also used an optimality approach to predict the conditions under which

¹Recently, Ward (1992, 1993) has proposed the concept of "satisficing" as an alternative conceptual framework for foraging theory. However, it is not clear at present whether this is a genuine alternative to OFT or just "optimization with constraints" (Nonacs & Dill 1993)

frequency-dependent selection should occur. To provide a framework for his predictions, he divided predator-prey interactions into two groups according to whether or not foraging efficiency could be substantially improved by practice. In the case where a predator can learn to increase its foraging efficiency, Visser (1981) states that it "...will be able to reduce the recognition, catching or handling time for the relatively common prey type much more than for the scarce prey type, due to a higher encounter rate with the common prey type.....This means that the encounter with and the profitability of the common prey type increases with respect to that of the rare prey type". This increased profitability should lead to apostatic selection (Hughes 1979, Staddon & Gendron 1983). This is exactly the type of explanation which could explain the adaptive significance of search images (i.e. it is a mechanism which leads to a reduction in recognition time).

When a predator is unable to improve its foraging efficiency, Visser (1981) *incorrectly* states that the null hypothesis (i.e. no frequency-dependence) is to be expected when prey are conspicuous. (As outlined above, Hubbard et al (1982) showed that the optimal diet model, in which perfect knowledge of the environment is assumed, predicts apostatic selection.) However, Visser correctly points out that when a predator is unable to improve its foraging efficiency and prey density becomes very high, confusion may become a factor (a similar point was made by Greenwood 1984). As we saw in Proximate Mechanisms, this means that the attention of the predator is likely to be drawn to the rare forms, which stand out in a "sea" of common forms. The adaptive significance of this is that the profitability of the rare prey types is increased since they are more easily (i.e. more quickly) recognized as single prey items. As a result, anti-apostatic selection is predicted and, as we have seen, selection is often anti-apostatic at high density. However, Engen & Stenseth (1984ab) developed a model, which did not include recognition time, which also predicted anti-apostatic selection by predators when prey are encountered simultaneously.

1.4.3. Predictions of FDS Based on Optimization of Nutrient Intake.

Although most OFT models assume maximization of energy intake rate, this is not always necessarily the case. Sometimes the forager may be constrained by nutrient requirements (Pulliam 1975). A classic example is that of the foraging moose (Belovsky 1978, 1981); sodium-rich plants are not available to the moose in winter, and this sodium constraint dictates the composition of the summer diet. Greenstone

(1979) has also shown that the spider *Pardosa ramulosa* also select its prey in a manner which optimizes amino acid intake.

When there are nutritional benefits to be gained from a mixed diet, anti-apostatic selection is predicted. Greenwood (1984) states that : "...to maintain its balanced diet when one food is rare, the animal must take a disproportionate amount of that food relative to what is available". Perez-Mellado et al (1991) suggested that such constraints could explain why the prey preferences of the lizard *Lacerta monticola* were negatively correlated with relative availability (i.e. anti-apostatic selection) for three out of the four major prey taxa of this species. Partridge & Maclean (1981) found that bank voles showed a short-term decrease in preference for a familiar, but slightly nutritionally deficient, grain diet (i.e. an *increase* in preference for alternative foods), but no decrease when the familiar food was supplemented with a nutritionally complete background diet.

It is conceivable that sensory-specific satiety has evolved as a mechanism for optimizing nutrient intake. Rolls (1986) states that: "Sensory-specific satiety helps to ensure the consumption of a varied, and therefore balanced, diet. Thus, when a variety of foods is available, there will be a tendency to switch from one food to another because of the decrease in palatability in any one food after consumption". However, care must be taken when invoking nutrient constraints to explain experimental data. Belovsky (1990) stated that "...the number of cases where additional nutrient constraints need to be included in OFT models is very small". He goes on to argue: "This implies that most nutrient demands for a forager are satisfied incidentally with the forager's optimization of some other nutrient currency". However, a nutrient-based approach may prove useful in the study of food selection by domestic cats, especially urban feral cats which must select their diet from an array of extremely abundant but nutritionally variable foods.

1.5. THE EFFECT OF INDIVIDUAL PREFERENCES ON SELECTION AT THE GROUP LEVEL.

Variation between individuals can have important consequences at the population or group level (Lomnicki 1988, Huston et al. 1988, DeAngelis & Gross 1992, Judson 1994). This is especially true of foraging behaviour since predators may vary considerably in their choice of prey. Cook (1965) stated that: "Examination of the

first few dozen of these [prey] must determine their [the predators] response to all the other potential prey that they may come across" [brackets added]. This will lead to variation in prey choice between predators due to the inherent stochasticity of prey sampling. Indeed, between-individual variation in preference has been documented in a variety of different predators (e.g. Murdoch & Oaten 1975, Ringler 1985, Desrochers 1992, Skulason et al. 1993, Wotton et al. 1993, Zerba & Collins 1992). Variation in food preferences may also be attributed to age, sex, genotype and competition (reviewed by Partridge & Green 1985).

P.L. Chesson (1984) modelled the effects of predator variance on FDS at the population level. He demonstrated that when there is variance between individual predators with constant frequency-independent preferences, the overall effect of the predator population on the prey population is anti-apostatic. Weale (1992) suggested that the overall effect would be small unless predator variance is particularly large. However, Sherratt & MacDougall (unpublished) have demonstrated that the effect can be quite large even with relatively little variation. Such a phenomenon could partly explain the anti-apostatic selection of pastry baits by blackbirds observed by Allen & Anderson (1984). It is likely that the effects of inter-individual variation may be of some importance in any study of frequency-dependent selection by groups of foragers.

1.6. FREQUENCY-DEPENDENT SELECTION AND THE DOMESTIC CAT: A PRELIMINARY ANALYSIS.

1.6.1. Are Domestication and Adaptation Mutually Exclusive?

In this introductory chapter, I have demonstrated that FDS can usually be interpreted in terms of its adaptive significance. "Adaptation" in this sense implicitly assumes that a behaviour is under some form of genetic control (*sensu* Dawkins 1976) and is selected for over an evolutionary timescale. This clearly poses a problem when searching for a framework within which to contemplate food selection by the domestic cat². The cat has, after all, only relatively recently spread into urban environments. It would therefore be foolhardy to assume that the cat is *genetically*

²Rural feral cats are a possible exception since they can be treated as truly wild animals. Furthermore, they also appear to occupy niches similar to that of their wild ancestors.

adapted to the urban environment. Recently, though, the concept of adaptation has been re-evaluated. Focus has shifted towards a hierarchical model of adaptation (O'Neil et al. 1986, Provenza & Cincotta 1993) in which learning within the lifetime of an individual (behavioural evolution by consequences) is considered as a parallel process to genetic adaptation. While relatively little genetic adaptation is likely to have occurred in the cat since its domestication, the scope for learning by consequences is enormous since cats are known to be adept at problem solving (e.g. the classic work of Thorndike, summarized in McFarland 1993) and cultural learning (John et al. 1968). It might therefore prove fruitful to assess differences in FDS between cats with different dietary histories in order to assess how experience modifies, or "adapts", foraging behaviour.

1.6.2. The Scope of the Study.

When attempting to test for FDS, a reasonably large degree of experimental manipulation is usually required in order to make data collection both predictable and practical. These practical constraints effectively ruled out rural feral cats as experimental subjects in this study (it might also be argued that cats which occupy an entirely rural niche, feeding only on live prey, are very much in the minority). Thus, the questions addressed in this thesis are limited to domestic cats in urban areas. In many ways this is fortunate since urban cats raise perhaps the most interesting questions about food selection, particularly with respect to their behavioural responses to life in an urban environment. The different types of cats used as experimental subjects in this thesis are described in chapter 2.

1.6.3. The Aims of the Study.

The aims of this study were necessarily wide-ranging, given both the lack of data on FDS by felids and the numerous parameters which have the potential to influence selectivity. On a broad scale, the primary objective was to elucidate, within an ecological context, the foraging decisions which urban domestic cats make in response to changes in the availability of different food types. FDS has a strong theoretical basis and therefore provided a convenient conceptual framework within which to interpret diet choice decisions. As an adjunct to this objective, it was anticipated that the insights into FDS by the domestic cat gained in this study could be used to draw more general conclusions and enhance our understanding of FDS

by other mammalian foragers in both urban and "natural" environments³.

To achieve these broad objectives, it was necessary to test for and examine the mechanisms of FDS by the domestic cat over a range of experimental conditions. I therefore tested for the occurrence of FDS using foods which differed in both their spatial and temporal availability using multi-frequency and training experiments respectively. Initially, I attempted to replicate the results of Miles (1989), that groups of domestic cats select anti-apostatically when food is presented at high density in multi-frequency experiments. These experiments were then extended to test for FDS by individual cats, and to elucidate the behavioural mechanisms which have the potential to cause this behaviour (for example, perceptual contrast, sensory-specific satiety).

A second line of investigation was to consider the effect of temporal rarity on preference for both nutritionally complete and nutritionally-defined catfoods, with a view to studying (i) the effect of different feeding regimes on preferences for foods which had not been recently encountered, and (ii) the possibility that any changes in preference reflected attempts by cats to select a nutritionally balanced diet. This line of investigation was relevant to all domestic cats, but particularly applied to urban feral cats which selected their diet from a variety of nutritionally variable food items.

Encompassing all of these objectives, and central to the thesis, was a comparative study of food selection by cats from different experiential backgrounds. Experiments were therefore carried out on three different types of cat; farm cats, rescue shelter cats and cattery cats (defined in chapter 2). It was anticipated that a comparative approach would prove fruitful in elucidating the "adaptive" significance of diet selection decisions by assessing the effect of previous experience and dietary history on foraging tactics (see section 1.6.1.).

³*As far as I am aware, the domestic cat has never been used as a "model" forager. This study could therefore also be viewed as an opportunity to assess the potential of the domestic cat as a model for studies of diet selection in general.*

Study Subjects, Sites & Methodology

The domestic cat provides an excellent opportunity to study FDS in a mammal since it is ubiquitous, easy to handle and much is known about its general feeding behaviour. Perhaps the biggest advantage, though, is that it is possible to study cats which come from very different backgrounds, ranging from those bred and reared in laboratories to feral cats. In the first section of this chapter I describe the different sites and subjects used in this study. In doing so, I shall pay particular attention to the types of foods which the cats at each location are currently exposed to, and the foods which they were likely to have been exposed to in the past. The foraging behaviour of cats from different experiential backgrounds is central to this thesis since previous foraging experiences are likely to play a crucial role in determining current food preferences and foraging strategies. This will provide the basis for a comparative study of food selection, which may be illuminating when attempting to unravel the different mechanisms of food selection which may be operating in domestic cats.

In the second part of the chapter, I describe the rationale behind the design of the experiments which are presented in this thesis. Although the experimental basis for testing for FDS (i.e. multi-frequency and training experiments) was briefly mentioned in Chapter 1, some facets of these experimental designs are quite subtle and therefore need to be stated explicitly.

2.1. STUDY SITES & SUBJECTS.

Data were obtained from more than 150 different individuals at four different study sites. The cats at these four sites could be conveniently grouped into three classes: farm cats, rescue shelter cats and cattery cats.

2.1.1. Farm Cats.

A large number of farms in the British Isles have a resident colony of feral (or semi-feral) cats. Such colonies may form because of the rich source of easily-obtainable food and warm shelter sites which farms offer. The composition of the diet of farm cats varies between different locations (see table 1.1), but usually includes live prey (which are also likely to be at high densities), farm scraps and cat food provided by the farmer (who may encourage cats to control rodent pests).

2.1.1.1. Firtree Farm.

In this study, I examined the feeding preferences of a small colony of farm cats at Firtree Farm, Firtree Lane, near Horton Heath, Southampton. At the beginning of the study, in October 1990, there were seven members of the colony; three neutered males (Sid, Dusty and Big Ginger) and four spayed females (Honey, Gertie, Penny and Black-Cap). With the exception of Big Ginger and Black-Cap all individuals were observed on a regular basis. Big Ginger was extremely wary of humans and was only sighted on a handful of occasions during the first 18 months of the study until his death in February 1992. At this time, Black-Cap moved to a nearby farm and was not sighted at Firtree Farm again. During 1992 and 1993 a second ginger cat, probably male, was sighted at the farm on a handful of occasions.

The Firtree Farm cats were provided with a garden shed (1.82 x 1.21m), to which they had access via a cat-flap (plate 2.1.). This shed served as a shelter, and was provisioned with boxes and newspaper as bedding material. All preference testing and supplementary feeding took place in the shed. As a result, most individuals spent a great deal of their time in or around this location. Care was also taken to ensure that the farm cats were kept as healthy as possible. The shed was cleaned out regularly, and periodically sprayed with pesticide to prevent flea infestations. Cats which were in poor health were trapped and taken for veterinary treatment.



Plate 2.1. *The feeding shed at Firtree Farm.*

In Chapter 1, I presented a classification of the feeding habits of the domestic cat (i.e. companion cats, urban feral cats and rural feral cats). I also stated that these groups are not discrete entities, but represent points on a continuous spectrum of



Plate 2.2. *The St. Francis Animal Welfare.*

...of the experimental subjects and ease of... However, data... since the cats would be unlikely to be present at the... the other, but

Although able to forage freely around the farm, the Firtree Farm cats received regular supplementary food from members of the Anthrozoology Institute at Southampton University in order to maintain their condition¹. This food consisted primarily of commercially available tinned cat food (usually Katkins Chunks, Pedigree Petfoods Ltd.), although dry foods were also fed occasionally. During non-experimental periods, the level of supplementary feeding was judged on an *ad hoc* basis via subjective estimates of the condition of the individuals; less food was presented in summer when alternative foods were more abundant, and when the cats appeared to be gaining weight. Typically, the level of supplementary feeding was around 300g of food per cat per day (approximately 75% of daily energy requirement). In addition to the supplementary feeding, the cats also caught live prey (intact or half-eaten carcasses of birds, voles and moles were found on a number of occasions) and probably foraged on farm scraps too. There was no evidence that these food sources constituted anything but a relatively minor proportion of the total diet.

In Chapter 1, I presented a classification of the feeding habits of the domestic cat (i.e. companion cats, urban feral cats and rural feral cats). I also stated that these groups are not discrete entities, but represent points on a continuous spectrum of food habits. On this spectrum, the Firtree Farm cats occupied a position between urban feral cats and companion cats; despite the fact that they were maintained primarily on proprietary foods throughout the study, they certainly had *experience* of scavenging for food.

2.1.2. Rescue Shelter Cats.

Animal rescue shelters are charitable organisations which care for unwanted or injured animals. A high proportion of the residents at these shelters are domestic cats, which usually come from a wide variety of backgrounds, ranging from abandoned pets and strays to feral cats. In terms of food habit classification, these rescue shelter cats can be considered to be very similar to the Firtree Farm cats; they are likely to be experienced at foraging on nutritionally variable resources even

¹ *There is a clear trade-off between the degree of ferality of the experimental subjects and ease of study. Without supplementary feeding the cats could be considered to be truly feral. However, data collection would then be considerably more difficult since the cats would be unlikely to be present at the feeding shed for experimental trials. Furthermore, individuals would be less healthy and, therefore, less likely to survive the entire duration of the study.*

though the bulk of their diet consists of nutritionally complete canned foods. Individuals from two rescue shelters were used in this study: The St. Francis Animal Welfare and Southampton Blue Cross.

2.1.2.1. The St. Francis Animal Welfare

The majority of experiments on rescue shelter cats were carried out at The St. Francis Animal Welfare. At the beginning of the study this shelter was located at Botley Road, Horton Heath, Eastleigh, Hampshire, U.K. In late 1992, the shelter relocated to a new site at nearby Mortimers Lane. Both sites offered very similar facilities, usually housing around 50 cats (plate 2.2.). At the Botley Road site, the cats were housed in four communal pens, each consisting of three small rooms with bedding material and a large outside run. One pen, the resident's pen, contained individuals which were unsuitable for homing as pets. These individuals included trapped feral cats and temperamental or old cats. The other three pens contained cats which were more socially adjusted towards humans and therefore more suitable for homing. At the Mortimers Lane Site, the set-up was very similar. There was a single residents pen and 5 communal pens for the other cats.

The St. Francis cats were fed twice daily, at approximately 9am and 3pm. The bulk of their diet consisted of a variety of tinned commercial cat foods. Because the shelter relied heavily on public donations of food, the cats received a wide variety of different brands (particularly "Whiskas" and "Kit-e-kat"). In addition, a *pot pourri* of household scraps were often available, including Pedigree Chum mixer, eggs, spaghetti and toast!

2.1.2.2. Southampton Blue Cross.

A second rescue shelter, The Blue Cross, Bubb Lane, Southampton, was occasionally used in the study. In general, The Blue Cross housed animals which were more socially tolerant of people than The St. Francis Animal Welfare. These cats were housed in groups of one to three in 20 pens. The pens consisted of a small inner room and a small covered outdoor area. There were also six to eight resident cats which roamed freely around the site. The cats were fed almost entirely on commercially available canned food ("Whiskas", "Arthur's", "Kit-e-kat"), with no table scraps. It was Blue Cross policy to feed dry kibble cat foods only in minimal

quantities because of the perceived risk of Feline Urological Syndrome. The cats were fed twice daily at variable times.

2.1.3. Cattery Cats.

For the purpose of this study, I shall define a "cattery cat" as a domestic cat which has been born and raised in a research institution for use in experiments to assess the quality of cat foods. The common usage of "cattery" is clearly much broader (i.e. any location used to breed or look after cats). However, I have deliberately chosen it here to avoid the use of the term "laboratory cat", which could easily conjure up misconceptions about both the conditions under which cats in scientific institutions are maintained and the types of experiments which are performed.

2.1.3.1. The Waltham Centre for Pet Nutrition.

Research into the feeding behaviour of cattery cats was carried out at The Waltham Centre for Pet Nutrition (WCPN), Melton Mowbray, Leicestershire, U.K. The cat palatability unit at WCPN housed around 150 cats (in six main groups, or "panels"). Each group consisted of approximately 25 cats of mixed sex (neutered males, intact females) and age (one to nine years old). All cats were British shorthairs, and virtually all were tame and easily handled. These cats were used exclusively for palatability testing.

Each group was housed in two large interconnected, adjacent rooms. An inner, heated room contained beds, a heated floor strip, and numerous toys. Shelves and wooden boxes added 3-dimensionality to the environment. The second, outer, room was not heated and was less well furnished, but afforded an outside view through large windows. The condition of the cats was monitored carefully; each cat was weighed every week and regular veterinary examinations were carried out.

The WCPN cats received a preference test each day and an overnight, ad-lib maintenance diet. It was not necessary to feed precise quantities of food since cats appear to regulate their energy intake quite effectively (Castonguay 1981, Kane et al. 1987, Bradshaw 1991). The maintenance diet consisted of a wide variety of canned and dry commercial cat foods.

Compared to other cats (including companion cats), cattery cats can be considered to be naive foragers. These individuals had been raised exclusively on a nutritionally complete diet of high-quality commercial cat foods. Although the cattery cats were undoubtedly sensitive to the types of foods with which they were presented, their food preferences were unlikely to have had adverse effects on their health. (Contrast this with the shelter and farm cats, which are, or had been, required to select their diet from an array of nutritionally variable foods.)

2.2. METHODOLOGY.

The experimental techniques commonly used to test for frequency-dependent food selection are relatively straightforward. As outlined in Chapter 1, there are two main experimental approaches; multi-frequency experiments and training experiments. In this thesis, I will present the results of experiments which utilize both of these approaches.

2.2.1. Experimental Foods.

The foods used in most experiments were standard, commercially available cat foods. Two types of food were used; dry and canned (moist). These foods were used in different types of experiment. Dry foods consist of discrete pieces which can easily be counted and are therefore appropriate for use in multi-frequency experiments (Chapters 4 to 6). Canned foods are convenient for dichotomous preference testing in training-type experiments (Chapters 7 and 8).

2.2.1.1. Canned foods.

Three different types of canned food were used as experimental foods; "Katkins Chunks", "Kit-e-kat" (both Pedigree Petfoods Ltd.) and "Arthur's" (formerly "Kattomeat", Spillers Ltd.). "Whiskas" (Pedigree Petfoods Ltd.) was also used as a maintenance diet for some experiments with dry foods on WCPN cats. All of these foods were considered by their manufacturers to be nutritionally complete². However, this should not be taken to imply that the foods were sensorily and

² a food can be considered to be nutritionally complete if it can be fed over a long period of time with no deleterious effects on the health of the cat.

nutritionally identical; both macronutrient and micronutrient composition can vary considerably within the acceptable bounds of a "nutritionally complete" diet, and many different artificial flavour systems may be used in commercial cat foods. The macronutrient composition of these foods are presented in table 2.1. In general, nutritional and sensory differences were far greater between different brands than they were between different flavours of the same brand (J.W.S. Bradshaw, *personal communication*). However, there may still be variation between different production batches of the same flavour of a particular brand (for example, because of slightly different cooking times). For this reason, the foods used in any single experiment in this study all came from the same production batch.

In addition to these commercially available foods, two foods were made exclusively for the study by Pedigree Petfoods. These were a high protein/low fat food (the "HP" diet) and a low protein/high fat diet (the "LP" diet). The nutritional composition of these foods are shown in table 2.1. The LP diet was prepared partly through manipulation in the laboratory; the original factory-produced food (80.4% water, 9.6% protein, 6.7% fat, 2.2% ash, 92.7 kcal/100g) was diluted with the addition of 58% of a flavoured, palatable food gel (with negligible nutritional content) to produce a food with the same calorie density as food HP, and with a lower protein composition. In table 2.1, the food LP refers to this diluted form.

	Arthur's "turkey"	Katkins "liver"	Kit-e-kat "rabbit"	Whiskas standard	HP	LP
% protein	7.73	7.0	7.01	8.70	11.3	6.05
% fat	4.03	4.0	4.41	4.1	2.3	4.2
% water	85	79.8	84.6	84.0	83.2	87.1
ME (kcal/100g)	65.6	61.84	62.05	55.64	58.7	58.7

Table 2.1. *Nutritional composition of canned foods used in the study. HP and LP are the specially formulated "high protein" and "low protein" diets. ME = "metabolizable energy". (Source : WCPN).*

2.2.1.2. Dry foods.

Two brands of dry foods were used in experimental trials; "Brekies" (Pedigree

Petfoods Ltd.) and "Go-Cat" (Friskies Ltd.), henceforth be abbreviated to "Br" and "GC" respectively. These foods were considered to be highly palatable relative to other commercial brands of dry food. They were also very high in protein (typical nutritional composition; Br: 30.0% protein, 7.5% fat, 9.0% ash, 2.5% fibre; GC: 30.0% protein, 8.0% fat, 7.5% ash, 3.0% fibre). Water was always freely available to the cats whenever such dry foods were being used.

Three varieties of GC (mackerel & herring, lamb & beef, rabbit & liver) and three varieties of Br (liver, chicken, pilchard) were used in this study. Although nutritionally similar, the two brands had very different sensory properties. Visually, all dry foods were a shade of brown (plate 2.3.) but differed in their shape. All varieties of Br were three pointed stars, while pieces of GC were either fish-shaped (mackerel & herring) or four-pointed stars (lamb & beef, rabbit & liver). Both brands also produced extremely characteristic odours and could be easily discriminated by the human nose. Individual pieces of GC (approximately 0.3g) were also slightly heavier than pieces of Br (approximately 0.2g).

2.2.2. High-Density, Multi-Frequency Experiments.

2.2.2.1. Rationale.

In Chapters 4, 5 and 6 I test for FDS by domestic cats in a variety of high-density, multi-frequency experiments using dry foods. In such experiments, preference is usually measured over a range of different relative frequencies of food types.

Usually, these include fairly extreme frequencies, such as 9:1 and 1:9. The rationale behind the choice of such frequencies is simple: if selection is frequency-dependent then the greatest differences in preference are likely to be observed when there are large differences in the availability of food types. Although frequency-dependence can be tested for using just two extreme frequencies, it is usually preferable to have at least three frequencies to give some indication of the nature of the preference change over the whole frequency spectrum. The majority of experiments presented in this thesis test preferences at several different frequencies.

2.2.2.2. Experimental considerations.

There are several important factors which must be considered when designing multi-

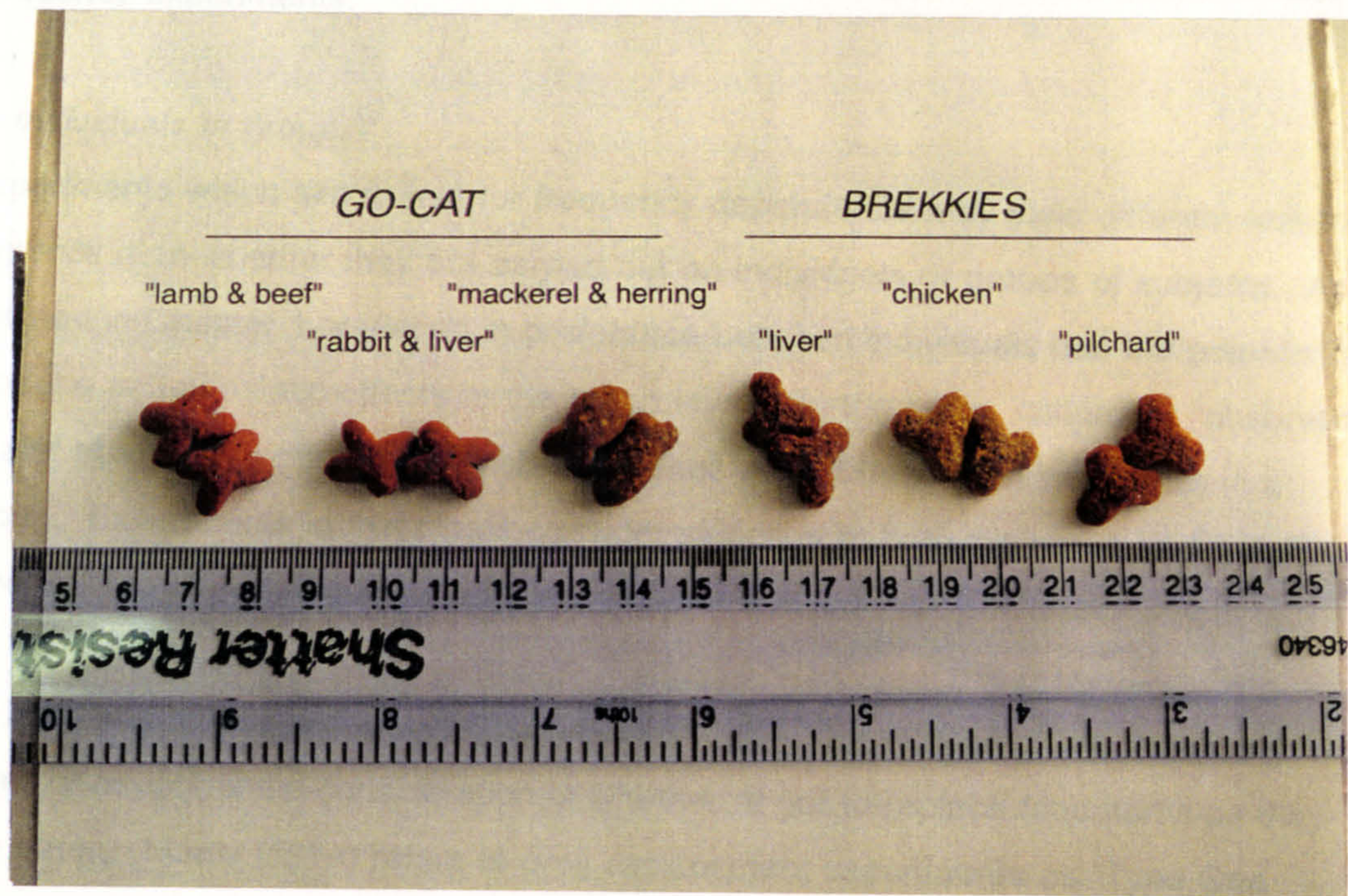


Plate 2.3. The different types of dry cat food used in the study.



Plate 2.4. Food dish containing 9:1 ratio of two evenly distributed dry foods, as used in chapters 4, 5 and 6.

frequency experiments:

a) Individuals or groups?

Experiments which aim to test for frequency-dependence may yield different results depending on whether they are carried out on individuals or groups of subjects. As I outlined in Chapter 1, variation in preference between individuals has the potential to produce anti-apostatic effects at the group level. Furthermore, cultural or "observer" (Galef et al. 1985) effects might also influence the preference of individuals in a group. Experiments in this thesis consider selection at both the group and individual levels.

b) Type one versus type two selection.

A major experimental consideration is whether or not to replace food items as they are eaten. Manly (1974) refers to prey-replacement experiments as "Type One Selection Experiments" (or TOSEs) and no-replacement experiments "Type Two Selection Experiments" (or TTSEs). This terminology will be adopted throughout this thesis. In practical terms, TOSEs are easier to analyse than TTSEs because food frequencies remain constant throughout experimental trials (see Chapter 3), but can present experimental difficulties since the very act of food replacement may influence the behaviour of the forager. In this study, all experiments are TTSEs because (i) when food is at high density it is not easy to see which food items have been consumed, so replacement would be difficult, and (ii) the act of replacement would almost certainly disturb the foraging cat.

c) The spatial distribution of food.

Statistical tests used to demonstrate frequency-dependence generally require that the available food items are randomly distributed in space; the probability of a forager encountering a given prey item at a given moment is based on the assumption that the prey are randomly distributed in space. In many cases, though, it is impractical to generate random positions for every single food item. Indeed, a number of studies (e.g. Allen & Anderson 1984, Allen et al. 1990, Greenwood et al. 1984ab) have not formally randomized food distribution, instead resorting to a more "haphazard" distribution. In the experimental methods presented in Chapters 4, 5 and 6, the large numbers of food items required for testing each day dictated that it was not feasible to rigorously randomize the positions of each item. However, rather than mix the foods "haphazardly", I arranged them in a regular, evenly dispersed

distribution (plate 2.4.). The use of this regular dispersion at high food densities is justified, and its implications for statistical testing examined, in chapter 3 (section 3.5.)

d) Trial length.

Experimental trials can be terminated after either (i) a fixed time period ("hard selection") or (ii) a certain number of food items have been eaten ("soft selection"). In practical terms, the choice of method is not crucial since the statistical techniques used to model each of these scenarios produce very similar estimates of preference (Weale 1992). Since it is often very difficult to control precisely the number of food items consumed in a trial, it is usually convenient to stop after a "reasonable" number of food items have been eaten. This should certainly be more than 10, otherwise estimates of selectivity are likely to be very poor (Murdoch et al. 1975), and probably less than 50% of the total available to prevent food frequencies changing too much during a trial and to prevent *all* of any rare foods from being consumed.

2.2.3. Training Experiments.

The experiments described in chapters 7 and 8 are based on "training experiments" (see Chapter 1). In such experiments, preference changes (in a dichotomous preference test) are measured relative to the food type consumed over a defined time period prior to the test. In other words, preferences for foods which vary in their *temporal frequency* are being measured. This represents a far simpler approach, both experimentally and analytically, than multi-frequency experiments. Dichotomous preference tests are simple to perform and have very few potential sources of bias. Furthermore, virtually any simple index of preference (see Cock 1978) can be used.

The validity of training experiments as evidence for frequency-dependent selection has been called into question, notably by Greenwood & Elton (1979) and Greenwood (1985). Greenwood (1985) stresses that "...while it is true that training effects might give rise to pro-apostatic selection or might themselves depend on behavioural mechanisms that would do so, especially if the prey mixture was spatially or temporally heterogeneous, there is not necessarily a connection between the two phenomena". However, it is perhaps more useful to consider training experiments as a parallel approach to multi-frequency experiments which yield a different type of

data. I consider that both approaches can provide evidence for frequency-dependent effects. Perhaps the most important factor determining the relative importance of these two approaches is whether or not they have ecological analogues for the study species. This is true for both approaches in the present study; urban feral cats which scavenge on human household refuse may encounter some food types only rarely within their home range, and this is temporal, rather than spatial, rarity. However, the same cats are often faced with a simultaneous choice between different quantities of different food items (for example, in a dustbin), and selection in this type of situation can be investigated in multi-frequency experiments.

Statistical Analysis of Frequency-Dependent Selection Experiments

The statistical analysis of FDS experiments is, despite the apparent simplicity of experimental design, fraught with difficulties. It is probably fair to say that the majority of previous studies have paid too little attention to statistical methods. This is unfortunate since the available techniques must be applied with considerable care in order to avoid producing spurious results. In an attempt to clarify some of these analytical difficulties, I will devote an entire chapter to the subject of the statistical analysis of FDS experiments. There are three main reasons why I believe this is justified:

- (1) Important new methods of analysis have recently been proposed (Weale 1992) which may be more powerful than previous methods. It is therefore important to assess whether their use is justified.
- (2) Some of the methods described in this thesis for measuring FDS by domestic cats, particularly with reference to the spatial distribution of food items in multi-frequency experiments (see Chapter 2), may not strictly adhere to some of the assumptions of the available models. It will therefore be necessary to assess how this influences the way in which experimental results are interpreted.
- (3) In discussing analytical methods, I also present the results of original computer simulations which illustrate some of the difficulties of the available models.

In this chapter, I aim to present a practical account of some of the methods used to analyze FDS experiments. After outlining some of the general underlying principles of selectivity indices, I will go on to consider the advantages and disadvantages of the two most commonly used models; those of Greenwood & Elton (1979) and Manly (1972, 1973, 1974). I will then outline Weale's (1992) new methods for analysing frequency-dependent selective predation experiments and consider whether they really do represent an improvement over previous models. Finally, I will consider how prey dispersion might influence the interpretation of the statistical analysis of FDS experiments.

3.1. BASIC PRINCIPLES.

3.1.1. Preference and Selectivity.

A forager is said to have a preference for a given prey type when it consumes more of that prey than would be expected by chance alone, on the basis of its density (Cock 1978). The concept of preference, though, is deceptively complex. The very word "preference" implies that the forager has complete information about the available alternatives and therefore makes a direct choice between two food types. In reality, foods may be chosen by foragers because they have incomplete information about the alternatives. As a result, "selectivity" may be a better term to use in many cases. However, in the present study, preference is used in its true sense, so I shall retain its use. The terms "preference" and "selectivity" will therefore be used synonymously throughout this thesis.

3.1.2. Selectivity Indices and Frequency-Dependent Selection.

The simplest way to measure preference is in a dichotomous preference test. Both the experimental design and the statistical analysis of such tests are relatively straightforward. However, testing for FDS using multi-frequency experiments requires that preference should be measured over a range of relative food densities. Many different selectivity indices have been proposed to account for changes in frequency [e.g. Murdoch's (1969) C_i , Tinbergen's (1960) r_i , Chesson's (1978) α_i , Vanderploeg & Scavia's (1979ab) W_i ; see Cock (1978) and Weale (1992) for reviews]. These indices are descriptive rather than mechanistic and, although

superficially different, are based on the same general, weighted stochastic model of foraging behaviour. These indices can be referred to as w_{ij} -based (Weale 1992, after O'Neil 1969), with w_{ij} representing a weighting factor, or measure of selectivity. The probability of consuming prey type i at time j , p_{ij} , is given by

$$p_{ij} = \frac{w_{ij}D_{ij}}{\sum_{s=1}^m w_{sj}D_{sj}} \quad (3.1)$$

where m is the number of food types available and D_{ij} is the availability (density) of food type i at time j .

Since p_{ij} is a proportion, it is necessary to relativize w_{ij} values (Weale 1992). This is usually done in one of two ways, either by setting $w_{mj}=1$ or $\sum w_{ij}=1$. In the former case, values for w_{ij} lie between zero and infinity with $w_{ij}=1$ representing no selection. In the latter, w_{ij} values lie between zero and one with $w_{ij}=0.5$ representing no selection in the two-prey case.

3.1.3. Type One and Type Two Selection Experiments

Experimental design can have a major effect on the predicted proportions of food types consumed according to models of selective predation. Perhaps the most important factor in this respect is whether food items are replaced (Type One Selection Experiments, or TOSEs) or not (Type Two Selection Experiments, or TTSEs) as they are consumed by the forager. In a TOSE, the relative proportions of available prey remain constant throughout the experiment, and this makes statistical modelling relatively simple. However, the experiments reported in this thesis consist entirely of TTSEs, in which both the absolute and relative densities of prey may change during the course of an experimental trial. In this chapter I will therefore concentrate primarily on the analysis of TTSEs.

3.2. PREVIOUS DESCRIPTIVE MODELS.

During the past 20 years, statistical analysis of selection predation experiments has been carried out primarily using two different descriptive models: the Manly model

and the Elton-Greenwood model. Although they can be treated as special cases of a more general model (Gendron 1987), they are usually treated as different models in their own right. In this section, I describe the general properties of the two models and consider their use in TTSEs. The results of computer simulations are used to support the main arguments.

3.2.1. Elton and Greenwood's Exponential Model.

3.2.1.1. The model.

Elton & Greenwood (1970, 1987; Greenwood & Elton 1979) proposed, on intuitive grounds, an exponential model to describe prey selection. For the two-prey case:

$$e_1/e_2 = (VD_1/D_2)^b \quad (3.2)$$

Here, V is a measure of frequency-independent selectivity and b is a parameter which describes the strength of frequency-dependent selection. FDS is apostatic when $b > 1$ and anti-apostatic when $b < 1$. Absence of FDS is represented by $b = 1$. The standard methods use to fit the model (see below) assume that prey densities remain constant throughout an experimental trial (i.e. the model is, strictly speaking, only applicable to a TOSE).

One of the major advantages of the Elton-Greenwood model is that separate parameters for frequency-dependent and frequency-independent selection are explicitly included. Greenwood & Elton (1979) describe how to obtain estimates of these parameters. Logarithmic transformation of equation (3.2) gives:

$$\log e = b \log V + b \log D \quad (3.3)$$

where $e = e_1/e_2$ and $D = D_1/D_2$. Least squares linear regression can then be performed on the data, with $y = \log e$ and $x = \log D$, to obtain estimates of b and $b \log V$ (from which V can be calculated). Data are visualized by plotting $\log(e_1/e_2)$ against $\log(D_1/D_2)$.

3.2.1.2. The applicability of the Elton-Greenwood model to TTSEs - some computer simulations.

One of Manly's (1973) criticisms of the Elton-Greenwood model was that it can only

be used in a TOSE. Greenwood & Elton (1979) countered by stating that "if selection is frequency-dependent, then one will obtain larger values of b if the relative prey densities are kept constant, than if they are allowed to change but the value of b will still be comparable between experiments of similar design". To quantify these effects, I used computer simulation techniques (using Turbo Pascal v7.0, Borland International Ltd.) to compare the effects of FDS on the Elton-Greenwood model for TOSEs and TTSEs. The program listing is given in appendix 1.

The algorithm to determine selectivity in these simulations was based on Gendron's (1987) expression of the Elton-Greenwood model in terms of w_{ij} :

$$w_{ij} = \frac{V_i^b D_{ij}^{b-1}}{\sum_{k=1}^m V_k^b D_{kj}^{b-1}} \quad (3.4)$$

where m is the number of different food types. In all simulations presented here, $m=2$. Thus, when there is no frequency-independent selection (i.e. $V_i=1$ for all i), equation (3.4) becomes:

$$w_1 = \frac{D_1^{b-1}}{D_1^{b-1} + D_2^{b-1}} \quad (3.5)$$

In this case, w is equivalent to Manly's β (i.e. $w_1 + w_2 = 1$). The instantaneous probability of consuming an item of food type 1 is then obtained from equation (3.1.).

The simulations modelled an animal foraging on two randomly distributed food types (100 in total). Selectivity was simulated over 19 different relative frequencies, ranging from 5% to 95%, for both TOSEs and TTSEs under conditions of apostatic selection ($b=1.5$), random selection ($b=1$) and anti-apostatic selection ($b=0.5$). The number of food items eaten in each trial, E , was 50.

Trials in which either $e_1=0$ or $e_2=0$ could not be calculated by the standard Elton-Greenwood method since they produced the undefined values of $\log(0)$ or $\log(\infty)$. To overcome this, the numbers eaten in simulated trials were calculated as the average of 10 replicates. The mean values of $\log(e_1/e_2)$ at each frequency were then calculated from 100 iterations, with each iteration made up of these 10 replicates.

The results of the simulations demonstrate that the Elton-Greenwood model is virtually unbiased in both TTSEs and TOSEs when there is no selection ($b=1$; figure 3.1.). When there is anti-apostatic selection ($b=0.5$), the TTSE model produces a highly conservative estimate of anti-apostatic selection (figure 3.2.), especially at extreme frequencies [frequencies of 10% and 90% correspond to values $\log(D_1/D_2)$ of -0.954 and +0.954]. In the case of apostatic selection ($b=1.5$), the TTSE model produced only a slightly conservative estimate of FDS.

The fact that trials in which $e_1=0$ or $e_2=0$ cannot be analyzed is a major drawback of the Elton-Greenwood model, as Elton and Greenwood themselves have recognized. Unfortunately, such values are likely to occur relatively frequently when testing for FDS since selectivity is usually estimated at fairly extreme food ratios (i.e. when one food is very rare and therefore more likely to be completely overlooked). Indeed, further Monte Carlo simulations demonstrated that 681 out of 1000 trials could not be analyzed at a food ratio of 10:90 when $E=10$ and $b=1.5$ (i.e. moderate apostatic selection), although this reduced to 85 out of 1000 when $E=50$. This clearly places a considerable constraint upon analysis. Elton & Greenwood (1979) suggested that this difficulty can be overcome by combining data from replicate trials (as was done in the simulation). In general, however, when e_1/e_2 is very small or very large (values which are given undue weight in the regression analysis) Elton & Greenwood advocate the use of a rather tricky (and, in fact, rarely used) non-linear least squares method to determine parameter estimates. In such cases, it is usually more convenient (and far simpler) to adopt a different descriptive model altogether.

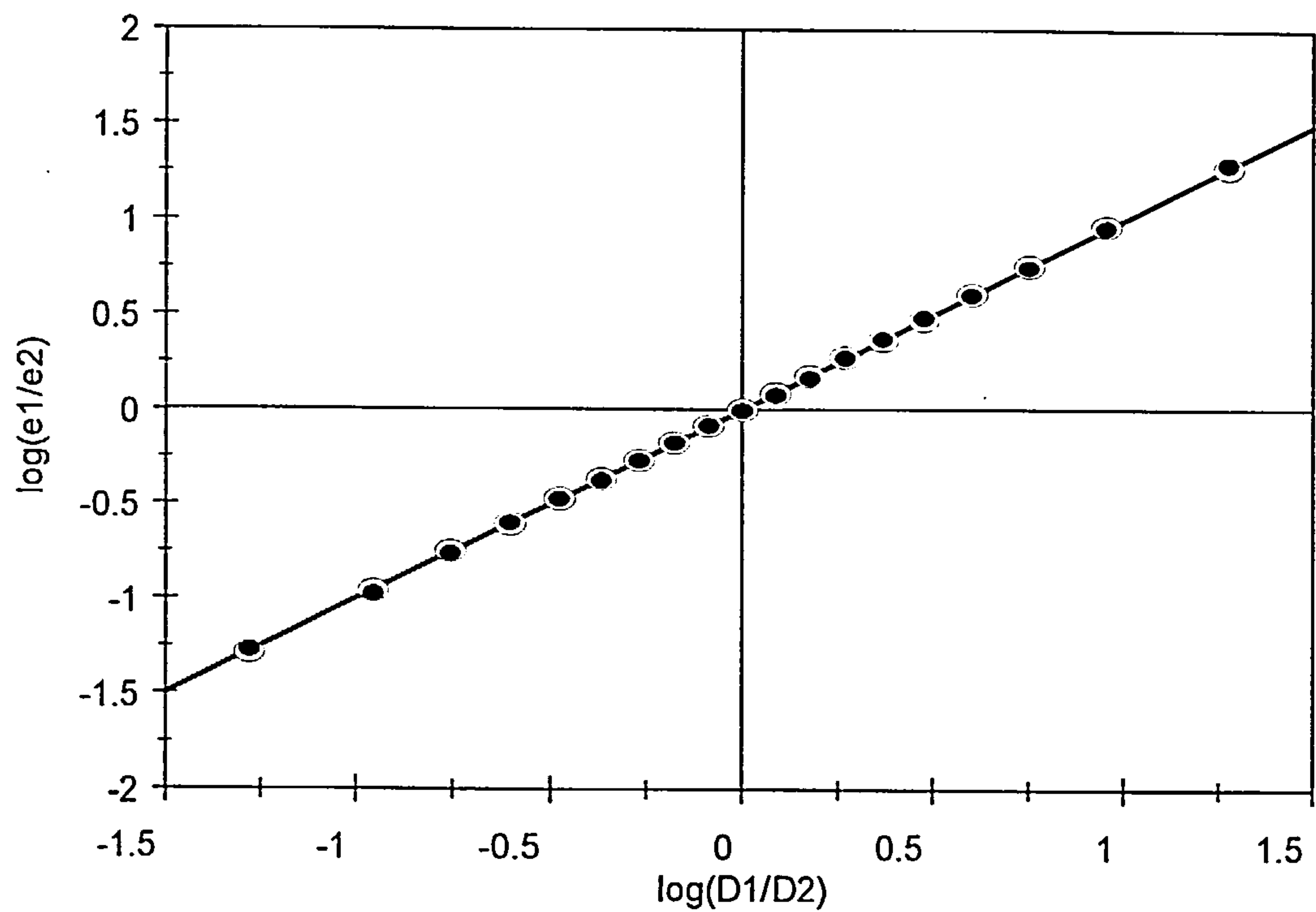


Figure 3.1. Comparison of Elton-Greenwood model in a TTSE (O) and a TOSE (●) under random predation ($b=1$, $E=50$). Each data point is calculated from 100 iterations. The total number of food items available at start of "trial" was 100. The solid, thick line represents the line of no selection.

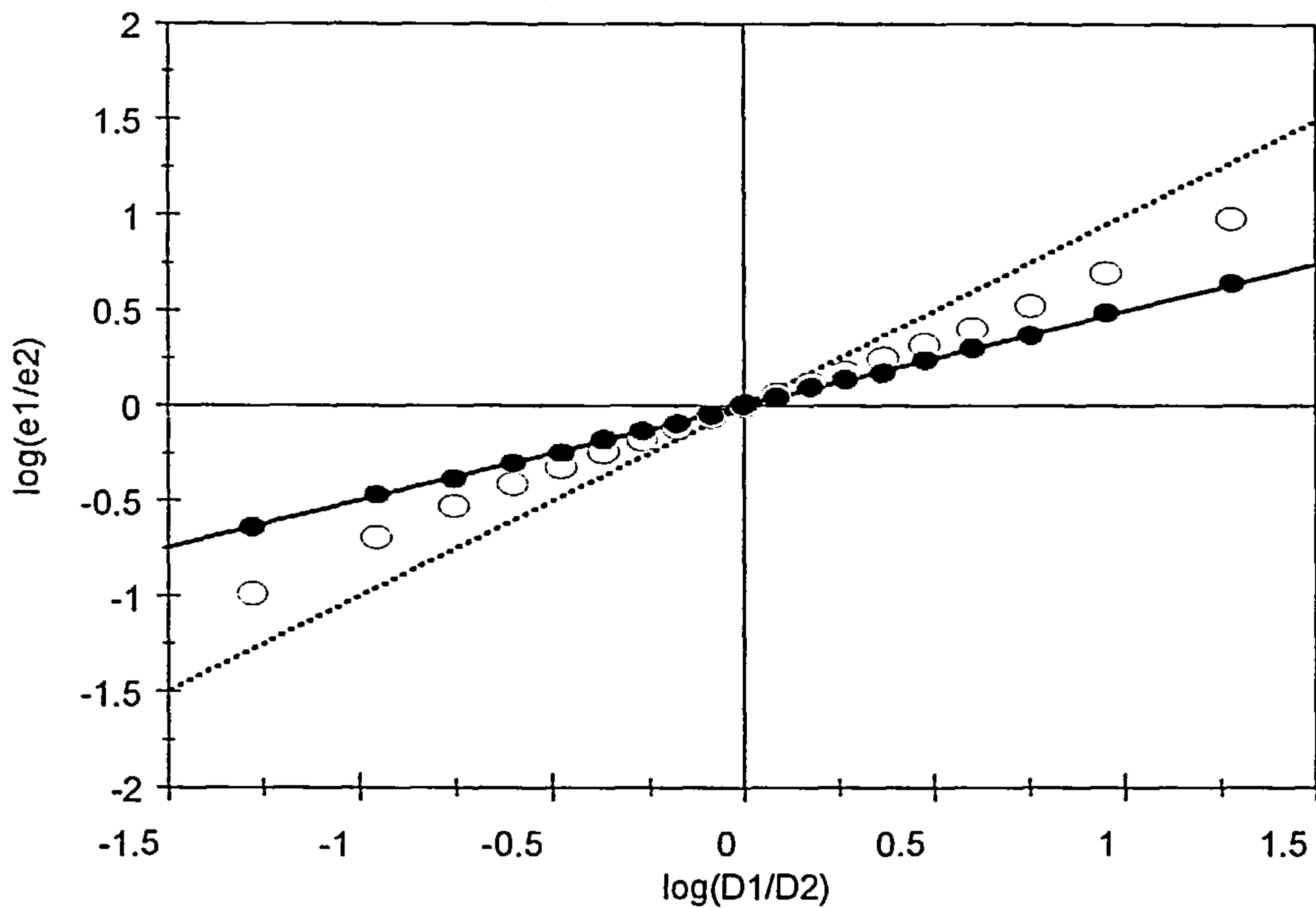


Figure 3.2. Comparison of Elton-Greenwood model in a TTSE (O) and a TOSE (●) under anti-apostatic selection ($b=0.5$, $E=50$). Each data point is calculated from 100 iterations. The total number of food items available at start of "trial" was 100. The solid, thick line represents the expected fit of the model when $b=0.5$ and the dashed line represents the line of no selection.

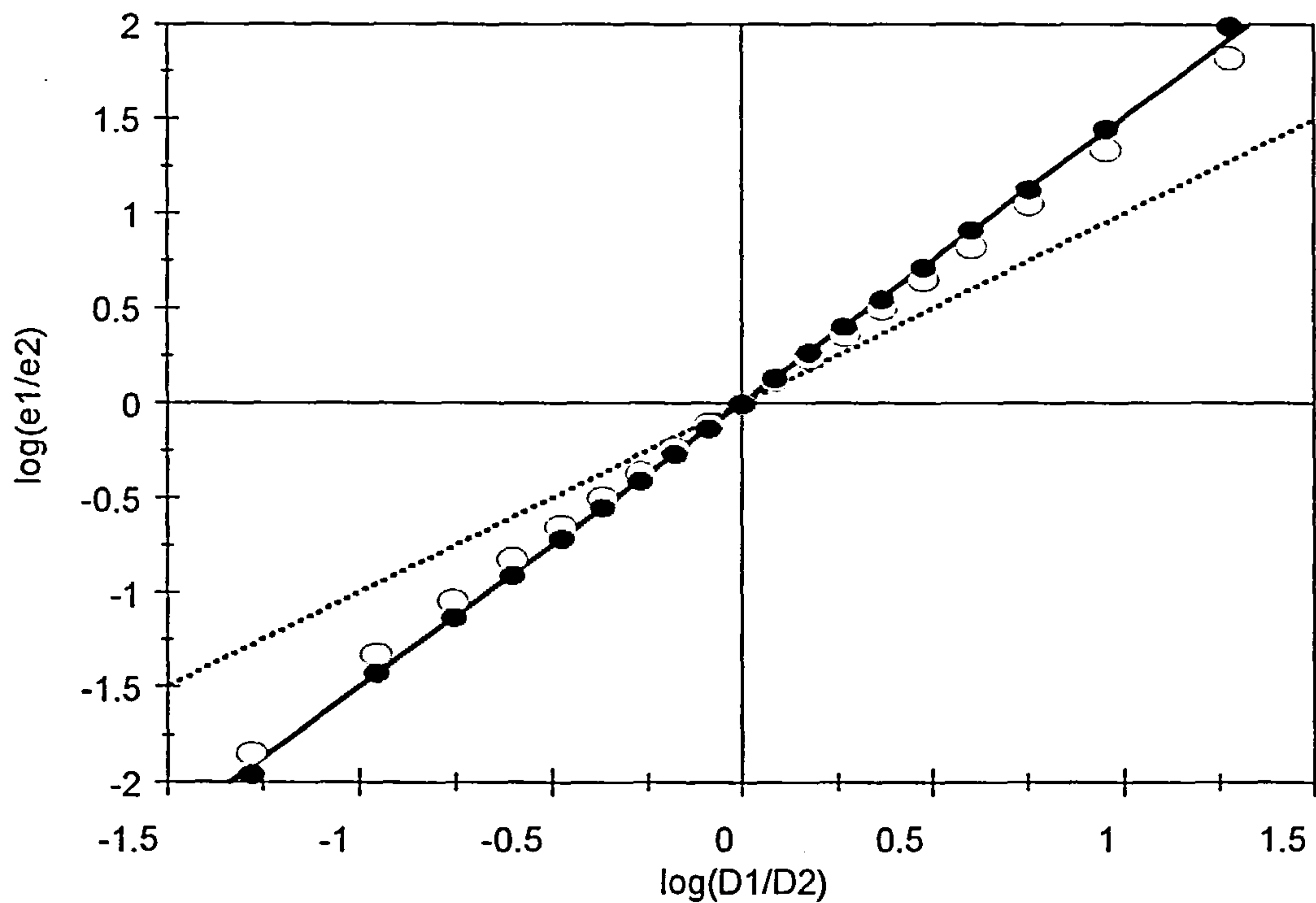


Figure 3.3. Comparison of Elton-Greenwood model in a TTSE (O) and a TOSE (●) under apostatic selection ($b=1.5$, $E=50$). Each data point is calculated from 100 iterations. The total number of food items available at start of "trial" was 100. The solid, thick line represents the expected fit of model when $b=1.5$ and the dashed line represents the line of no selection.

3.2.2. Manly's Linear Model.

3.2.2.1. The model.

Manly (1972, 1973, 1974), with useful additions by Chesson (1978), proposed a descriptive model based on a selection coefficient, β , which he assumed to be a linear function of prey density:

$$\beta_i = mD_i + c \quad (3.6)$$

β is equivalent to w_{ij} under the constraint $\sum w_{mj}=1$. Thus, in the two-prey case, $\beta_1+\beta_2=1$. Equation (3.1) can then be re-written as:

$$p_{ij} = \frac{\beta_j D_j}{\sum_{s=1}^m \beta_s D_s} \quad (3.7)$$

Manly (1974) demonstrated that in a TTSE (no replacement) with constant preference throughout a trial, β can be estimated from the following expression:

$$\beta_i = \frac{\log((D_i - e_i)/D_i)}{\sum_{j=1}^m \log((D_j - e_j)/D_j)} \quad (3.8)$$

$\beta_1=1$ represents exclusive preference for prey type 1, while $\beta_1=0$ represents exclusive preference for prey 2. In the two-prey case, $\beta_1=\beta_2=0.5$ represents no selection (but see below for a discussion of bias in beta).

β has been used extensively in the analysis of frequency-dependent selective predation experiments (e.g. Allen & Anderson 1984, Allen et al. 1990, Bantock et al. 1975, Greenwood et al. 1981, Gianino & Jones 1989, Cooper 1984ab, Tucker 1991, Tucker & Allen 1988, 1991, 1993). Usually, linear regression or ANOVA techniques have been applied to assess changes in selectivity between different frequencies.

3.2.2.2. The assumption of constant preference.

When using β in a TTSE it is necessary to assume that the preference of the forager remains constant throughout an experimental trial (Manly 1973). Greenwood & Elton

(1979) considered that this assumption was unrealistic. They suggested that β will change as learning occurs and prey numbers deplete. This is certainly a valid criticism, and one which it is important to consider before using β values to analyze experimental data. However, it is also worth noting that this is likely to be a general criticism of all descriptive models of TTSEs. Unless the foraging behaviour of the predator is well understood or the exact sequence of prey consumed is known, it will always be necessary to make some assumption about how the predator modifies its selectivity throughout a trial. The simplest assumption is to assume that preference does not change. However, it is always wise to attempt to test whether this assumption is actually adhered to in experimental trials.

3.2.2.3. The sampling distribution of β - computer simulations.

Although β has been used extensively, relatively little attention has been paid to important statistical factors such as bias and sampling distribution. In reality, these can have profound effects on the interpretation of experimental data and can lead to type I errors (i.e. falsely rejecting the null hypothesis). Perhaps the major problem with β is that it is biased. Manly (1974) was aware of the problem, and suggested that estimates of β would be reasonably accurate if the expected numbers of both foods eaten in a trial were greater than five. Testing for FDS, though, requires that selectivity is measured at extreme frequencies, and simulations by Weale (1992) have shown there is a considerable bias in β under many FDS scenarios. In the case of a TTSE, this bias is generally apostatic when less than half the prey are eaten and anti-apostatic when more than half of the prey have been consumed. Computer simulations written using Turbo Pascal (listings in Appendix 2) show the extent of the bias in β in TTSEs (figure 3.4.) when two food types are available ($N=100$). These results have important implications for previous studies of frequency-dependence, many of which have studied selection by avian predators in TTSEs. Usually, less than half of the available prey (pastry baits) are consumed in such experiments, which will produce an apostatic bias in β . However, since the results have purportedly shown apostatic selection, it is conceivable that the true extent of selection has been over-estimated. In such cases, it may prove wise to use simulation techniques to estimate the "true" null hypothesis based on the frequencies and numbers eaten in experimental trials.

A second difficulty with β is that it is far from normally distributed. Weale (1992) has

shown that the distribution of β is extremely skewed at extreme ratios (again, depending upon the number of food items eaten). Some authors (e.g. Cooper 1984ab, Allen & Anderson 1984, Tucker & Allen 1988, 1991, 1993, Tucker 1991) have used an arcsine transformation in an attempt to normalize the data. However, this transformation has little effect on the skewness and heteroscedasticity of the data (Weale 1992); its only effect is to convert the 0 to 1 scale of β into a slightly unwieldy 0 to 90. β is also heteroscedastic (figure 3.5.). Given this lack of normality and non-homogeneity of variance, it is perhaps surprising to note that parametric techniques (ANOVA and least squares linear regression, in particular) have generally been used to test for differences between β values at different frequencies. Unfortunately, non-parametric tests do not necessarily provide a viable alternative. Despite their "distribution free" tag, non-parametric tests such as the Kruskal-Wallis test still assume that samples are taken from the same underlying distribution (Fowler & Cohen 1990). Unfortunately, β is skewed in different directions at different ends of the frequency spectrum, thus precluding the use of such techniques. In addition, non-parametric tests do not alleviate the problem of bias.

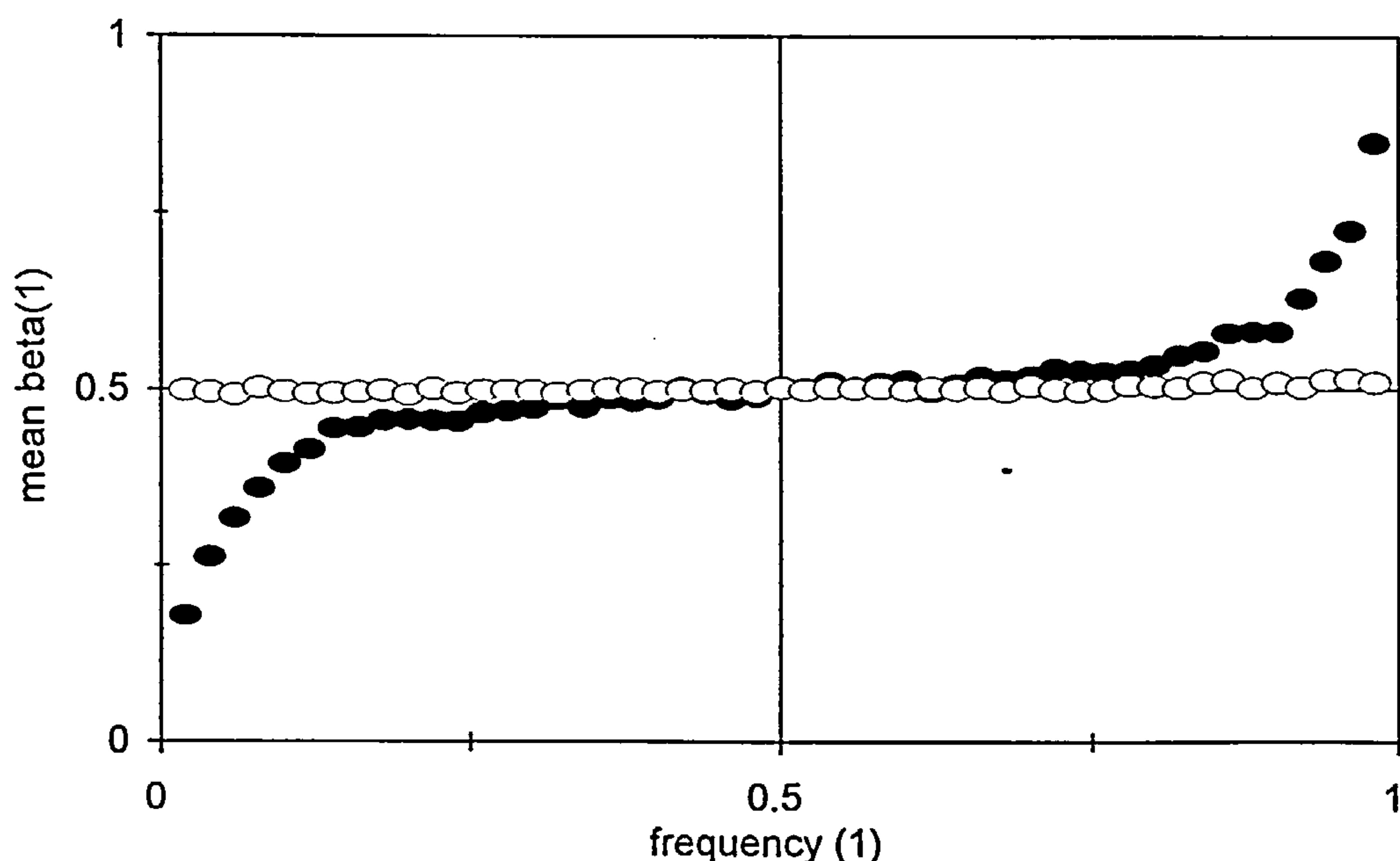


Figure 3.4. Bias in Manly's β (mean of 1000 iterations) in a TTSE when $E=10$ (●) and $E=50$ (○). Total number of prey = 100.

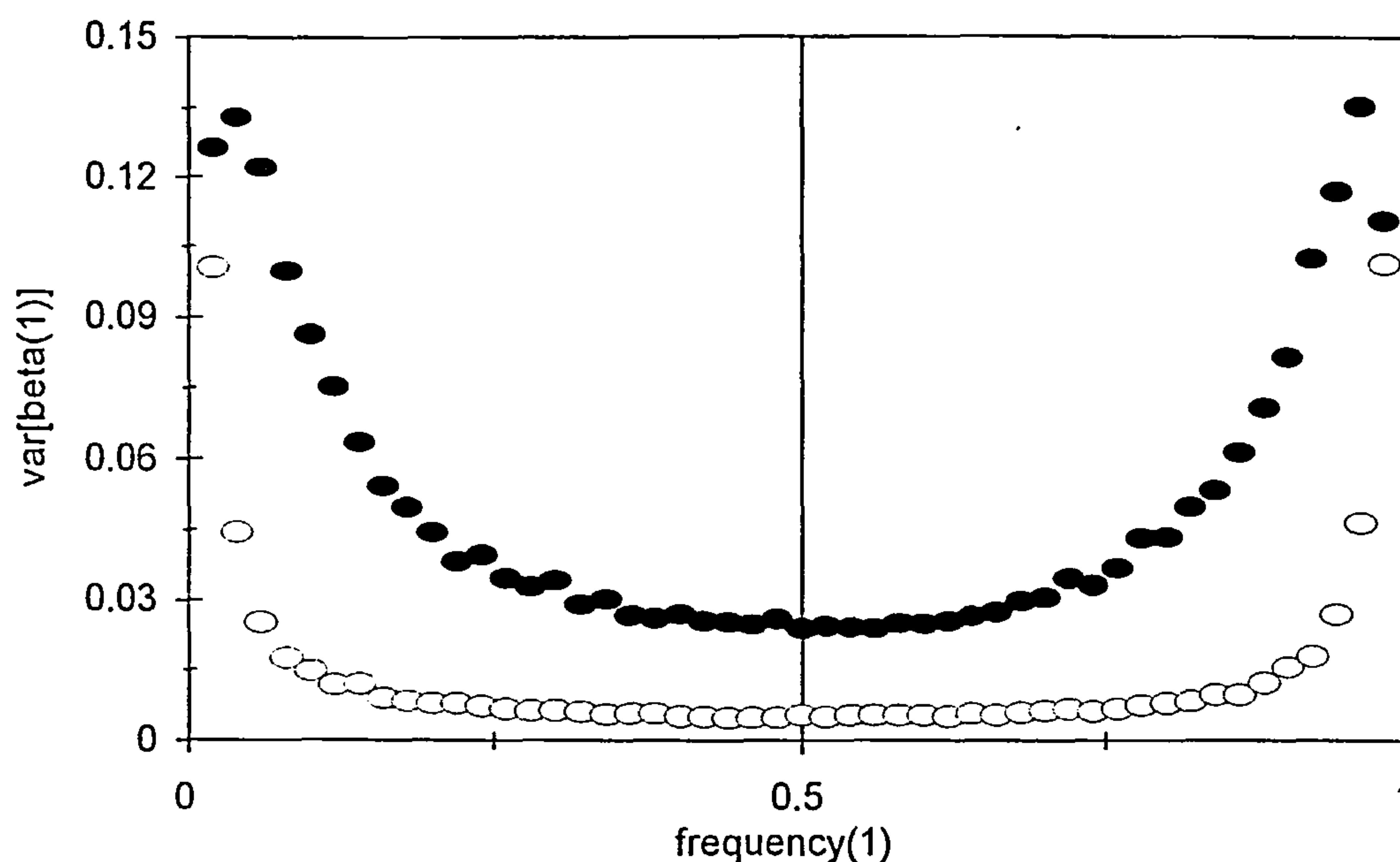


Figure 3.5. Variance in Manly's β (mean of 1000 iterations) in a TTSE when $E=10$ (●) and $E=50$ (○). Total number of prey = 100.

3.3. A NEW APPROACH: GENERALIZED LINEAR MODELS.

Weale (1992) has attempted to overcome some of the problems associated with the analysis of FDS experiments using the methods of Elton & Greenwood and Manly by developing a hierarchy of models using the technique of Generalized Linear Modelling (Nelder & Wedderburn 1972). These models build on previous applications of Generalized Linear Models (GLMs) by Heisey (1985) and Manly (1985).

3.3.1. An Introduction to Generalized Linear Models and GLIM.

GLMs, first introduced by Nelder & Wedderburn (1972), represent a convenient, flexible framework for converting certain, complex non-linear algorithms into fairly simple linear models. GLMs are defined by three components (Nelder & Wedderburn 1972, Aitkin et al. 1989):

- (1) A probability distribution $f(y)$ for the dependent (response) variable y (e.g.

normal, binomial, poisson).

- (2) A linear regression function (linear predictor) for the p explanatory variables.

$$\eta = \beta'x = \beta_0x_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_px_p$$

- (3) A link function $g(\mu)$ which relates the linear predictor η to the mean μ :

$$\eta = g(\mu)$$

In the case of, for example, a standard regression analysis (with normally distributed data) this link function is the identity $\eta = g(\mu) = \mu$. The significance of the link function will become clear in the next section.

The computer software package GLIM (Generalized Linear Interactive Modelling, National Algorithms Group) is designed to fit such models.

3.3.2. Modelling TTSEs with GLIM.

3.3.2.1. The TTSE algorithm.

The difficulty with modelling a TTSE is incorporating the effects of changing frequency. Manly (1976) suggested that a double exponential fitness function represented a convenient way to describe the probability of an individual surviving selection for a given period of time. Weale (1992) used this approach to fit a Proportional Hazards model (Manly 1985) to predict the expected proportion of each food type eaten in a TTSE:

$$E(e_j/D_{ij}) = 1 - \exp(\exp(\ln w_{ij} + g_j)) \quad (3.9)$$

In equation (3.9), w_{ij} is the weighting factor described above, and g_j is the logarithm of some function of time representing the time spent foraging. (e_j/D_{ij}) is expected to follow a binomial distribution. Equation (3.9) can be rearranged to form a GLM, in the following form:

$$\ln(-\ln(1 - \frac{e_j}{D_{ij}})) = \ln w_{ij} + g_j \quad (3.10)$$

The left hand side is the link function (a "complementary log-log link" in GLIM

jargon). The right hand side forms the linear predictor, in terms of the explanatory variable $\ln w_{ij}$.

3.3.2.2. Weale's hierarchy of frequency-dependent selection models.

Weale (1992) described a hierarchy of models which can be fitted to describe a range of FDS scenarios. These models are based on relative likelihood. This means that different models are compared to see how much better one fits the data over the others. Furthermore, these models must be nested (hierarchical) - when comparing two models, say model n and model $(n-1)$, model $(n-1)$ must always be a special case of model n .

Weale's models are exponential and appear superficially similar to the Elton-Greenwood model. Weale's C and s are equivalent to Elton & Greenwoods V^b and $(b-1)$ respectively (although, of course, the estimation of model parameters is entirely different). The hierarchy is presented in table 3.1. The most complex model, "FDS + additional effect 1" allows foragers to adopt different frequency-dependent responses for different food types. Taking natural logs of the expressions in table 3.1. produces linear terms in terms of $\ln w_{ij}$, and these can be fitted as the right-hand side of equation (3.10) in GLIM to produce estimates of C and s .

Parameter estimates are calculated by GLIM using the iterative method of *maximum likelihood*. In this method, the parameter estimates are essentially those values for which the observed data are most probable. As with all TTSE models dealt with here, it is necessary to assume constant preference throughout a trial.

When each model is fitted, GLIM produces an estimate of deviance (which can be best thought of as analogous to the residual sum of squares in an ANOVA) and degrees of freedom. The difference between the deviances in the fit of successive models approximately follows a χ^2 distribution.

3.3.2.3. Visualization of fitted GLIM models.

Visualization of Weale's (1992) exponential FDS models is less intuitive than that of either the Manly or Elton-Greenwood models. However, once understood it is an extremely useful technique. As a starting point, to visualize individual data points,

	Description	Exponential Models	Linearized Version
MODEL 1	no selection	$w_{ij} = 1$	$\ln w_{ij} = 0$
MODEL 2	simple preference	$w_{ij} = C_i$	$\ln w_{ij} = \ln C_i$
MODEL 3	simple FDS	$w_{ij} = C_i(D_{ij})^s$	$\ln w_{ij} = \ln C_i + s \ln D_{ij}$
MODEL 4	FDS + "additional effect 1"	$w_{ij} = C_i(D_{ij})^{s_i}$	$\ln w_{ij} = \ln C_i + s_i \ln D_{ij}$

Table 3.1. Weale's (1992) hierarchy of w_{ij} -based exponential frequency-dependent selection models.

the values for $\ln w_1$ in a single TTSE trial can be calculated by applying the equation:

$$\ln w_1 = \ln \left[\frac{\ln((D_1 - e_1)/D_1)}{\ln((D_2 - e_2)/D_2)} \right] \tag{3.11}$$

If the constraint $C_1=1$ is applied to the "simple FDS" model, $w_{ij}=C_i(D_{ij})^s$, in the two-prey case then w_1 , relativized to let $w_2=1$, is given by:

$$w_1 = \frac{D_1^s}{C_2 D_2^s} \tag{3.12}$$

After taking natural logs, equation (3.12) becomes:

$$\ln w_1 = -\ln C_2 + s \ln(D_1/D_2) \tag{3.13}$$

Equation (3.13) is then the straight line described by the fitted GLIM model, with $\ln(D_1/D_2)$ on the abscissa and $\ln w_1$ on the ordinate. GLIM provides the parameter estimates for s and C_2 . Since $\ln w_2$ is constrained to equal 0, "no selection" is represented by the line $\ln w_1=0$ (i.e. $\ln w_1=\ln w_2$).

3.4. MODEL COMPARISONS.

In a preliminary analysis, M.E. Weale (unpublished data) carried out computer simulations to compare the results of different analytical models in various foraging scenarios. These models were:

- Model 1:* Manly's linear model [β].
- Model 2:* Manly's linear model, arcsine transformed [$\arcsin(\beta)$].
- Model 3:* Elton & Greenwood's exponential model [E-G].
- Model 4:* Weale's generalized linear models [GLM].

All simulations modelled selection by a predator feeding on a total of 100 randomly-distributed prey at five different frequencies: 10:90, 30:70, 50:50, 70:30, 90:10. A total of 50 prey items were consumed in each simulated TTSE trial. Three different foraging scenarios were simulated:

- Simulation A:* Random predation [$w_1=1, w_2=1$].
- Simulation B:* Random predation with extraneous variance [$\ln w_1=0, \ln w_2 \sim N(0,1)$].
- Simulation C:* Constant preference for prey type 2 [$w_1=1, w_2=2$].

The results from Monte Carlo simulations of these scenarios (400 iterations for simulation A, 100 for simulations B and C) are shown in table 3.2. In simulations A and C, Weale's GLMs produced the best description of the simulated predation events. These models resulted in the appropriate number of type I errors required to adopt conventional significance levels (i.e. approximately 5% type I errors). Type I errors occurred more frequently in the other three models. Furthermore, although there was a slight bias towards apostatic type I errors, overall the number of trials with apostatic selection was approximately the same as would be expected by chance (i.e. 50%). All other models were less accurate, generally producing apostatic biases (e.g. the Manly model in simulation A and the Elton-Greenwood model in simulation C). However, some serious problems were encountered with the GLMs in simulation B (high extraneous variance). In this simulation, the rate of type I errors rose to an enormous 37%, while the other models actually improved their performance. It is clear from this that GLMs should only be used when models provide a good fit to the data (i.e. deviance = degrees of freedom). When there is high extraneous variance, alternative models should be used.

simulation	FDS model	% type I errors (p<0.05)	fraction of apostatic type I errors	% apostatic selection (s>0)	% food 1 preference (lnV ₂ <0)
A	β	10.75	33/43	61.25	50
	arcsin(β)	11.5	34/46	61.5	50.25
	E-G	11	22/44	49.75	50.75
	GLM	5.25	14/21	50.5	51.5
B	β	6	3/6	49	51
	arcsin(β)	9	5/9	45	49
	E-G	3	1/3	44	50
	GLM	37	11/37	41	46
C	β	11	9/11	48	43
	arcsin(β)	11	9/11	47	32
	E-G	13	13/13	74	100
	GLM	7	6/7	51	51

Table 3.2. Results of FDS simulations by M.E. Weale (unpublished) of Manly's β , arcsin-transformed β , Elton-Greenwood model and TTSE generalized linear model. Simulation A assumed constant, random preference (400 iterations), simulation B is the same but with large extraneous variance (100 iterations), while simulation C assumed a constant overall preference for prey 2 (100 iterations).

The simulations presented in table 3.2. are limited in their scope. However, they do suggest that GLMs represent a genuine improvement over previous models under basic foraging scenarios when there is no extraneous variance. In addition, Weale's (1992) re-analysis of data from classic FDS studies (e.g. Popham 1943, Gendron 1986) have demonstrated the validity of the models over a range of selective behaviour.

3.5. THE EFFECT OF PREY DISPERSION ON ANALYSIS.

All of the descriptive FDS models outlined in this chapter are based on the assumption that prey items are randomly dispersed in space. In many cases, though, it is impractical to generate formally random positions for every single food

item, especially if a large number of trials are carried out in a day. As a result, some experimenters have dispersed food items in manners variously described as "thoroughly mingled" (Allen & Anderson 1984), "haphazard" (Allen et al. 1990) and "scattered" (Greenwood et al. 1984a). It is clear, though, that any departure from true randomness has the *potential* to produce biases in food selectivity (e.g. see Gianino & Jones 1989). In the high-density, multi-frequency experiments reported in this thesis (chapters 4, 5 and 6) the two food types were regularly dispersed among each other. This must be considered as a potential source of selectivity bias. However, there are three lines of reasoning which suggest that such an approach is entirely justified: (a) the nature of dispersion is unlikely to be important at high food densities, (b) regular dispersion of the two food types will, if anything, produce conservative estimates of selection, (c) when it is not practical to randomize, regular dispersion may be the best option. Since this issue is fundamental to the analysis of FDS experiments, I shall consider these arguments in some detail.

3.5.1. The Effect of High Food Density.

Perhaps the most convincing circumstance under which regular dispersion of prey can be justified is when prey are available at very high densities. If the total area covered is small enough (as is the case with the food dishes used in preference tests in the present study) then all food items will be encountered by the forager *simultaneously*. In this situation, the actual dispersion of the food items may be largely irrelevant. Although random and regular dispersion are entirely different in a mathematical sense, a forager would be unlikely to *perceive* them as fundamentally different when encountered simultaneously. Thus, any preferences which the forager might have can be fully expressed because complete information is available about the available choices. However, this argument is likely to be less applicable when prey densities are low enough for encounters to be sequential. An environment consisting of regularly-dispersed, low-density prey is inherently more predictable than one in which prey are randomly dispersed. It is therefore possible that a forager will express different preferences when it possesses a detailed knowledge of the available choices (via increased predictability due to regular prey distribution) than when prey encounters are quite unpredictable (when prey are distributed randomly).

3.5.2. The Effect of Dispersion on Type I Errors.

The regular dispersion of high-density foods will, if anything, tend to produce conservative statistical tests (i.e. the risk of type I errors will be reduced). However, the overall effect will depend on the behaviour of the forager. As I argued in section 3.5.1., if a forager has a strong preference (frequency-dependent or -independent) when prey are at a high density then it is likely to express this preference regardless of prey dispersion. However, even in a forager with an active preference there will always be a random error component in selection. When prey are regularly distributed, the effect of this error component will depend upon the behaviour of the cat. To understand this, consider a cat with no preference feeding on a high density mixture of food. If the cat selects each successive food item from a random point in space ("spatial randomness"), then the distribution of the prey does not affect the instantaneous probability that the next food type taken is of a given type. If cats select with this sort of underlying behaviour when they show a preference then we would not expect prey distribution to influence statistical analysis. However, consider an alternative scenario in which the cat is a *systematic* random forager. In other words, any food item taken is spatially adjacent to the previous food item taken ("systematic randomness"). In this case, regular dispersion of prey will tend to reduce "runs of bad luck" (i.e. selecting, by chance, a disproportionately long sequence of one food type) and lead to low sample variance (a general characteristic of a regular dispersion; Fowler & Cohen 1990). The upshot of this is that statistical tests will tend to be conservative; the probability of obtaining a spuriously significant result is low. In reality, the behaviour of a foraging cat is likely to fall somewhere between the two extremes of spatial randomness and systematic randomness. As a result, the significance levels quoted in this thesis (chapters 4,5 and 6) are likely to be slightly conservative estimates.

3.5.3. Is 'Haphazard' Food Dispersion a Valid Alternative?

Distributing prey in a "haphazard" manner appears to be an accepted experimental technique in the FDS literature (see above). Researchers appear to have adopted this approach on the assumption that it produces a good approximation of random dispersal. However, it is possible that, due to the unavoidable subjective biases of humans, a "haphazard" distribution of food items is not a good approximation of a random distribution. Thus, if formal randomization is not possible, it could be argued

that a regular dispersion of prey at least allows an experimenter the opportunity to explicitly consider the effect of dispersion on selectivity rather than blindly assume randomness.

3.6. DISCUSSION.

The original aim of this chapter was to clarify the use of different statistical models in the analysis of FDS experiments. Perhaps more than anything, though, it has served to illustrate that such analysis is almost bewilderingly complex. The simulations presented here demonstrate that there is no single FDS model which is consistently superior to its competitors. However, throughout this thesis I will use Weale's (1992) hierarchy of GLMs as the primary method of analysis. Although there are undoubtedly problems associated with this model (notably the effect of extraneous variance), it has been chosen largely by default. The Elton-Greenwood model is not strictly applicable to TTSEs (all experiments in this thesis are TTSEs); using it for this purpose tends to underestimate the magnitude of FDS, particularly when selection is anti-apostatic, while overestimating statistical significance. Furthermore, it often impractical to use when none of a particular food type is eaten in a trial (as is often the case in FDS trials). The Manly model, on the other hand, is applicable to TTSEs, but is biased and also tends to produce type I errors. Weale's methods, while being less "user-friendly" than either the Manly or Elton-Greenwood models appear to represent a genuine improvement both in terms of lack of bias, proportion of type I errors and statistical sophistication (for example, assuming that the underlying data is binomially rather than normally distributed). It would be slightly rash, though, to fully embrace these models to the complete exclusion of the other two. Where there is any doubt as to the statistical interpretation of a data set (for example, when $0.01 < p < 0.05$ for data sets in which there is high extraneous variance) results should be confirmed by an appropriate alternative technique.

Frequency-Dependent Selection by Groups of Cats

Miles (1989), in the only explicit study of FDS by domestic cats to date, demonstrated that groups of rescue shelter cats select anti-apostatically when presented with different ratios of dry cat food at high densities. As a preliminary investigation it is clearly necessary to carry out similar experiments on groups of cats in order to confirm Miles' findings. If vindicated, these results may act as a platform on which to further explore the FDS by the domestic cat. In addition, selection experiments on groups of cats have the potential to explore some of the effects of individual food preferences on group selectivity. A large number of FDS studies, especially those on wild predators, have investigated the selective behaviour of groups of individuals rather than the individuals themselves (e.g. Allen & Clarke 1968, Allen 1972, 1974, Cooper 1984ab, Greenwood et al. 1981, Harvey et al. 1975, Reid 1987, Greenwood et al. *in press*). From the perspective of population processes, this is understandable. After all, the selection acting on a prey population is imposed by a whole group of predators, and it is usually the selection itself which is the focus of interest (although it would be naive to assume that the individuals within the group behave in an identical manner; Lomnicki 1988). When we study foraging *behaviour*, rather than its consequences, it is more usual to focus on the individuals themselves. However, from an ecological viewpoint, it may prove valuable to consider how the summed effects of individual behaviour are manifested at the group or population level. Although mathematical models have shown that variation in food preferences alone can produce frequency-dependent effects at the

population level (Chesson 1984, Sherratt & MacDougall *unpublished*), empirical evidence for this phenomenon is scarce. An artificial and easily manipulated system, such as domestic cats feeding on dry cat foods, may be useful in providing evidence for these effects. This chapter therefore examines the food selection of groups of cats feeding on a high-density "patch" containing two types of dry cat food. I initially present details of experiments designed to test for FDS in two different groups of cats: the Firtree Farm cats and a similar-sized group of WCPN (cattery) cats. I then go on to use preference data from individual cats to model the effect of between-individual preferences on group preferences. This model is then used to interpret the empirical findings.

4.1. EXPERIMENTS 1 & 2: SELECTION BY GROUPS OF FARM AND CATTERY CATS.

4.1.1. Methods.

Experiments were carried out to test for the occurrence of FDS and measure individual frequency-independent preferences in two different groups of cats. In experiment 1, the subjects were the seven cats which were present at Firtree Farm during late 1990/early 1991. In experiment 2, the subjects were a group of six WCPN cats of mixed age and sex. During experimental periods, the maintenance diet of the two groups of cats was limited to a single brand of commercial canned food ("Katkins Chunks", Pedigree Petfoods Ltd., for the Firtree Farm cats, and "Whiskas", Pedigree Petfoods Ltd., for the WCPN cats)

4.1.1.1. Testing for frequency-dependence.

(a) Experiment 1 : Farm cats.

Experimental trials were performed on 20 non-consecutive days between 16th October and 19th December 1990. On each day of the experiment, the cats were presented with 1:9 (108:972) or 9:1 (972:108) ratios of two dry foods (Br "liver" and GC "mackerel & herring" varieties). Four large foil trays (inner diameter 260 mm) containing a mixture of Br and GC in the required ratio were simultaneously presented to the experimental group. A total of 270 whole pieces of food were placed in a single layer in each tray (5085 pieces/m²). The two food types were *evenly* interspersed with each other since it was not practical to randomize the

positions of each food item (see Chapters 2 & 3). In each trial, the four trays were of identical composition (a total of 1080 pieces of food). Preliminary experiments suggested that this amount of food would result in a sufficient amount (approximately half) of the food remaining at the end of a trial. The trays were arranged as the corners of a square, spaced by approximately 12 inches.

The experimental ratios were placed in the feeding shed at between 1600 and 1700 hours at the beginning of each trial, and left overnight. The food remaining was collected and counted at between 1000 and 1200 hours the following day. The amount of food eaten in each trial could not be easily controlled, and it was not possible to tell which individuals had sampled from the trays during each trial. However, it also meant that the cats were able to eat without the presence, and possible influence, of a human observer.

20 trials were performed in total; 10 with Br as the common form and 10 with GC common. The choice of common form for each trial was determined randomly (Greenwood 1985). At least 30 hours were allowed between successive trials, during which time the cats received no dry food.

(b) Experiment 2 : Cattery cats.

The six experimental subjects were housed in a pair of connected rooms (identical to the panel rooms described in Chapter 2, but approximately half the size) for the duration of the experiment. Preference testing was carried out between 4th May and 9th June 1993. The experimental methods were virtually identical to Experiment 1; the group of cats were presented with 1:9 (108:972) and 9:1 (972:108) ratios of Br "liver" and GC "mackerel & herring" in the manner described for Experiment 1. Each experimental trial started at 1500 hours and was terminated at 0800 hours the following day, after which the remaining food was counted. At least 30 hours were allowed to elapse between successive group preference trials, although on five occasions during the experiment individual preferences were assessed between trials. Sixteen trials were carried out in total, eight with Br common and eight with GC common. The sequence of presentation of frequencies was performed in a random order.

4.1.1.2. Individual preference tests.

(a) *Farm cats.*

Frequency-independent preferences for Br "liver" and GC "mackerel & herring" were obtained for the five individuals (Sid, Honey, Dusty, Gertie and Penny) who were least nervous in the presence of humans. Each individual completed a preference test on two consecutive days (18th and 19th February 1991). The farm cats received no dry food for six weeks prior to these preference tests.

In each preference test, individual cats were presented with 140 whole pieces of an even mixture of Br and GC as a single layer in the bottom of a foil dish with inner diameter 180mm (5502 pieces/m²). The two experimental foods were presented to the cats in a 1:1 (70:70) ratio. Each cat was allowed to feed for a maximum of 10 minutes during a test. The test was terminated before this time if, in the judgment of the experimenter, approximately 50% of the total number of pieces were consumed. At the end of each test, the numbers remaining of each of the two components were counted.

Since the farm cats were free-living, interference by other cats was often a problem. This difficulty was circumvented by placing the dish of food inside an inverted "stack'n'store" basket with a hole (140mm x 120mm) cut in the side which restricted access to one cat (plate 4.1). The basket had a series of wide slits on every side so that the subject cat could still view its surroundings and was therefore not forced into a state of vigilance, constantly interrupting the meal. Other cats could be dissuaded from approaching the feeding cat by firing a water pistol at the ground near to them, or by actively removing them.

(b) *Cattery cats.*

On five occasions during Experiment 2, after trials 1, 3, 6, 8 and 12, measures of frequency-independent preference were obtained for the cattery cats. Individual cats were each presented with a 1:1 ratio (70:70) of Br "liver" and GC "mackerel & herring" in the same manner as that described above for farm cats. Rather than use "stack'n'store" baskets to deter other individuals, individuals were confined to one of the two rooms in which they were housed for preference testing.



Plate 4.1. "Stack'n'store" basket method, used to obtain preference data from a single cat within a group of individuals.

4.1.2. Results.

4.1.2.1. Testing for frequency-dependence.

(a) Experiment 1 : Farm cats.

The experimental data were analyzed using Weale's (1992) GLIM models for TTSEs (see Chapter 3). $\ln w_{Br}$ values were calculated for each trial using equation (3.10.). The full transcript of the GLIM analysis is presented in appendix 3. Fitting the null model (model 1, linearized version) in table 3.1. produced a very poor fit to the data (deviance=111.57, df=20). This was not significantly improved by adding a term (model 2) to account for frequency-independent preference (deviance=109.5, df=19, $\chi^2_{[1]}=2.073$, $p>0.1$). However, adding a term for frequency-dependence (model 3) produced a very highly significant improvement in the fit of the model (deviance=63.33, df=18, $\chi^2_{[1]}=46.16$, $p<0.001$). From the parameter estimates which GLIM provides, the "best fit" model can be expressed as:

$$\begin{aligned} w_{Br} &= D^{-0.1006} \\ w_{GC} &= 0.929D^{-0.1006} \end{aligned}$$

The negative value of the exponent in these equations indicates that selection was *anti-apostatic* (figure 4.1.). The choice of axes ($\ln D_{Br}/\ln D_{GC}$ v $\ln w_{Br}$) was discussed in section 3.3.2.3.

The large amount of extraneous variance (deviance $\gg$ d.f.) in the "best fit" model could, conceivably, have produced spurious anti-apostatic results (section 3.4.). However, performing a standard one-way ANOVA on Manly's (1974) β -values (equation 3.7.), which generally produce a conservative estimate of anti-apostatic selection, also demonstrated a highly significant anti-apostatic effect (Br common: mean $\beta_{Br} = 0.46$, SD = 0.07; Br rare: mean $\beta_{Br} = 0.57$, SD = 0.07; $F_{1,18} = 12.656$, $p<0.01$).

Weale's (1992) hierarchy of GLMs for analysing TTSEs assume that predator preference (w_{ij}) is constant throughout experimental trials, thus allowing trials in which different numbers of food items have been consumed to be compared. In Experiment 1, significantly more food items were consumed by the cats in trials where Br was common than those in which GC was common (Br common: mean number eaten = 653.5, SD = 165.87; GC common: mean number eaten = 442, SD = 98.85; ANOVA: $F_{1,18} = 11.99$, $p<0.01$). Since there was no direct observation of

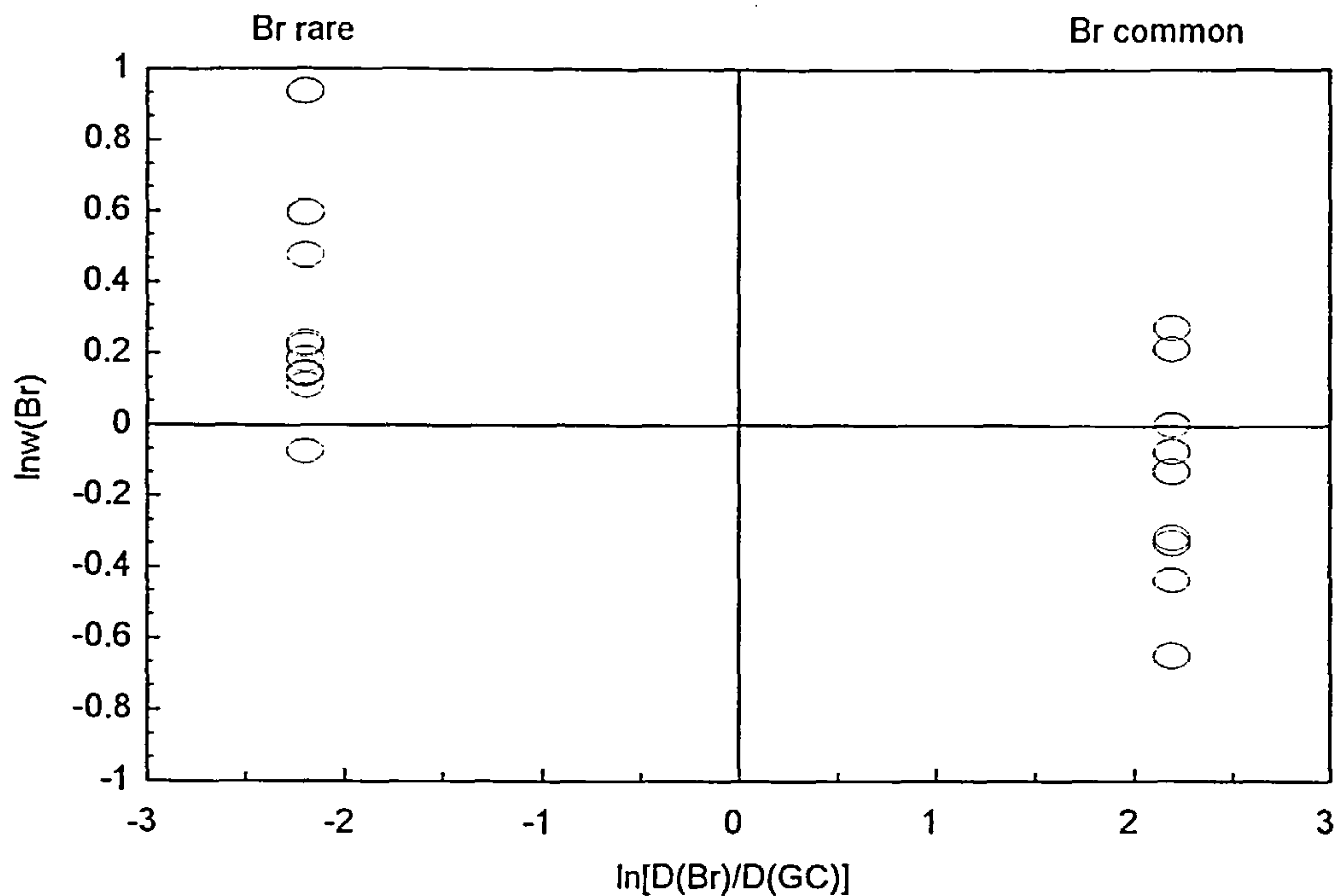


Figure 4.1. *The effect of frequency ($\ln D_{Br}/\ln D_{GC}$) on selectivity ($\ln w_{Br}$) by Firtree Farm cats in Experiment 1.*

feeding in this experiment, it was only possible to assess crudely whether the assumption of constant preference held for this experiment. This was done by plotting $\ln w_{Br}$ against total number of food items eaten for each trial at each frequency. Any large, systematic preference changes ought to be associated with the total number of pieces of food consumed. However, no significant correlation was found between $\ln w_{Br}$ and number eaten when Br was common (Spearman rank correlation: $r_s = -0.0667$, $n=10$, $p>0.5$) or rare ($r_s = -0.3212$, $n=10$, $p>0.1$), suggesting that preference remained roughly constant during each trial.

(b) Experiment 2 : Cattery cats.

Data were analyzed using the same methods as for Experiment 1. Fitting a null model (model 1) produced a deviance of 34.597 with 16 degrees of freedom. Fitting model 2 produced a very highly significant reduction in deviance (deviance=21.954, $df=15$, $\chi^2=12.64$, $p<0.001$), and inspection of GLIM parameter estimates revealed that this represented an overall preference for GC. There was also a significant frequency-dependent effect when model 3 was fitted (deviance=11.373, $df=14$, $\chi^2=10.58$, $p<0.005$). This model was an excellent fit to the data (figure 4.2.). From

GLIM parameter estimates, the best fit model can be described as:

$$w_{Br} = D^{-0.06107}$$

$$w_{GC} = 1.123D^{-0.06107}$$

The negative value of the exponent indicates that, as in experiment 1, selection was *anti-apostatic*.

Significantly more food items were eaten in trials when Br was common than when GC was common (Br common: mean number eaten = 516.38, SD = 155.54; GC common: mean number eaten = 336.88, SD = 72.37; ANOVA: $F_{1,14} = 8.76$, $p < 0.05$). However, preference was again assumed to be constant throughout a trial since there was no significant correlation between $\ln w_{Br}$ and total number eaten when Br was both common (Spearman rank correlation: $r_s = 0.3571$, $n = 8$, $p > 0.1$) and rare ($r_s = -0.2857$, $n = 8$, $p > 0.1$).

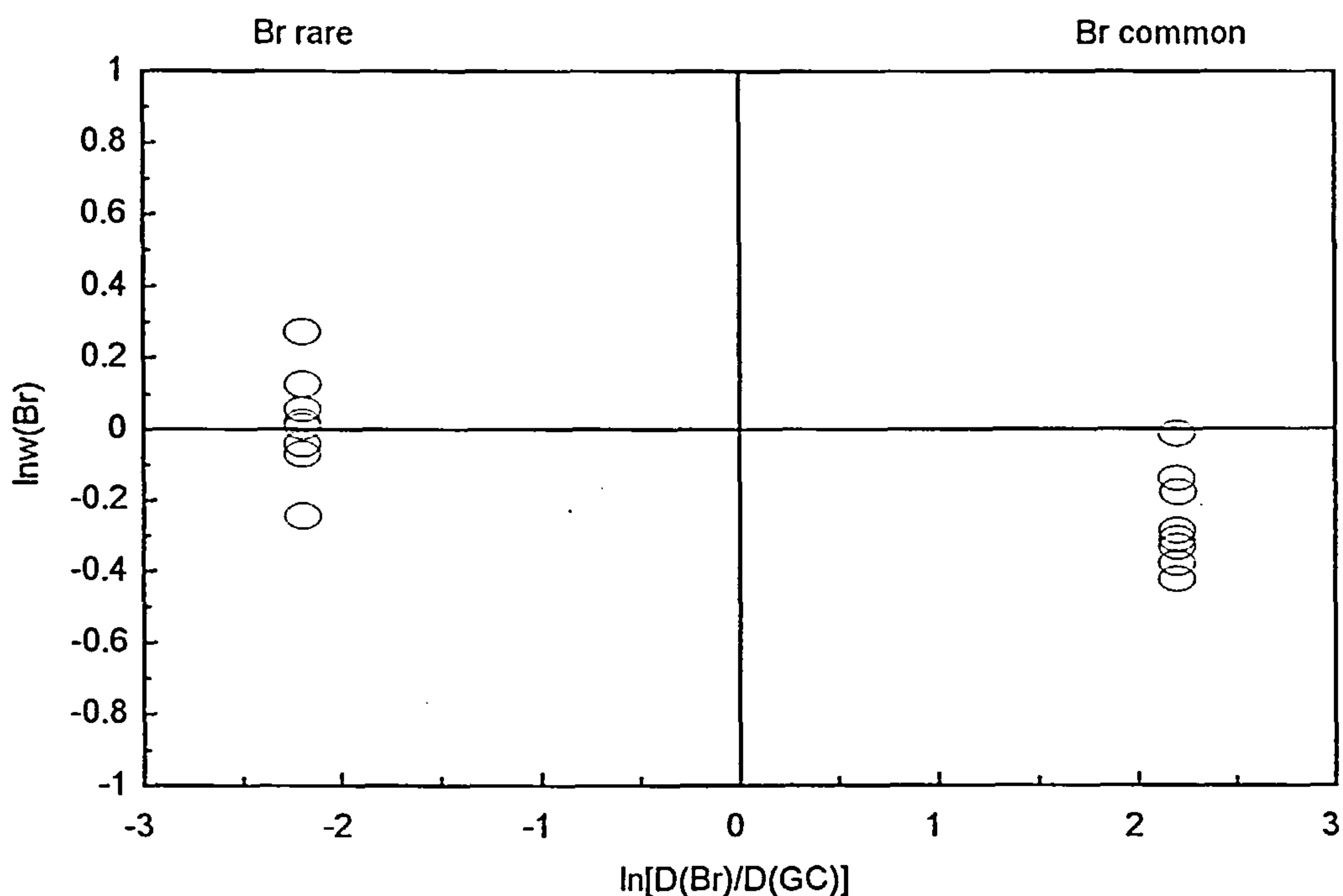


Figure 4.2. The effect of frequency ($\ln D_{Br} / \ln D_{GC}$) on selectivity ($\ln w_{Br}$) by WCPN cats in Experiment 2.

4.1.2.2. Individual preference tests.

(a) Farm cats.

The numbers of pieces of Br and GC eaten in each individual preference test (initial number = 70:70) and the calculated β_{Br} values are shown in table 4.1. Observation of the data suggested that there was considerable inter- and intra-individual variation in preference. The largest deviance from the null hypothesis ($\beta_{Br}= 0.5$) for each individual is displayed in bold in table 4.1. (These values will used in the model described in section 4.3.)

CAT	TEST 1		TEST 2	
	Br:GC eaten	β_{Br}	Br:GC eaten	β_{Br}
SID	38:25	0.361	28:24	0.451
HONEY	37:36	0.489	12:23	0.679
DUSTY	28:28	0.5	6:12	0.676
PENNY	15:11	0.415	8:5	0.379
GERTIE	8:6	0.682	9:10	0.528

Table 4.1. Number of food items eaten (Br:GC) and β -values for Firtree Farm cats. Bold β_{Br} are largest deviations from equal preference ($\beta_{Br}=0.5$) by each individual.

(b) Cattery cats.

The data obtained from the WCPN in the individual preference tests is presented in table 4.2. One individual, C462, did not complete a single test, while cat H142 only completed three out of the five tests. Mean β_{Br} values and their standard deviation were calculated for the five cats which completed preference tests. (cat C435: mean $\beta_{Br}=0.506$, SD=0.039; cat C710: mean $\beta_{Br}=0.376$, SD=0.1251; cat C455: mean $\beta_{Br}=0.539$, SD=0.116; cat C594: mean $\beta_{Br}=0.413$, SD=0.099; cat H142: mean $\beta_{Br}=0.462$, SD=0.181).

CAT	TEST 1	TEST 2	TEST 3	TEST 4	TEST 5
C435	17:18 (0.48)	25:23 (0.52)	15:12 (0.56)	23:26 (0.46)	15:15 (0.50)
C710	7:14 (0.32)	19:16 (0.55)	5:7 (0.41)	4:14 (0.20)	14:21 (0.38)
C455	20:10 (0.69)	13:18 (0.41)	12:15 (0.44)	19:13 (0.60)	23:19 (0.55)
C594	14:15 (0.48)	8:21 (0.25)	7:11 (0.36)	11:11 (0.5)	10:12 (0.45)
H142	-	3:8 (0.27)	10:10 (0.5)	8:5 (0.62)	-

Table 4.2. Individual preferences (Br eaten : GC eaten) of WCPN cattery cats. β_{Br} values are in parentheses.

4.2. MODELLING THE EFFECT OF INDIVIDUAL VARIATION ON SELECTION.

One possible explanation for the anti-apostatic selection observed in experiments 1 and 2 is that it is caused by inter-individual variation in the frequency-independent component of selection (P.L. Chesson 1984). This effect can be best illustrated by considering a simple, hypothetical example. Imagine two predators feeding on a mixed population of 90 prey X and 10 prey Y. Predator 1 has exclusive preference for prey X and predator 2 exclusive preference for prey Y. If both predators are able to consume 9 prey items in the available foraging time, then a total of 81 prey X and 1 prey Y will remain at the end of the foraging period. In other words, more of prey Y (rare) have been eaten than would be expected by chance alone on the basis of the original frequencies of the two prey. Conversely, with the same predators there would be disproportionate predation on prey X when it is rare. In general, variation between predators can lead to anti-apostatic selection even though individuals themselves are not selecting anti-apostatically. The frequency-independent preference data obtained for the Firtree Farm and WCPN cats allow this effect to be crudely modelled.

4.2.1. The Model.

Manly's β values were used as the preference index for the model since β is easier to conceptualize and visualize than w_{ij} values when $w_{mj}=1$ (as with GLM analysis). In addition, $\ln w_{ij}$ values are not always calculable (equation 3.10.) since $\ln(0)$ can arise when all of one prey type are eaten. Computer modelling is simplified by avoiding the use of such expressions.

Group preference for food type i in a given trial of an FDS experiment in which n food types are available is given by $\beta_{i(g)}$:

$$\beta_{i(g)} = \frac{\log(D_i/(D_i - e_i))}{\sum_{j=1}^n \log(D_j/(D_j - e_j))} \quad (4.1)$$

where D_i is the total number (density) of food i available to the group, and e_i is the total numbers of food i remaining at the end of the trial. Let ϵ_i be the number of items of food i eaten by each of the n individuals in the group:

$$\epsilon_{ik} = F_{ik} N_k \quad (4.2)$$

(F_{ik} is the frequency of food i in the diet of the k th individual, and N_k is the total number of food items eaten per trial by the k th individual.) The total number of food i items consumed by the group is the sum of the number consumed by each individual:

$$e_i = \sum_{k=1}^n \epsilon_{ik} \quad (4.3)$$

In a TTSE, the probability, P_{ik} , that the next food type consumed by a given forager will be of type i , is given by:

$$P_{ik} = \frac{\beta_{ik} D_{ik}}{\sum_{j=1}^n \beta_{jk} D_{jk}} \quad (4.4)$$

where D_{ik} represents the number of prey i currently remaining in the trial (being a TTSE, D_{ik} decreases during a trial), and β_{ik} represents the constant preference of that forager for prey i throughout the trial. In a TOSE, the D 's are constant throughout a trial so $F_{ik} = P_{ik}$. In a TTSE, though, the D 's change as food depletion

occurs, so $F_{ik}=f(D_{ik})$. Thus

$$\varepsilon_{ik}=f(D_{ik})N_k \quad (4.5)$$

Although we have seen that a double exponential function can be used to relate selectivity to consumption at a given density in a TTSE (equation 3.8.), by far the most convenient method of obtaining estimates of group preference is to use computer simulation techniques.

4.2.2. Computer Simulations.

Computer simulations of the effect of intra- and inter-individual variation on group FDS were written using *Turbo Pascal* version 7.0 (Borland International Ltd.). The data obtained in the individual preference tests in experiments 1 and 2 (tables 4.1. and 4.2.) were used to provide estimates of variation for the model.

4.2.2.1. Simulation of selection by cattery cats.

Although data was only collected for five out of the six cats in the experiment, it was still possible to model, albeit rather crudely, the preferences of the whole group. The *Turbo Pascal* program written for this purpose is presented in appendix 4. Although the aim of the simulations was to recreate the conditions of experiment 2 as faithfully as possible, three main assumptions were made:

(a) *Numbers eaten.*

The number of food items consumed in each experimental trial varied a great deal. I therefore assumed that the number eaten in each trial at each frequency in the simulations were the same as the *mean* number eaten in experimental trials at each frequency (i.e. 516 when Br is common and 337 when GC is common).

(b) *The underlying distribution of β values.*

Since only five β_{Br} values were obtained for each individual, it was necessary to make an assumption about the underlying distribution from which these values were sampled. In one simulation, I assumed that the distribution was normal, since this distribution is both widespread in biological systems and intuitively appealing. However, for comparative purposes, a second simulation was carried out using a uniform (square) distribution delineated by the maximum and minimum β_{Br} values

obtained for each cat. Although unlikely to represent the true distribution, this had the advantage of not generating β_{Br} values outside those which were determined experimentally. Data files containing random β values according to the required distribution, based on the experimental data for each cat, were generated using the statistical software package *Statgraphics* version 5.0.

(c) Predator behaviour and prey distribution.

The simulation assumed that food items were randomly distributed in space. As stated in chapter 2, this was not the case in the present experiments. However, since the random β values for each cat were generated from experimental results, the regular arrangement of prey is implicitly included in the simulation. Furthermore, if it is assumed that the predator selects successive food items from random points in space, as in these simulations, then the spatial arrangement of the prey is unlikely to affect the outcome of the simulation.

100 iterations (trials) were carried out for each frequency, from which the mean β_{Br} value was calculated. The results of the simulations agreed well with the observed values of mean β_{Br} , both qualitatively and quantitatively (figure 4.3.). Experimental results, simulation 1 (normal) and simulation 2 (uniform) all show anti-apostatic selection and an overall preference for GC. Perhaps not surprisingly, the predicted magnitude of anti-apostatic selection is larger for a normal distribution than for a uniform distribution (due to the greater variance). However, the fact that two completely different distributions produce very similar results suggests that the overall effect is robust.

4.2.2.2. Simulation of selection by farm cats.

The individual preference data obtained for the Firtree Farm cats (table 4.1.) is less comprehensive than that obtained for the cattery cats, with only two preference tests being carried out per individual. These data points are too few to calculate a mean and standard deviation, or to assume a range. As a result, only the most extreme β_{Br} values were taken from each cat, and used to model a single trial. Although generally unsatisfactory, this method does provide a rough estimate of the magnitude of FDS which can be predicted from the observed differences between cats. The magnitude of the anti-apostatic effect predicted by the model was close to that observed in experiment 1 (figure 4.4.). However, the simulation over-estimated the

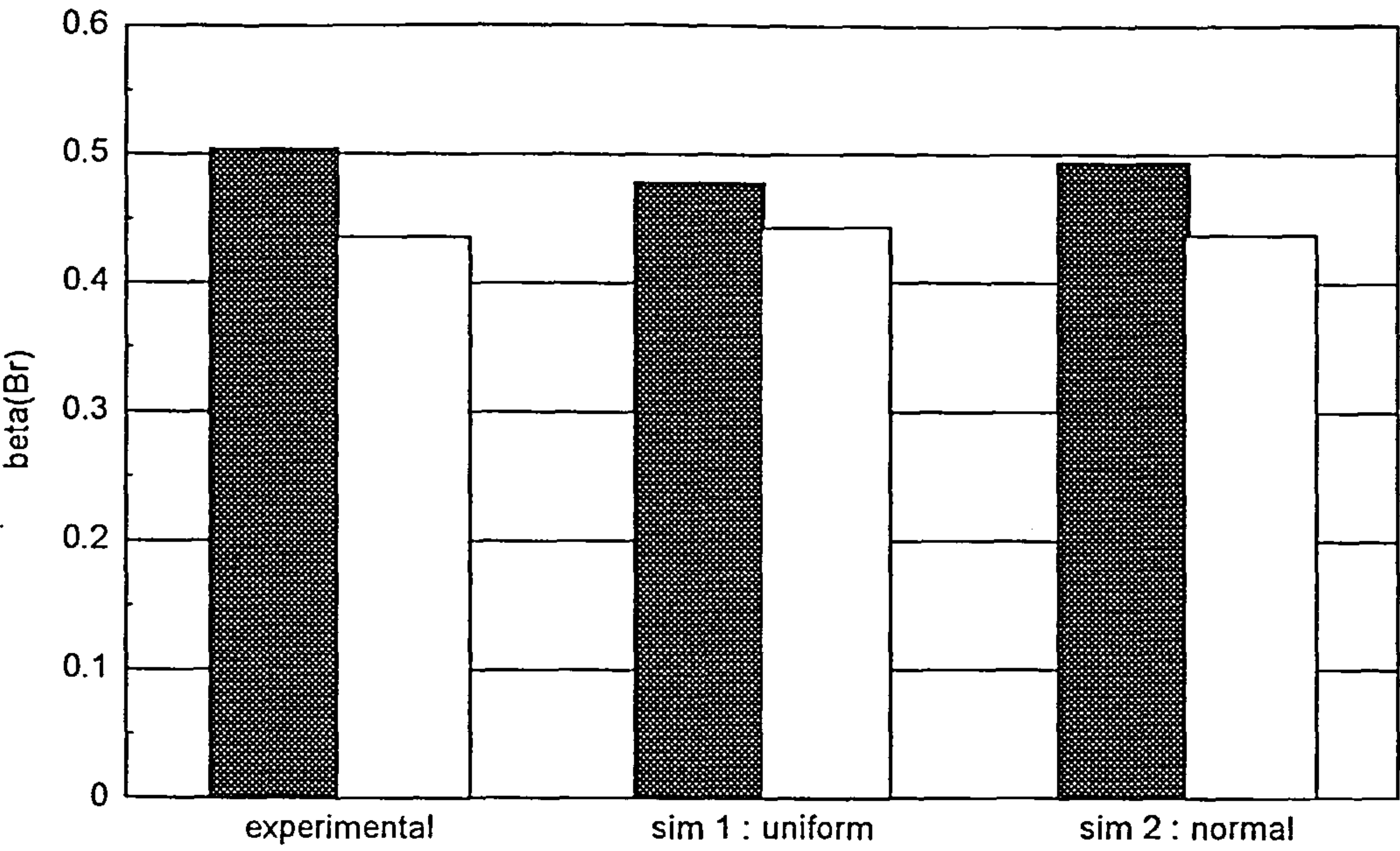


Figure 4.3. Comparison of experiment 2 data with group foraging computer simulations based on inter-individual variation in preference (■ Br rare □ Br common).

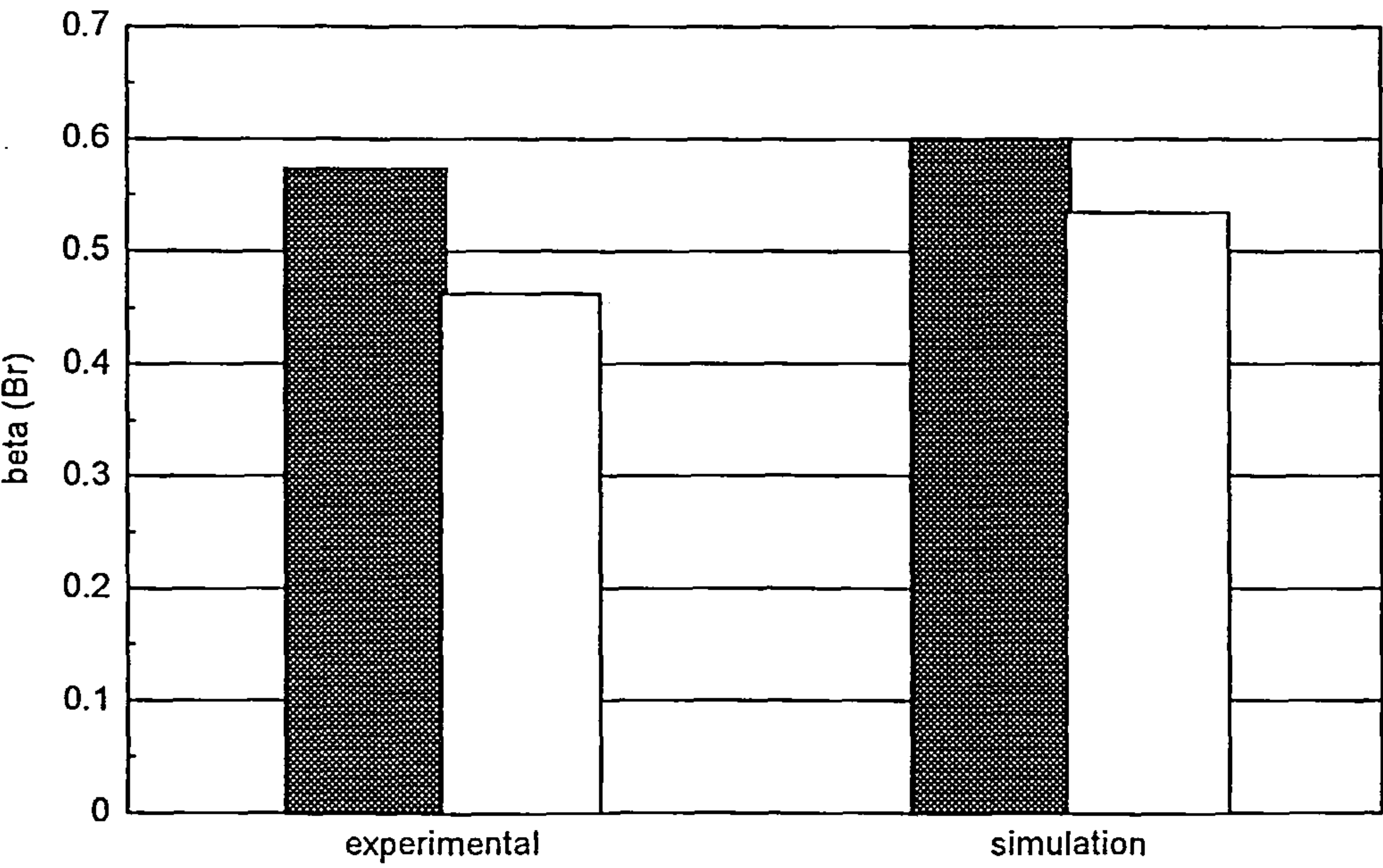


Figure 4.4. Comparison of experiment 1 data with results of group foraging simulation based on most extreme preferences of each individual (■ Br rare □ Br common).

group frequency-independent preference for Br. This is not surprising, though, given that individual data from an odd number of cats (five) were used. In this situation, there will always be a bias in group preference towards whichever food the majority of individuals prefer.

4.3. DISCUSSION.

4.3.1. Overview.

The experiments presented in this chapter add to the growing body of evidence (Allen 1972, Allen & Anderson 1984, Raymond 1987, Horsley et al. 1979, Wilson et al. 1990, Greenwood et al. *in press*) that anti-apostatic selection by groups of foragers occurs when absolute prey densities are very high. Furthermore, the results of experiments 1 and 2 are in close agreement with those obtained by Miles (1989) in the only other study carried out to date on FDS by domestic cats. This is reassuring because Miles' experimental protocol was, in some respects, quite different to that of experiments 1 and 2. Rather than presenting trays of food simultaneously and overnight, he presented four foil dishes sequentially over a period of one or two hours to a group of rescue shelter cats. He also did not randomize the presentation sequence of the two different frequencies, opting instead to alternate frequencies in successive trials. In addition, he mixed the two foods in a "haphazard" manner, as opposed to the regular distribution used in these experiments. The similarity between the results obtained by Miles and those of experiments 1 and 2 therefore suggests that anti-apostatic selection by groups of domestic cats is a genuine, robust phenomenon among groups of cats from different backgrounds and not merely due to the minutiae of experimental design. It is clear, though, that there are some facets of this work (methodological, analytical and theoretical) which require further discussion.

4.3.2. Methods & Analysis: A Critique.

The use of groups of cats (or any animals, for that matter) raises some important methodological issues. One problem when testing for FDS in a single group of cats is deciding the order of presentation of different frequencies. With literal (true) replication (Martin & Bateson 1986), in which a different group of individuals is used

for each trial, presentation sequence is not likely to be a problem since all trials will be independent (although it is still advisable to randomize as a precaution against systematic climatic effects or the effect of endogenous rhythms). However, to carry out around 20 experimental trials, each with a different group of five or six foragers is immensely impractical unless the subjects are both extremely common and easily accessible. Although the domestic cat is common, it is by no means practical to use different individuals in each trial. As a result, it was necessary to use the same group throughout all trials. Unfortunately, this makes it possible that the selection observed in a particular trial might be influenced by the experimental frequencies experienced in previous trials. This is especially likely to be true if different frequencies are alternated, as in the case of Miles (1989), since individual foragers are then likely to be able to learn the sequence. This could lead to expectation being confounded with the effect of frequency on selection. Indeed, expectation can play an important role in determining food preferences in the wild (Zach & Falls 1976). Although the problem of expectation is overcome by randomizing the sequence of presentation, the random sequence of ratios presented in previous trials can still influence current preference. In the present experiments, though, there were clear differences between selectivity at each frequency. Since each trial was preceded by a different sequence of trials, it is very unlikely that presentation sequence might have produced the same spurious results for both experiments.

A further difficulty with the use of groups of animals when considering the effects of inter-individual variation is the accurate measurement of individual preferences. Preference is a dynamic process, and so the result of any preference test can only reveal a "window" of preference. The method used in experiment 2 (measuring frequency-independent preferences for individuals between group FDS trials) is useful in that it is predictive; by measuring the inter-individual variation, predictions can be made about the nature of the group preference. It is extremely difficult, however, to obtain enough individual data to be confident about the underlying distribution of preference in such cases. An alternative method, though, is to measure the preferences of individuals *during* a group foraging bout. This was not possible in the experiments presented here since the food was at such a high density that it was not possible to observe which particular food items an individual was consuming. Indeed, measuring the preferences of a whole group of predators feeding in a patch simultaneously is likely to be an extremely difficult task in any experimental system.

The major analytical difficulty encountered in this chapter was the large amount of extraneous variance detected when fitting the TTSE GLMs to the data from experiment 1. Weale (*unpublished*; see Chapter 3) has shown that high extraneous variance tends to produce a large number of anti-apostatic type I errors in TTSE GLMs. This may be offset to some extent by the regular arrangement of food items in the experimental trays, which tends to produce conservative estimates of anti-apostatic selection. However, the very high significance level of the anti-apostatic effect, coupled with confirmation by a more conservative analysis based on Manly's β values, means that great confidence can be placed in the conclusion that selection was anti-apostatic. No such problems were encountered for experiment 2 since the "best-fit" model was an extremely good fit to the experimental data.

4.3.3. Ecological Implications of Inter-Individual Variation in Selectivity.

Perhaps the most important issue to emerge from these experiments and computer simulations are their ecological implications. To date, the effect of individual variation upon group or population processes has, with a few notable exceptions (Chesson 1984, Lomnicki 1988, DeAngelis & Gross 1992, Judson 1994), been largely overlooked. Yet the tendency for anti-apostatic selection to occur when there is inter-individual variation in preference is, potentially, of great importance in population dynamics. There is no doubt that generalist predators often show large differences in preference between individuals (illustrated graphically for several different species by Murdoch & Oaten 1975). It is therefore likely that anti-apostatic effects are occurring in many natural systems. Anti-apostatic selection, though, produces an extremely destabilizing effect on prey populations; once a prey species becomes rare it will tend to go (locally) extinct (Low *unpublished*).

Given that inter-individual variation is likely to be quite common, it is surprising to find that anti-apostatic selection is rarely observed in FDS experiments, except at high densities. One possible reason for this is that prey are generally presented to predators in a fairly homogeneous (i.e. random) mixture in artificial experiments. Since prey preferences are likely to be influenced by the prey items encountered in the immediate past (Cook 1965), it might be expected that greater variation would arise when prey are distributed in a heterogeneous manner (patchily). For example, Murdoch et al. (1975) found extreme variation in preferences between guppies feeding on tubificid worms and *Drosophila* because these prey species occupied

either the bottom or the surface of the tank, and individual guppies tended to spend a large proportion of time in one location only. However, this leads us into uncharted territory: environmental heterogeneity is generally accepted to promote stability in prey populations (Murdoch 1977) yet, as I have outlined above, can also potentially generate conditions that lead to instability via anti-apostatic effects. Modelling the relative influence of these effects on stability might prove to be a fruitful area for future research.

4.3.4. Computer Simulations: Is There Room for FDS by Individuals?

The simulations of the effect of inter-individual variation in frequency-independent preference on group FDS produced an exceptionally good fit to the empirical data, particularly in experiment 2. It might therefore be considered unparsimonious to entertain notions of FDS by individuals. As with all behavioural models, though, a note of caution must be sounded. Because the models closely predicted group FDS it may be tempting to conclude that the mechanisms which were explicitly included in the model were those *which actually caused* the experimental results. Although it is clear from the computer simulations that wherever inter-individual variation occurs there will tend to be an anti-apostatic effect, it is entirely conceivable that the observed data could be due, at least in part, to anti-apostatic selection by individual cats. This would not be surprising since what little evidence there is (Thorne 1982, Bradshaw et al. summarized in Bradshaw 1992) suggests that individual domestic cats prefer rare food items. Furthermore, there are several behavioural mechanisms, (e.g. sensory contrast, sensory-specific satiety, benefits to mixed diets; see Chapter 1) which might produce increased preferences for rare food types in domestic cats. These behavioural mechanisms, as well as causing individual anti-apostatic selection, might also cause variation to decrease at extreme frequencies. The resulting group effect might therefore be a combination of individual variation *and* individual FDS. To date, though, FDS by individual cats has not been tested for. Experiments which address the hypothesis that individual cats select anti-apostatically are presented in the next chapter.

Frequency-Dependent Selection by Individual Cats

In chapter 4 it was demonstrated that groups of farm and cattery cats select anti-apostatically when presented with a high-density mixture of two dry foods, a result consistent with previous studies of FDS by vertebrate foragers when food items are at high densities (Greenwood et al. 1984ab, Allen & Anderson 1984, Greenwood et al. *in press*, Wilson et al. 1990). Although much of the observed anti-apostatic selection could be explained in terms of inter-individual variation in preference, selection by individual cats was not explicitly addressed. There is, however, evidence that individual mammals (mice) select anti-apostatically at high food densities (Greenwood et al. 1984ab). Furthermore, studies of food selection by the domestic cat, although not explicitly testing for FDS, have shown that cats tend to show increased preferences for food types which they do not normally encounter (Bradshaw et al. summarized in Bradshaw 1992, Thorne 1982). It can therefore be predicted that selection by individual cats in high-density, multi-frequency experiments will be anti-apostatic. In this chapter, I present experiments on rescue shelter and cattery cats which test this hypothesis.

The foraging experiences of rescue shelter cats are very different from those of cattery cats; the majority of shelter cats have experience of scavenging and are often required to select food from a nutritionally variable array of foods, while cattery cats have been raised and maintained only on nutritionally complete commercial foods (see chapter 2). A second objective of this chapter is therefore to examine whether

these differences in foraging experience might produce differences in food selection.

If previous foraging experience influences the strength of FDS in cats, it might also influence the sensitivity of cats to systematic changes in food availability. In testing for FDS I have therefore used two different approaches for presenting different ratios of foods in multi-frequency experiments. In the first, the different ratios are presented to each experimental cat in a random order ("random presentation"). This approach is most applicable when testing for FDS is the sole consideration of the experiment. In the second approach, the food ratios presented to individuals are gradually and systematically changed in successive trials from one extreme frequency to the other ("sequential presentation"). In a natural situation, the relative availability of different prey types may change gradually with time. This could apply to urban feral cats in terms of both live prey availability and composition of household waste. Comparing selection under each of these presentation regimes may shed some light on the response of cats from different backgrounds to subtle, systematic, changes in food availability.

5.1. METHODS.

5.1.1. Experiments 3a - 3e : Selection by Cattery Cats.

Five experiments were carried out using WCPN cats as experimental subjects. All experiments lasted for five consecutive days, with each subject in each experiment being subjected to one preference test each day, at approximately 1300 hours. In each test, individual cats were presented with 140 whole pieces of a mixture of Br and GC as a single layer in the bottom of a foil dish (inner diameter 180mm), a density of 5502 pieces/m². The two foods were regularly distributed among each other (see section 3.5. for rationale). Each cat was assigned to its own regular feeding box (figure 5.1). Each preference test lasted for a maximum duration of five minutes. The test was terminated before this time if, in the judgment of the experimenter, half of the total number of pieces had been consumed. Trials in which less than 10 pieces of food were eaten were rejected since these are likely to produce poor estimates of selectivity (Murdoch et al. 1975). At the end of each test, the numbers remaining of each of the two foods were counted.

Each cat was tested at five different ratios of Br:GC; 14:126 (10% Br), 42:98 (30% Br), 70:70 (50% Br), 98:42 (70% Br) and 126:14 (90% Br). In experiments 3a-3c, the frequencies were presented in a different random order to each cat. In experiments 3d-3e, the subjects were divided into two groups. The ratio Br:GC was gradually changed over the five days in the order 14:126, 42:98, 70:70, 98:42 and 126:14 in group 1 and, in the reverse order, from 126:14 to 14:126 in group 2. This is a similar experimental design to that used by Murdoch et al.

(1975) in their study of switching by fish. The dates, experimental foods, identity of individual cats and order of presentation of different frequencies are summarized in table 5.1. During the experimental periods, no dry food was fed to the cats other than that which was presented in experimental trials. The amount of maintenance diet provided for the cats on the evening prior to each day of the experiment averaged 233g of canned food (various varieties of "Kit-e-kat", Pedigree Petfoods) per cat.

5.1.2. Experiments 4a-4c : Selection by Rescue Shelter Cats.

Three experiments were carried out using rescue shelter cats from the St. Francis Animal Welfare. Experiments 4a and 4b used an identical design to experiments 3a - 3c (i.e. random presentation of frequencies), while experiment 4c used the same design as experiments 3d and 3e (sequential presentation of frequencies). The basic experimental details are summarized in table 5.2. The choice of subjects used in each experiment was determined by several preliminary feeding trials; individuals which were extremely wary of humans or overly social (to the extent of preferring human attention to food) could not be reliably tested on a regular basis and were rejected as experimental subjects.

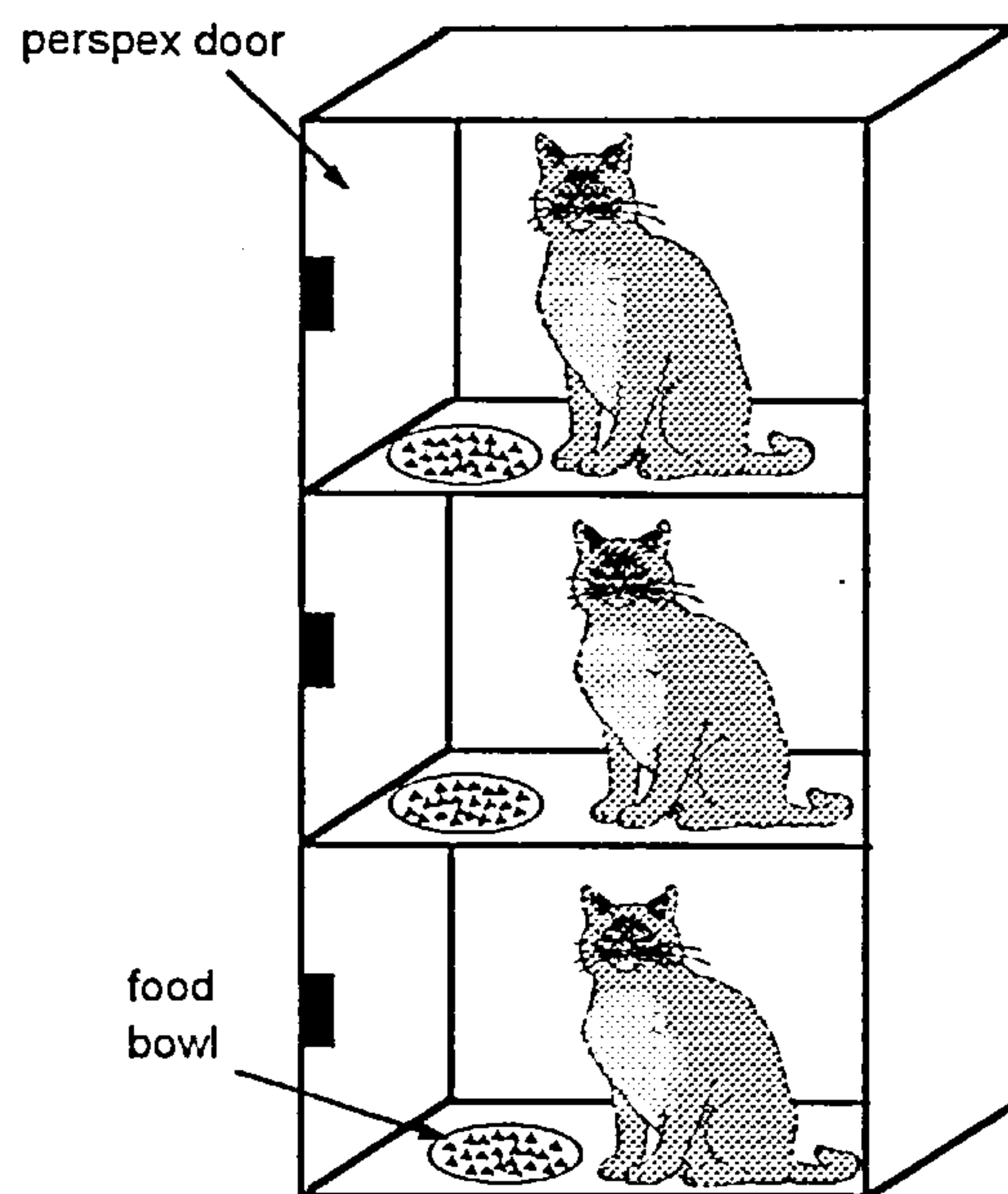


Figure 5.1. *Experimental 3-cat feeding box used in preference testing of cattery cats.*

The preference testing protocol was also identical to that of experiments 3a-3e, with the exception that feeding boxes were not used. Instead, the "stack'n'store" basket method described in section 4.1.1.2. was used to prevent other, non-experimental, cats from interfering with those being tested. Preference tests were always carried out at between 1100 and 1200 hours.

During experimental periods no Br or GC was given to the cats other than that presented in preference tests. However, the staff at St. Francis liked to give regular dry food "treats" to the cats. To prevent Br or GC being given, the shelter was supplied with "Meow-mix" (Quaker Foods Ltd) as an alternative dry food. Meow-mix had very different sensory properties to Br and GC, and was also less palatable (J.W.S. Bradshaw, *personal communication*).

EXP. NO.	DATE	INDIVIDUALS USED	EXPERIMENTAL FOODS	ORDER OF FREQUENCIES
3a	3-7/2/92	C403, D318, C467, C566, C592, C656, G5, G67, G586, H70	Br "pilchard" GC "lamb & beef"	random
3b	9-13/3/92	C403, D318, C467, C566, C592, C595, C656, G5, G67, G586, H70	Br "pilchard" GC "lamb & beef"	random
3c	10-15/5/93	C403, C409, C460, C470, C471, C597, C611, C656, C704, D271, H12	Br "chicken" GC "rabbit & liver"	random
3d	17-21/2/92	C403, D318, C467, C566, C656, C592, C595, C611, G5, G67, G586,	Br "pilchard" GC "lamb & beef"	sequential
3e	9-13/3/92	C704, C431, C463, C227, C424, C432, C470, C688, C250, C425, C443, H71	Br "pilchard" GC "lamb & beef"	sequential

Table 5.1. General details of experiments 3a-3e.

EXP. NO.	DATE	INDIVIDUALS USED	EXPERIMENTAL FOODS	ORDER OF FREQUENCIES
4a	18-22/5/92	LGBW, SNOW, TW, BLH, TWT, LHBH, BOB, TAB, TORT, BW, TT, BC	Br "pilchard" GC "rabbit & liver"	random
4b	28/6-2/7/93	BOB, LHBW, TAB, LBW2, EXLH, BLK, BLG, BLY, SMBW, LHFB, LHSB, GRW	Br "chicken" GC "rabbit & liver"	random
4c	25-29/5/92	LGBW, SNOW, TW, BLH, TWT, LHBH, BOB, TAB, TORT, BW, TT, BC	Br "pilchard" GC "rabbit & liver"	sequential

Table 5.2. General details of experiments 4a-4c.

5.2. RESULTS.

5.2.1. Experiments 3a-3c : Selection by Cattery Cats.

Experiments 3a-3c were analyzed using the standard TTSE version of Weale's (1992) generalized linear models (see chapter 3). The deviances and degrees of freedom in each experiment for models 1 (no selection), 2 (frequency-independent selection) and 3 (frequency-dependent selection) are summarized in table 5.3. The values of χ^2 and estimates of p in table 5.3. refer to the improvement in the fit of model n over model $(n-1)$.

In experiment 3a, one cat (C595) failed to eat 10 pieces of food at three of the five different ratios of Br:GC and was subsequently removed from the analysis. All other individuals in experiments 3a - 3e successfully completed at least four of the five preference tests.

In experiments with random presentation of frequencies (3a, 3b and 3c), GLIM analysis revealed no statistically significant frequency-dependent selection (model 3). Because of this, there was no need to fit model 4 (FDS + "additional effect 1"). In experiments 3a and 3b, model 2 produced a very highly significant improvement in

EXPT.	MODEL 1	MODEL 2	MODEL 3
3a	deviance = 126.82 d.f. = 44	deviance = 64.27 d.f. = 43 $\chi^2_{[1]} = 62.55$ $p < 0.001$	deviance = 61.91 d.f. = 42 $\chi^2_{[1]} = 2.36$ $p > 0.1$
3b	deviance = 99.81 d.f. = 55	deviance = 58.94 d.f. = 54 $\chi^2_{[1]} = 40.87$ $p < 0.001$	deviance = 57.12 d.f. = 53 $\chi^2_{[1]} = 1.83$ $p > 0.1$
3c	deviance = 56.02 d.f. = 55	deviance = 52.53 d.f. = 54 $\chi^2_{[1]} = 3.49$ $p > 0.05$	deviance = 51.27 d.f. = 53 $\chi^2_{[1]} = 1.26$ $p > 0.1$
3d	deviance = 103.17 d.f. = 54	deviance = 79.47 d.f. = 53 $\chi^2_{[1]} = 23.71$ $p < 0.001$	deviance = 78.98 d.f. = 52 $\chi^2_{[1]} = 0.51$ $p > 0.1$
3e	deviance = 109.54 d.f. = 59	deviance = 59.73 d.f. = 58 $\chi^2_{[1]} = 49.82$ $p < 0.001$	deviance = 59.54 d.f. = 57 $\chi^2_{[1]} = 0.19$ $p > 0.5$

Table 5.3. Summary of GLIM analysis of selection by cattery cats in experiments 3a-3e. See text for details.

the fit of the model. Examination of GLIM parameter estimates showed that in both cases this was due to an overall preference for GC. Model 1 (no selection) provided the best fit to the data in experiment 3c. The fitted models provided a good fit (i.e. deviance $\approx$ d.f.) to the data in experiments 3b and 3c. In experiment 3a, though, there was a reasonable amount of extraneous variance (i.e. deviance $>$ d.f.). However, some confidence can be placed in the analysis of experiment 3a since extraneous variance tends to produce type I errors (section 3.4.), yet no significant FDS was detected. From the parameter estimates, the overall best fit models in each experiment were:

Experiment 3a

$$w_{Br} = 1$$
$$w_{GC} = 1.556$$

Experiment 3b

$$w_{Br} = 1$$
$$w_{GC} = 1.366$$

Experiment 3c

$$w_{Br} = w_{GC} = 1$$

Although there was no significant FDS, it was still very useful to assess frequency-dependent trends in the data. Thus, fitting model 3 to each data set revealed an anti-apostatic trend (i.e. a negative value of the exponent s) in all three cases:

$$\begin{aligned} \text{Experiment 3a} \quad w_{Br} &= D^{-0.074} \\ w_{GC} &= 1.536D^{-0.074} \end{aligned}$$

$$\begin{aligned} \text{Experiment 3b} \quad w_{Br} &= D^{-0.057} \\ w_{GC} &= 1.353D^{-0.057} \end{aligned}$$

$$\begin{aligned} \text{Experiment 3c} \quad w_{Br} &= D^{-0.053} \\ w_{GC} &= 1.105D^{-0.053} \end{aligned}$$

The best-fit models and model 3 for experiments 3a-3c are visualized in figure 5.2. The fitted lines to the $\ln w_{Br}$ values were generated using the method outlined in section 3.3.2.3.

Analyses of experiments 3d and 3e (table 5.3.) were based on the pooled data from the two groups (recall that in each experiment the five frequencies were presented to the two groups in opposite orders). To justify pooling, it was necessary to demonstrate that there were no significant differences in selectivity between the groups. This was done in GLIM by generating additional models which allow an interaction between group and either food type (for overall preference) or density (for FDS) and comparing these to non-interaction models (i.e. models 2 and 3 for the combined data from both groups). In both experiment 3d and experiment 3e adding an interaction model produced no significant improvement in fit over model 2 (experiment 3d: $\chi^2_{[1]}=0.157$, $p>0.5$; experiment 3e: $\chi^2_{[1]}=0.221$, $p>0.5$) or model 3 (experiment 3d: $\chi^2_{[1]}=0.156$, $p>0.5$; experiment 3e: $\chi^2_{[1]}=2.128$, $p>0.1$). Pooling of data was therefore justified. GLIM analysis of the pooled data showed a very highly significant preference for GC in experiments 3d and 3e, but no significant FDS (table 5.3). From GLIM parameter estimates, the best-fit models for experiments 3d and 3e were:

$$\begin{aligned} \text{Experiment 3d} \quad w_{Br} &= 1 \\ w_{GC} &= 1.248 \end{aligned}$$

$$\begin{aligned} \text{Experiment 3e} \quad w_{Br} &= 1 \\ w_{GC} &= 1.387 \end{aligned}$$

The fitted FDS models (model 3) for these experiments were:

Experiment 3d

$$w_{Br} = D^{0.028}$$
$$w_{GC} = 1.254D^{0.028}$$

Experiment 3e

$$w_{Br} = D^{-0.018}$$
$$w_{GC} = 1.382D^{-0.018}$$

These analytical methods assumed that preference was constant throughout each experimental trial (Weale 1992). This assumption was, as in chapter 4, crudely tested by examining correlations between the number of food items eaten in each trial and $\ln w_{Br}$ (table 5.4.). In this analysis, correlations were only carried out for the two extreme 9:1 frequencies in each experiment since these are the frequencies at which preference changes are most likely to be revealed. There were no significant correlations, so it was cautiously assumed that preference was constant.

% Br	EXPT.	r_s	n	p
10	3a	-0.273	7	>0.5
	3b	-0.114	11	>0.5
	3c	0.428	11	>0.1
	3d	-0.167	9	>0.5
	3e	0.4035	12	>0.1
90	3a	0.214	8	>0.5
	3b	0.246	11	>0.1
	3c	-0.100	11	>0.5
	3d	-0.298	11	>0.1
	3e	0.150	12	>0.5

Table 5.4. Spearman rank correlation of $\ln w_{Br}$ against number of food items eaten by each cat for $Br=10\%$ and $Br=90\%$ in experiments 3a - 3e.

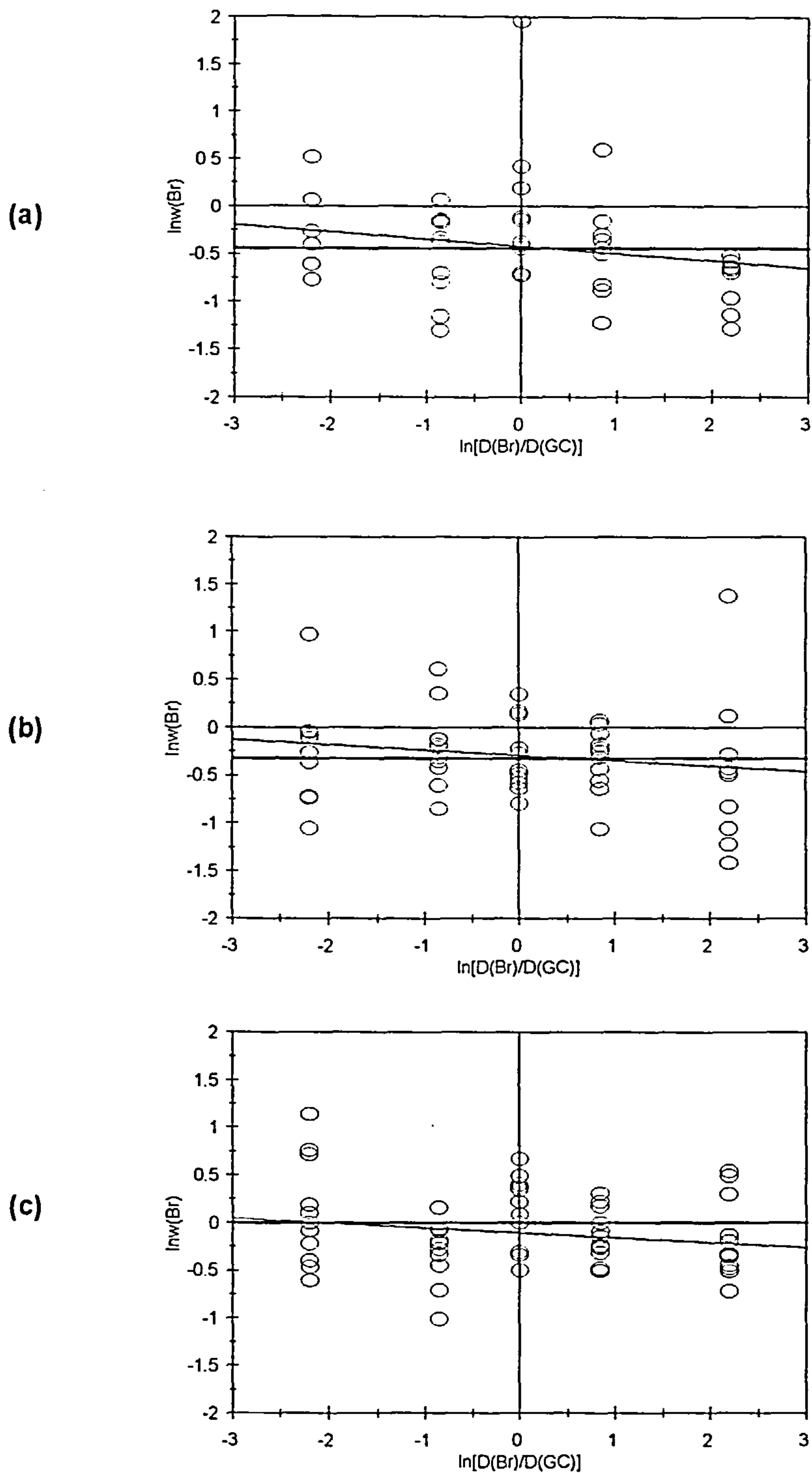


Figure 5.2. Plots of relative frequency of Br ($\ln(D_{Br}/D_{GC})$) against preference for Br ($\ln w_{Br}$) in (a) experiment 3a, (b) experiment 3b and (c) experiment 3c. The "best-fit" model in all cases is represented by a thick, solid line (gradient = 0) and the FDS trend by a thin, solid line (gradient $\neq 0$).

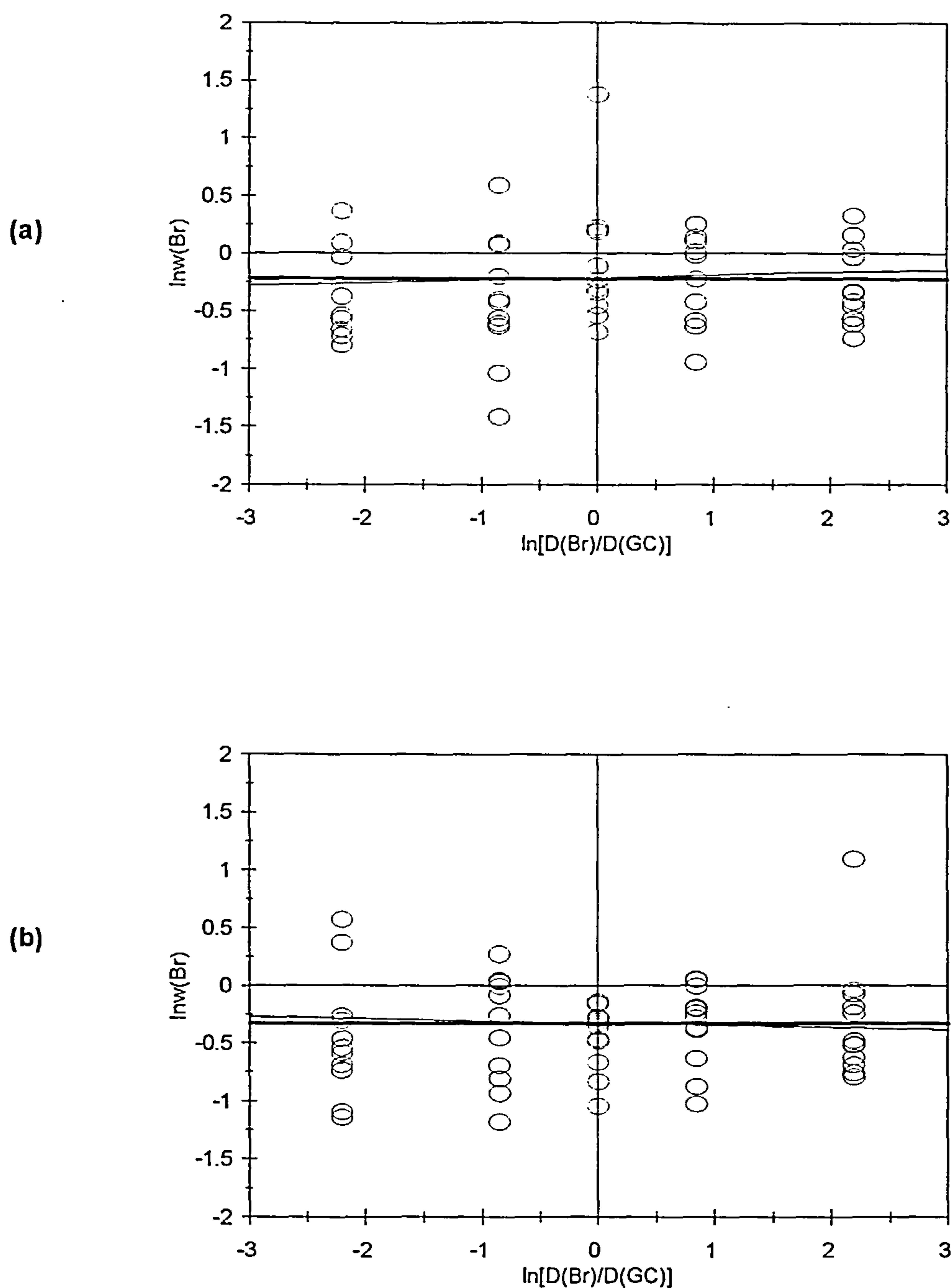


Figure 5.3. Plots of relative frequency of Br ($\ln(D_{Br}/D_{GC})$) against preference for Br ($\ln w_{Br}$) in (a) experiment 3d and (b) experiment 3e. The "best-fit" model in each case is represented by a thick, solid line (gradient = 0) and the FDS trend by a thin, solid line (gradient $\neq 0$).

5.2.2. Experiments 4a - 4c : Selection by Rescue Shelter Cats.

Three individuals in experiment 4b (EXLH, LHFB and LHSB) failed to consume 10 pieces of food in at least two preference tests and were subsequently removed from the analysis. The results of fitting GLIM TTSE models to the data from experiments 4a-4c are presented in table 5.5. In all experiments there were significant overall preferences (for Br in experiments 4a and 4c, and for GC in experiment 4b). GLIM analysis revealed highly significant anti-apostatic selection in experiments 4b and 4c but no significant FDS in experiment 4a. Fitting model 4 (FDS + "additional effect 1") did not produce a significant improvement in the fit of any of the three experiments.

EXPT.	MODEL 1	MODEL 2	MODEL 3	MODEL 4
4a	deviance=109.97 df=57	deviance=77.31 df=56 $\chi^2_{[1]}=32.66$ p<0.001	deviance=73.58 df=55 $\chi^2_{[1]}=3.73$ p>0.05	deviance=73.52 df=54 $\chi^2_{[1]}=0.064$ p>0.5
4b	deviance=52.28 df=40	deviance=43.07 df=39 $\chi^2_{[1]}=9.2$ p<0.005	deviance=34.47 df=38 $\chi^2_{[1]}=8.61$ p<0.005	deviance=33.54 df=37 $\chi^2_{[1]}=0.93$ p>0.1
4c	deviance=137.43 df=57	deviance=115.6 df=56 $\chi^2_{[1]}=21.76$ p<0.001	deviance=95.07 df=55 $\chi^2_{[1]}=20.60$ p<0.001	deviance=94.59 df=54 $\chi^2_{[1]}=0.482$ p>0.1

Table 5.5. Results of GLIM analysis of experiments 4a - 4c.

From the GLIM parameter estimates, the best fit models were:

Experiment 4a

$$\begin{aligned}w_{Br} &= 1 \\w_{GC} &= 0.748\end{aligned}$$

Experiment 4b

$$\begin{aligned}w_{Br} &= D^{-0.148} \\w_{GC} &= 1.18D^{-0.148}\end{aligned}$$

Experiment 4c

$$\begin{aligned}w_{Br} &= D^{-0.185} \\w_{GC} &= 0.794D^{-0.185}\end{aligned}$$

When model 3 (simple FDS) is fitted to the data from experiment 4a, the relationship between preference and density became:

$$w_{Br} = D^{-0.078}$$
$$w_{GC} = 0.751D^{-0.078}$$

The analysis of experiment 4c in table 5.5. was based on the pooled data from the two experimental groups. To justify this pooling, GLIM models were constructed to test for differences between the groups. Adding a group term to model 1 in table 5.5. produced a significant reduction in deviance ($\chi^2_{[1]}=5.415$, $p<0.025$), indicating a difference in the frequency-independent preferences of the two groups. There was no significant reduction in deviance when a group term was added to model 3 ($\chi^2_{[1]}=0.18$, $p>0.5$), indicating that there was no difference in the strength of FDS in the two groups. Since FDS was, ultimately, the focus of interest, pooling of data was justified.

Experiments 4a and 4c both showed a high degree of extraneous variance (deviance >> d.f.). Since experiment 4a was of borderline significance and 4c was highly significant, the more conservative test of a linear regression of frequency (% Br available) against β_{Br} was carried out to safeguard against the possibility of type I errors. The results were consistent with those obtained by GLIM analysis (experiment 4a: $\beta_{Br} = 0.607 - 0.00085\text{freq}(\text{Br})$, $t=1.542$, $df=55$, $p>0.1$; experiment 4c: $\beta_{Br} = 0.666 - 0.002\text{freq}(\text{Br})$, $t=3.569$, $df=55$, $p<0.001$).

In experiments 4a to 4c, there were no significant correlations between $\ln w_{Br}$ and total number of food items consumed in each trial at 10% and 90% Br (table 5.6), suggesting that preference remained roughly constant throughout the trial.

% Br	EXPT.	r_s	n	p
10	4a	-0.174	11	>0.5
	4b	-0.6587	8	>0.05
	4c	-0.077	12	>0.5
90	4a	0.070	12	>0.5
	4b	0.3253	8	>0.1
	4c	0.4924	10	>0.1

Table 5.6. Spearman rank correlation of $\ln w_{Br}$ v number of food items eaten by each cat for Br = 10% and Br = 90% in experiments 4a - 4c.

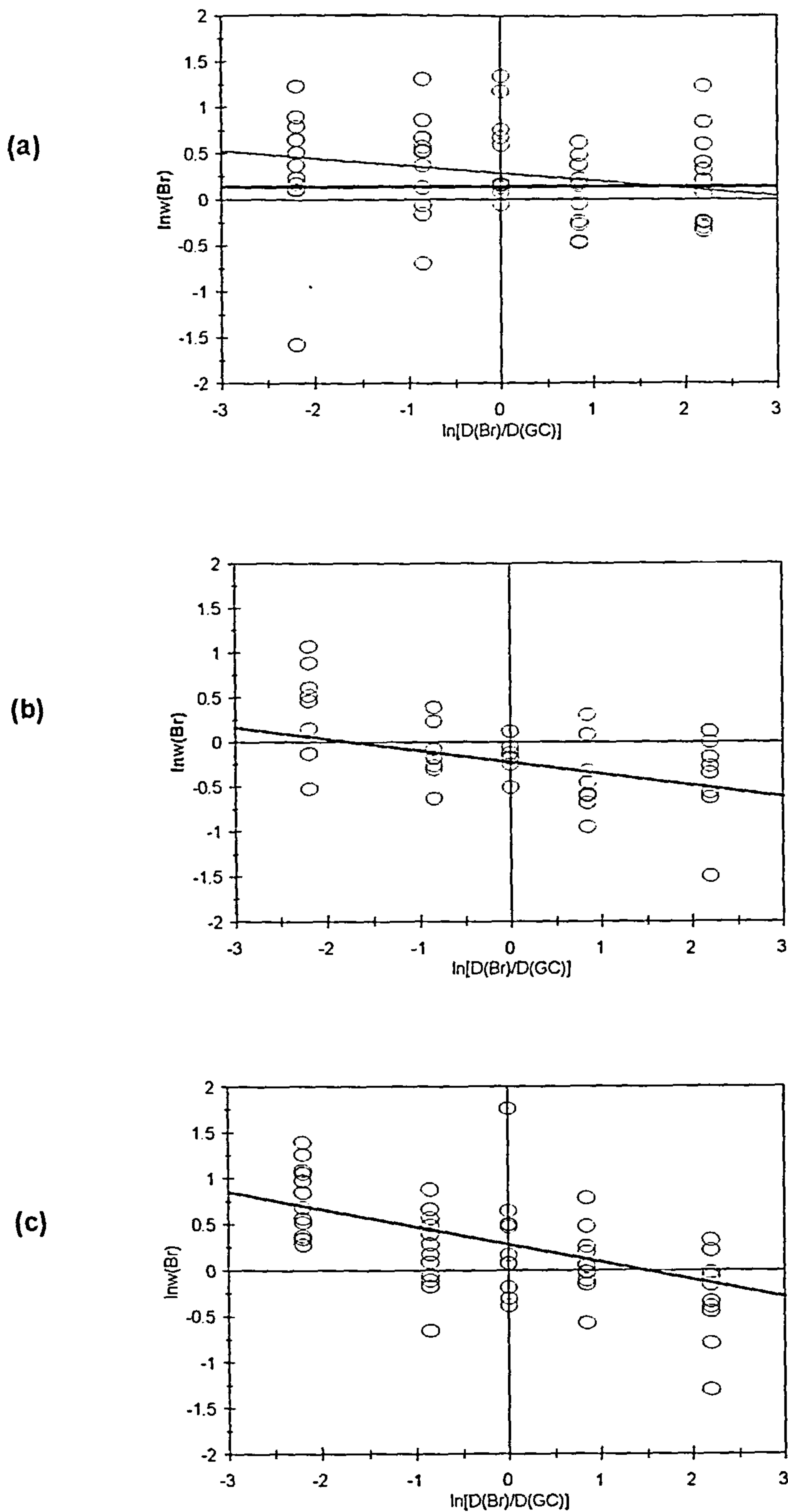


Figure 5.4. Plots of relative frequency of Br ($\ln(D_{Br}/D_{GC})$) against preference for Br ($\ln w_{Br}$) in (a) experiment 4a, (b) experiment 4b and (c) experiment 4c. The "best-fit" model is represented by a thick, solid line and the FDS trend (when the "best-fit" model is not frequency-dependent) by a thin, solid line.

5.2.3. Comparison of Selection by Cattery and Rescue Shelter Cats.

Differences in FDS between rescue shelter and cattery cats were investigated using a number of techniques. A simple visual comparison of the value of s , the frequency-dependent parameter in Weale's (1992) hierarchy of FDS models, among experiments (figure 5.5) revealed that rescue shelter cats selected more anti-apostatically than cattery cats in all experiments. Statistical comparison between the results of different experiments were, for most combinations, not valid since there was little consistency between the food types used and the presentation sequence of different frequencies. It was, however, possible to perform a GLIM analysis to compare selection between experiments 3c and 4b as the same foods (Br "chicken" and GC "rabbit & liver") and presentation sequence (random) were used. However, there were no significant differences between either frequency-independent ($\chi^2_{[1]}=1.008, p>0.1$) or frequency-dependent selection ($\chi^2_{[1]}=2.178, p>0.05$) between the shelter and cattery cat groups. As a second line of investigation, standard TTSE GLIM analysis was carried out on the data from each *individual* in experiments 3a - 3e and 4a - 4c. It is clear (figure 5.6.) that proportionately more rescue shelter cats selected anti-apostatically than did cattery cats. This was particularly apparent in experiments with sequential presentation of frequencies. It is also worth noting (see discussion) that the number of food items eaten in each trial was not significantly different between any of the eight experiments (one-way ANOVA on log transformed counts of total number eaten for Br=50%: $F_{(7,88)}=1.383, p>0.1$; figure 5.7.).

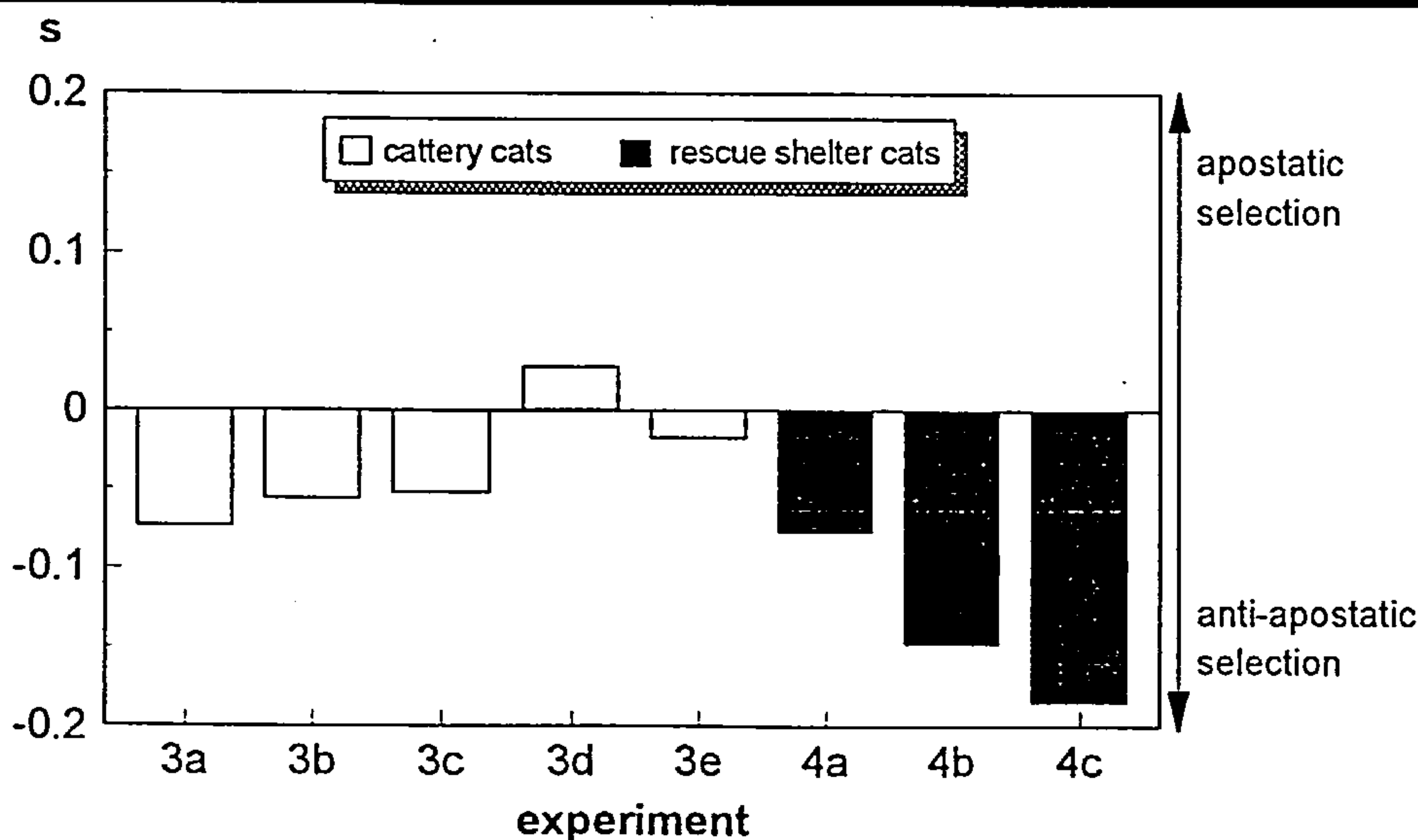


Figure 5.5. Summary histogram of strength of FDS (s) in experiments 4a-4e (cattery cats) and 3a-3c (rescue shelter cats).

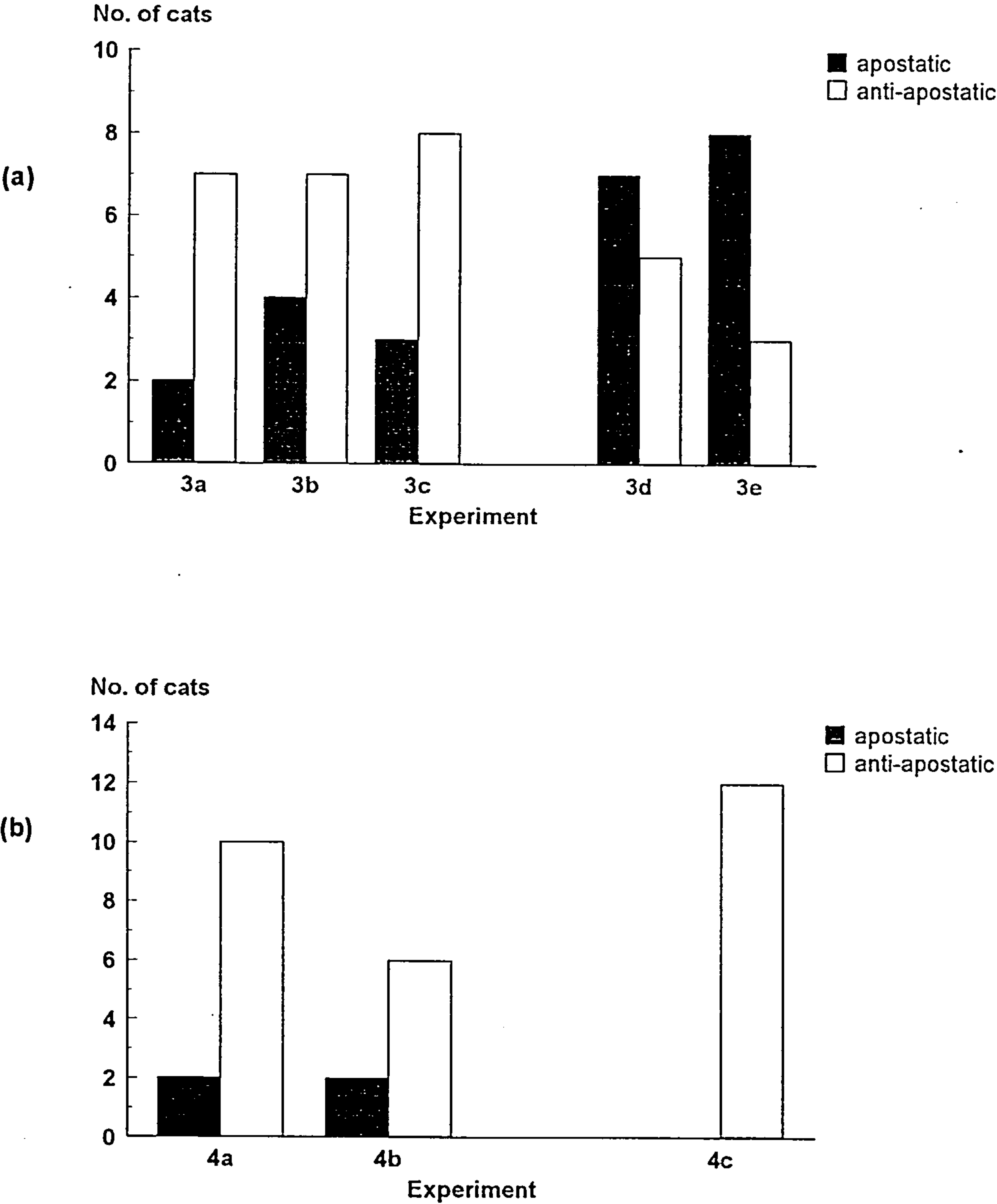


Figure 5.6. Number of individual cats selecting apostatically and anti-apostatically, based on GLIM analysis, in (a) experiments 3a-3e (cattery cats), (b) experiments 4a-4c (rescue shelter cats).

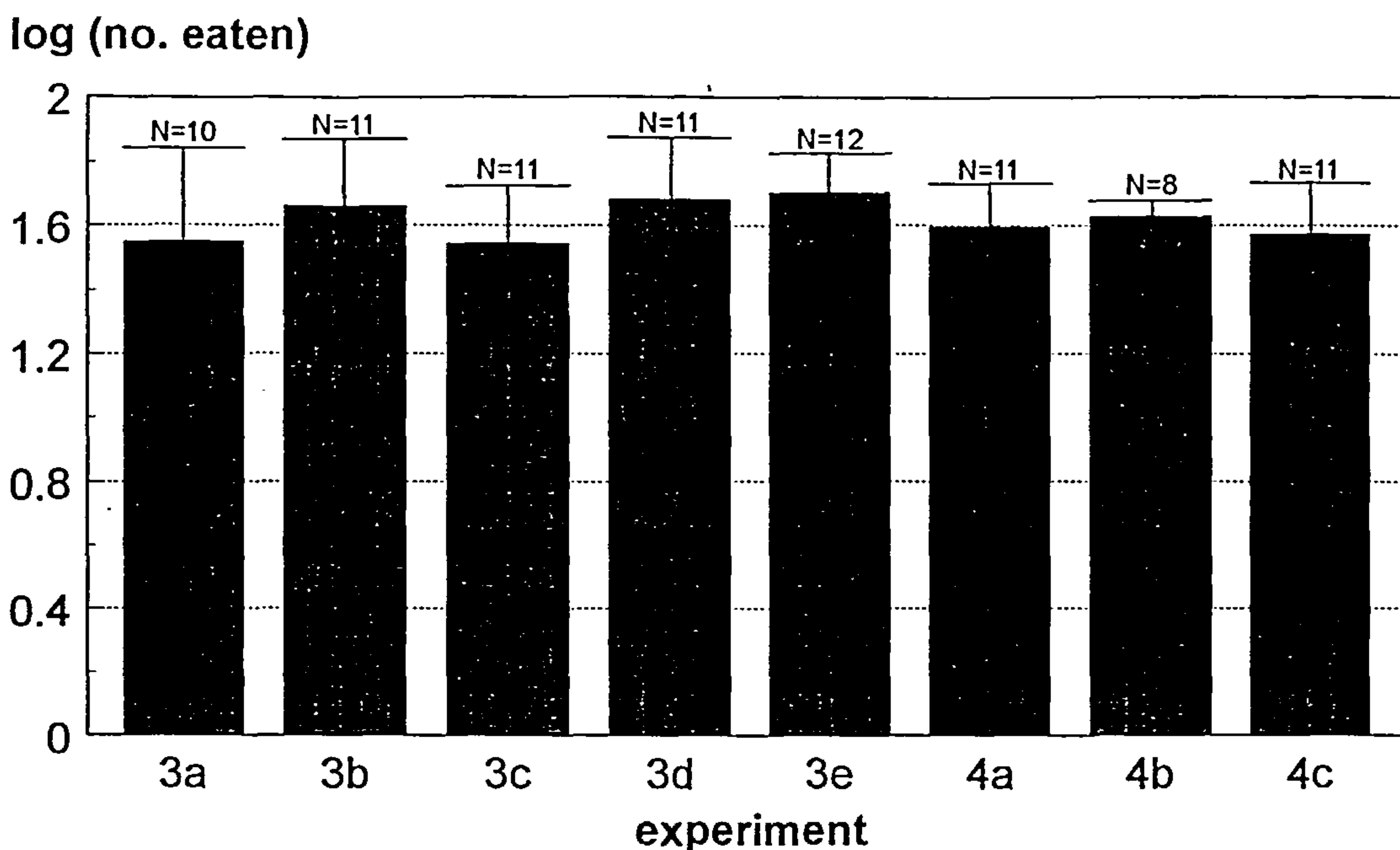


Figure 5.7. Log transformed number of food items (mean + SD) consumed by cats at $Br=50\%$ in experiments 3a-3e and 4a-4c [NOTE: $\text{antilog}(1.6)=39.8$].

5.3. DISCUSSION.

5.3.1. Overview.

Studies of FDS by individual vertebrate foragers at high food densities (Horsley et al. 1979, Greenwood et al. 1984ab, Allen & Anderson 1984) have generally resulted in anti-apostatic selection. However, the results of the eight experiments presented in this chapter provide only limited support for the prediction that individual domestic cats select anti-apostatically under such conditions. Although the majority of individual cattery cats (71%) showed anti-apostatic trends when frequencies were presented in a random order, statistically significant anti-apostatic effects were only observed in rescue shelter cats. Caution must be exercised, though, before concluding that there were fundamental differences between cats from different experiential backgrounds as it is conceivable that uncontrollable variables between study sites influenced the food selection behaviour of otherwise similar cats. It will therefore be necessary to carefully assess the minutiae of these experiments before any positive conclusions can be drawn.

5.3.2. Criticisms of Methods & Analysis.

5.3.2.1. Uncontrollable variables in the comparison of selection by rescue shelter and cattery cats.

In section 5.2.3. the strength of anti-apostatic selection by shelter cats in experiment 4b was statistically compared to that of cattery cats in experiment 3c. This was justified on the grounds that these two experiments were of identical design and used the same brands and varieties of dry food. Despite this similarity, there were still (unavoidably) uncontrolled variables between the two study locations. These variables may have important consequences in the interpretation of between-site differences in selection.

(a) Maintenance diet during experimental periods.

Although both cattery and shelter cats were primarily maintained on a diet of commercial cat foods, the quality of this food was generally superior at WCPN. Furthermore, shelter cats also received greater nutritional variety in their diet (by virtue of being fed table scraps). The idea that domestic cats can be classified according to their food habits is of central importance to this thesis. However, this classification also poses an experimental problem. For direct comparison of selection by cats from different experiential backgrounds experiments, strictly speaking, ought to be conducted under identical conditions. This includes the composition of the maintenance diet. But this is a double-edged sword: carrying out such manipulations would require that one or both cat groups would have to change their regular maintenance diet. This, in turn, might lead to atypical selectivity. In designing these experiments, this dilemma did not arise since logistic factors (i.e. lack of precise experimental control over the subjects) largely dictated the choice of maintenance diet. In general, though, it would seem preferable to study food selection under the regular feeding regime of the cats, as long as all other factors are controlled for.

(b) Hunger levels during experimental trials.

The fact that there were no statistically significant differences between the numbers of food items eaten in the eight experiments presented in this chapter suggests that hunger levels at the start of all experiments were approximately equal. However, this interpretation is confounded by the acts of (i) stopping all trials after five minutes and

(ii) stopping selected trials after a significant proportion of the available foods were eaten. While the majority of experimental trials were not affected (most cats became satiated before the five minutes had elapsed, having eaten less than half of the available food items), these two processes will tend to produce conservative estimates of the number of food items eaten. Furthermore, since the cattery cats, unlike the rescue shelter cats, were not fed on the morning prior to testing there are grounds for predicting that there were differences in the hunger levels of the two groups. If this were the case, it might have important implications for selectivity (see below).

(c) Temperature.

Experiments on shelter cats were carried out at ambient external temperature, while those on cattery cats were done at a precisely regulated room temperature (approximately 20°C). Since preferences can be influenced by the temperature at which the foods are offered (Edney 1973), with foods at temperatures of 35-40°C generally being preferred to foods at other temperatures (Robinson & Thorne 1990), these temperature differences could conceivably have resulted in different selectivity between the two sites. However, in the present case this is unlikely since the three experiments on shelter cats were all carried out between May and July so that ambient temperature, although variable, was generally around 20°C.

5.3.2.2. Repeated testing of experimental subjects.

Some individual cats from both WCPN and the St. Francis Animal Welfare were used as experimental subjects on more than one occasion. There was therefore a risk that results might be confounded by the effects of some individuals modifying their selection behaviour in experiments based on their experience in previous experiments. However, this is not supported by the data. For example, experiment 3b exactly repeated experiment 3a, with all foods and subjects being identical. The fitted GLMs were remarkably similar, both in terms of frequency-dependent and frequency-independent preferences. The cats did not therefore appear to modify their selectivity on the basis of very recent experience.

5.3.2.3. Outlier rejection.

In figures 5.2. to 5.4. several major outlying points can be observed. In most cases,

removal of such outliers would result in a clearer, perhaps significant, relationship between density and preference. Although removal of major outliers may be tempting, there are no *a priori* grounds for doing so, and these points must be considered to be part of the underlying distribution of preferences.

5.3.3. Behavioural Mechanisms of Anti-Apostatic Selection: Some Hypotheses.

Despite the fact that selection experiments on cattery cats produced no significant FDS, the general trend (particularly with random presentation of frequencies) was anti-apostatic. Furthermore, the majority of individual cats (figure 5.6.) demonstrated individual anti-apostatic trends. We must therefore seek to explain the *differences* in the strength of anti-apostatic selection between rescue shelter and cattery cats rather than simply attempting to explain why one group selected anti-apostatically and the other did not.

In their demonstration of anti-apostatic selection by mice feeding on coloured and flavoured rat cake at high densities, Greenwood et al (1984b) suggested three types of explanation for the behaviour: (a) rare forms stand out among common forms (either by olfactory or visual cues) and are therefore easier to locate, (b) initial sampling of food leads to disproportionately more rare types being taken, and (c) there are benefits to a mixed diet. In addition to these, I would add two further mechanisms; (d) maximization of energy intake (i.e. a traditional OFT approach), and (e) sensory-specific satiety. Care must be taken when interpreting these five hypotheses since they do not all address the same type of behavioural mechanisms; hypotheses (c) and (d) are based on a functional interpretation of food selection, while (a), (b) and (e) are based on proximate mechanisms of behaviour. To avoid confusion, I shall make a formal distinction between these two levels of behavioural mechanism.

5.3.3.1. Functional hypotheses.

(a) *There are benefits to a mixed diet.*

Anti-apostatic selection is always predicted to occur when there are nutritional benefits to be gained from the consumption of a mixed diet (Greenwood 1984). Although a mixed diet may be selected as a consequence of any potential proximate mechanism of anti-apostatic selection (section 5.3.3.2), it is possible that the strong

anti-apostatic selection observed in rescue shelter cats occurred because there were greater *direct* nutritional benefits associated with a mixed diet in these cats than for cattery cats¹. Furthermore, the rescue shelter cats may have *learned* about these benefits through previous foraging experiences. The effect of nutrient experience on selection is discussed further in section 5.3.4.2.

(b) Maximization of energy intake.

In general, the majority of examples of FDS can be explained in functional terms by assuming that the predator selects food items in a manner which optimizes its long-term rate of energy intake (e.g. Visser 1981, Hubbard et al. 1982; see also section 1.4.2.). However, it is highly unlikely that such adopting such a framework will enhance our understanding of the mechanisms which caused anti-apostatic selection in the experiments presented in this chapter. The first, and most fundamental, argument against this approach is that it is difficult to justify applying optimality arguments to a domestic animal (see sections 1.1.3. & 1.6.1.). However, the use of optimization techniques to interpret these experiments can be rejected purely by considering the nature of the experiments themselves. OFT models usually consider situations in which food items differ in their profitability (i.e. energy content per unit handling time). Yet the energy intake rate of cats during a meal (i.e. a high density of food) is remarkably constant for a wide range of both canned and dry cat foods (Sarah Cook, *unpublished*). Thus, any pair of experimental foods (Br and GC in this case) can be considered to be approximately equally profitable², making the use of OFT models inappropriate. Furthermore, the cats in these experiments (i) were living in an environment where energy was not limited (for example, the WCPN cats were fed ad libitum), and (ii) often became satiated before preference tests were terminated. Thus, there are no grounds for predicting that cats will select in a manner which optimizes their rate of energy intake.

¹Although the foods in these experiments were nutritionally complete, foods with different sensory characteristics will, in general, have different nutritional composition.

²In their OFT model of simultaneous encounters, Waddington & Holden (1979) included a distance component in the expression for profitability [profitability = energy/(handling time + pursuit time)]. However, in experiments 3a-3e and 4a-4c food items are so close to the cat that pursuit time is effectively negligible.

5.3.3.2. Proximate hypotheses.

(a) Perceptual contrast.

The foods used in these experiments differed both in terms of their visual and olfactory properties. It is therefore possible that some form of perceptual contrast may have lead to individuals preferentially removing the rare food items. Although cats have very poor vision when objects are less than 10-20cm away (Bradshaw 1992) it is not inconceivable that the observed selection was due to visual contrast between food items. However, given the dominant role of olfaction in food selection by the domestic cat (Rofe & Anderson 1970) it is more likely that any perceptual contrast was based on olfaction. Olfactory contrast is presumed to be analogous to the mechanism of visual contrast (Greenwood et al. 1984a), yet olfactory mechanisms of food selection are poorly understood. Indeed, the same predictions about selectivity as the olfactory contrast hypothesis could be made by invoking an entirely different olfactory mechanism - desensitization. Desensitization may occur when an olfactory stimulus is repeatedly encountered (e.g. Lawless & Stevens 1989). During an experimental trial, cats may become desensitized to the odour of the common food type. This might produce an increase in detectability and/or palatability for the rare foods types, resulting in anti-apostatic selection. This mechanism would, at a behavioural level, be indistinguishable from sensory-specific satiety (see below).

(b) Sampling.

At the start of a foraging bout, foragers may sample different food types in order to gain information about the available alternatives (Stephens & Krebs 1986). Sampling equal numbers of available food types will always tend to produce anti-apostatic selection. While it is possible that sampling might have occurred in these experiments, I believe that it is unlikely since all experimental cats were both extremely familiar with the experimental foods and, because of the high density, were easily able to assess which foods were present. If sampling occurred, the strength of anti-apostatic selection would be predicted to decrease with time. The lack of correlation found between numbers eaten in each trial and $\ln w_{br}$ suggests, therefore, that it did not occur. However, it would be unwise to dismiss the hypothesis on the basis of a single, crude test.

(c) Sensory-specific satiety.

Despite the fact that sensory-specific satiety has predominantly been applied to diet selection by humans (Rolls 1986), short-term decreases in preference for recently consumed foods have also been demonstrated in rats (Morrison 1974). It is possible that this mechanism could account for the anti-apostatic selection observed in these experiments. If it did occur, it would be expected that preference for the rare food would increase with time, as satiety for the common food increases. The lack of correlation between number of food items eaten per trial and $\ln w_{Br}$ suggests that sensory-specific satiety is not the underlying mechanism of anti-apostatic selection. Again, though, this hypothesis should not be instantly discarded.

5.3.4. Variables Influencing The Strength Of Selection.

In addition to the hypotheses outlined above, there are two major factors which might have influenced selectivity by the cats in these experiments: hunger and learning. Although not mechanisms of anti-apostatic selection in their own right, they have the potential to influence the other mechanisms and, consequently, to influence the strength of anti-apostatic selection.

5.3.4.1. Hunger.

Diet selection is a dynamic process which is sensitive to the internal state of the forager. One such internal state which may influence food selectivity is hunger. The majority of experimental and theoretical work suggests that foragers become less selective with increasing hunger (e.g. Schoener 1971, Snyderman 1983, DeMott 1993, Heatwole & Heatwole 1968), although Richards (1983) has described a model in which predators are predicted to become less selective when satiated. In the experiments presented in this chapter, cattery cats may have been less satiated than rescue shelter cats at the start of each feeding trial (despite the fact that there were no significant differences between the amount of food eaten in each experiment; see section 5.4.2.1. for explanation). If cattery cats were hungrier than rescue shelter cats then this could account for the observed differences in the strength of anti-apostatic selection between these groups. At present, though, there is little empirical data concerning the effect of hunger on food selection by the domestic cat.

5.3.4.2. Experience and learning.

Perhaps the most striking result to emerge from the comparison of the results obtained from shelter and cattery cats is the magnitude of the difference between the strength of anti-apostatic selection when the experimental frequencies were presented sequentially to each cat. It is unlikely that such differences were caused by differences in the physiological mechanisms of food selection. It is more likely that shelter cats selected more anti-apostatically than cattery cats because of a superior ability to learn about *changes* in the ratios of foods which were presented to them. Such differences in learning ability might have been influenced by the effects of environment on the cognitive development of the individuals at the different locations. Cattery cats were raised in a relatively deprived cognitive environment³. Shelter cats, having spent most of their lives as companion or feral cats, would have been able to freely explore the natural environment, with its plethora of problem-solving opportunities. It may be that these environmental differences could have resulted in differing abilities to solve problems. Direct evidence for this is scarce, although there is some indirect evidence; Singer (1984) states that "...the adaptive processes in the adult brain, commonly described as "learning" processes, might differ only quantitatively from the processes of self-organization occurring during ontogeny". Among these "processes of self-organization", Singer cites the modification of the degree of binocularity in kittens by visual experience. However, since it has been demonstrated that the visual development of "caged" cats is different to that of "street" cats (Belkin et al. 1977). it may also be inferred that there are also differences in the learning processes of these cats. The distinction between "caged" and "street" cats is closely analogous to that of "cattery" and "shelter" cats.

This interpretation is also consistent with the hypothesis that shelter cats select anti-apostatically because there are benefits to a mixed diet. In such a situation, it would be predicted that individuals which have learned that there are benefits to mixed diet would be far more sensitive to changes in food availability than individuals which had few nutritional inadequacies. It is also possible that proximate behavioural mechanisms could produce different experimental results when ratios are presented sequentially rather than randomly (e.g. due to carry-over effects of sensory-specific

³By this, I mean that the cattery environment, although perfectly adequate for its purpose, presented fewer problem-solving opportunities than a natural environment would by virtue of its small size, lack of 3-dimensionality and ease of access to resources

satiety between successive trials). However, there are few grounds for expecting that this modification would be different in cattery and rescue shelter cats.

5.3.5. An Insight into the Foraging Tactics of Urban Feral Cats?

As a first approximation, it can be tentatively proposed that the anti-apostatic food selection observed in rescue shelter cats is predominantly due to the benefits of a mixed diet, learned through previous foraging experiences. This interpretation is consistent with other experiments on food selection by domestic cats which largely scavenge for food; Bradshaw et al. (summarized in Bradshaw 1992) have shown that feral farm cats, in dichotomous preference tests, prefer foods which are rarely encountered over foods which form a major part of their regular diet. These experiments may therefore offer some insight into the food selection behaviour of urban feral cats; when selecting from a nutritionally diverse array of food types in a patch (for example, pig swill or dustbins), there are likely to be nutritional benefits associated with the selection of rare food types. However, it is also clear that the effect of hunger and proximate behavioural mechanisms such as perceptual contrast, sensory-specific satiety and sampling cannot be ruled out at this stage. Indeed, they may be important when assessing differences between the selectivity of cattery cats and rescue shelter cats. These mechanisms will be considered in greater detail in chapter 6.

The Mechanistic Basis of Anti-Apostatic Selection

Experiments 4a-4c in chapter 5 demonstrated that individual cats from rescue shelters select anti-apostatically in high-density, multi-frequency experiments. In contrast, experiments 3a-3e found no significant frequency-dependent selection by cattery cats (although the majority of individuals displayed an anti-apostatic trend when frequencies were presented in a random order). Although these experiments were not designed to explicitly address the underlying behavioural mechanisms of selection, four hypothetical *proximate* mechanisms were proposed to account for the observed selection. These were (i) initial sampling of food items (Greenwood et al. 1984a), (ii) the effect of visual contrast, or "confusion" (e.g. Ohguchi 1978, 1981, Allen & Anderson 1984, Greenwood 1984), (iii) olfactory contrast (Greenwood et al. 1984a), and (iv) sensory-specific satiety (Rolls 1986). In this chapter, I present a series of experiments designed to assess the importance of these proximate mechanisms in causing anti-apostatic selection by the domestic cat. In addition, I consider the effect of hunger upon food selection.

This chapter consists of three experimental sections. In the first, I assess the effects of hunger upon the strength of anti-apostatic selection. Hunger has been suggested to influence both selectivity (Richards 1983, Snyderman 1983, Schoener 1971, Newman et al. 1994) and feeding rate (McCleery 1977, Croy & Hughes 1991, Hughes & Croy 1993, Newman et al. 1994). In chapter 5, I proposed that differences in the hunger levels of cattery and rescue shelter cats might have

resulted in the observed differences in the magnitude of anti-apostatic selection. Empirical evidence for the influence of hunger on selectivity, though, is scarce. Here, I test for FDS by cattery cats in high-density multi-frequency experiments under carefully manipulated hunger regimes.

In the second experimental section, changes in food preference over the duration of an experimental trial are considered. This investigation can be used to assess the effects of two possible mechanisms of anti-apostatic selection - sampling (Greenwood et al. 1984a) and sensory-specific satiety (Rolls 1986). These mechanisms both make different predictions about how preference should change over time; sampling predicts that the strength of anti-apostatic selection should diminish as the trial proceeds (since the need for sampling reduces over time), while sensory-specific satiety predicts that selection should become increasingly anti-apostatic with time as satiety to the common food type sets in. Preference changes may also have important implications for the analytical techniques employed in chapters 4, 5 and 6, which assume that preference remains constant throughout feeding trials (Weale 1992).

The final section examines the effect of visual contrast on selection. Although visual cues are not suspected to be important in determining food selection by the domestic cat (the visual acuity of the cat is poor at close range; Bradshaw 1992), the possibility that visual contrast might cause anti-apostatic selection should be eliminated by empirical evidence rather than on the strength of theoretical arguments alone. The visual contrast hypothesis predicts that the strength of anti-apostatic selection at high food densities will be proportional to the degree of contrast. The dry cat foods used in this study are amenable to manipulation of colour and brightness since they can be easily dyed using food colourings. In this chapter, I have not attempted to test the olfactory contrast hypothesis since, for reasons which will be outlined in the discussion, it appears to require an understanding of mammalian olfaction which is beyond our current comprehension.

6.1. EXPERIMENT 5 : THE EFFECT OF HUNGER ON SELECTION BY CATTERY CATS.

6.1.1. Methods.

Experimental trials were carried out at WCPN between 24th and 29th May 1993.

The experimental protocol and subjects were identical in every respect to experiment 3c in chapter 5 [i.e. selectivity was measured in each of the 12 cats for randomly presented high-density ratios (126:14, 98:42, 70:70, 42:98 and 14:126) of Br "chicken" and GC "rabbit & liver"; see section 5.1.1], with the exception that the maintenance diet was modified to influence the hunger levels of the subjects during experimental trials. In experiment 3c, the maintenance diet of the cats averaged 233g per cat per day, and cats received no food at all for around 5 hours before each preference test. This was considered to be a "high hunger" treatment. In this experiment, the maintenance diet of 233g per cat per day was supplemented by an additional period of ad libitum feeding between 0800 and 1100 hours on the each day of the experiment. This represented the "low hunger" treatment. The maintenance diet in all cases (including ad lib feeding period) consisted only of "Whiskas" canned food (Pedigree Petfoods Ltd.).

Preference testing was carried out at approximately 1300 hours each day for both treatments. At the end of each five-minute preference test (carried out in feeding boxes; figure 5.1) the numbers of pieces of Br and GC remaining were counted. Trials in which less than 10 food items were consumed were rejected (Murdoch et al. 1975).

6.1.2. Results.

One individual (C443) was excluded from the entire analysis since it repeatedly failed to consume 10 pieces of food in trials in experiment 5c; the use of paired comparisons in statistical tests (see below) required that individuals should meet criteria in *both* treatments.

The number of food items eaten by individual cats in each trial in experiment 5 (low hunger) was, as expected, consistently lower than that of experiment 3c (table 6.1), with the differences between the two treatments at frequencies of 10%, 50% and 70% being statistically significant (paired t-test; see table 6.1).

The null GLM for a TTSE (model 1) for experiment 5 (low hunger treatment) produced a good fit to the data (deviance=37.38, d.f.=57). No significant reductions in deviance resulted from fitting either a simple preference model (model 2: deviance=37.25, d.f.=56, $\chi^2_{[1]}=0.125$, $p>0.5$) or an FDS model (model 3:

deviance=35.296, d.f.=55, $\chi^2_{[1]}=1.95$, $p>0.1$). The "best-fit" model was therefore:

$$\begin{aligned}w_{Br} &= 1 \\w_{GC} &= 1\end{aligned}$$

The corresponding "best-fit" model for the high hunger treatment (experiment 3c; see chapter 5) also showed no selection :

$$\begin{aligned}w_{Br} &= 1 \\w_{GC} &= 1\end{aligned}$$

For the low hunger treatment, fitting model 3 using GLIM revealed an anti-apostatic trend:

$$\begin{aligned}w_{Br} &= D^{-0.072} \\w_{GC} &= 1.025D^{-0.072}\end{aligned}$$

A similar trend was apparent in the high hunger treatment:

$$\begin{aligned}w_{Br} &= D^{-0.053} \\w_{GC} &= 1.105D^{-0.053}\end{aligned}$$

The frequency-dependent and frequency-independent trends from experiments 3c (high hunger) and 5 (low hunger) were compared using GLIM by combining the two data sets and generating new models with a "treatment" classification variable.

There were no significant differences between either the frequency-independent ($\chi^2_{[1]}=1.99$, $p>0.1$) or frequency-dependent ($\chi^2_{[1]}=0.089$, $p>0.9$) components of selection¹.

In the low hunger treatment, there were no significant correlations between $\ln w_{Br}$ and total number eaten in each trial at 10% Br ($r_s=-0.139$, $n=12$, $p>0.5$) or 90% Br ($r_s=0.1261$, $n=9$, $p>0.5$), suggesting that selectivity for Br remained relatively constant over time. (A similar effect was observed in the high hunger treatment; see table 5.3)

¹The data set obtained by combining the data from experiments 3c and 5 was too large for GLIM to process. Consequently, data points for Br:GC = 70:70 were omitted from the analysis since these were least likely to affect frequency-dependent preferences.

% Br	hunger level	mean no. eaten (E)	mean logE	SD logE	t	df	p
10	low	27.818	1.348	0.290	2.148	10	<0.05
	high	34.818	1.492	0.223			
30	low	27.727	1.419	0.187	1.208	10	>0.1
	high	37.000	1.510	0.236			
50	low	23.818	1.310	0.246	3.57	10	<0.01
	high	37.909	1.541	0.186			
70	low	23.454	1.338	0.178	3.94	10	<0.01
	high	35.636	1.515	0.189			
90	low	32.222	1.440	0.268	1.007	10	>0.1
	high	36.222	1.507	0.227			

Table 6.1. Comparison of numbers of food items eaten at each frequency by cats in experiments 3c (high hunger) and 5 (low hunger). Paired t-tests were carried out on the log-transformed data. All probabilities were one-tailed as there was a prior expectation that more food items would be eaten in the high hunger treatment.

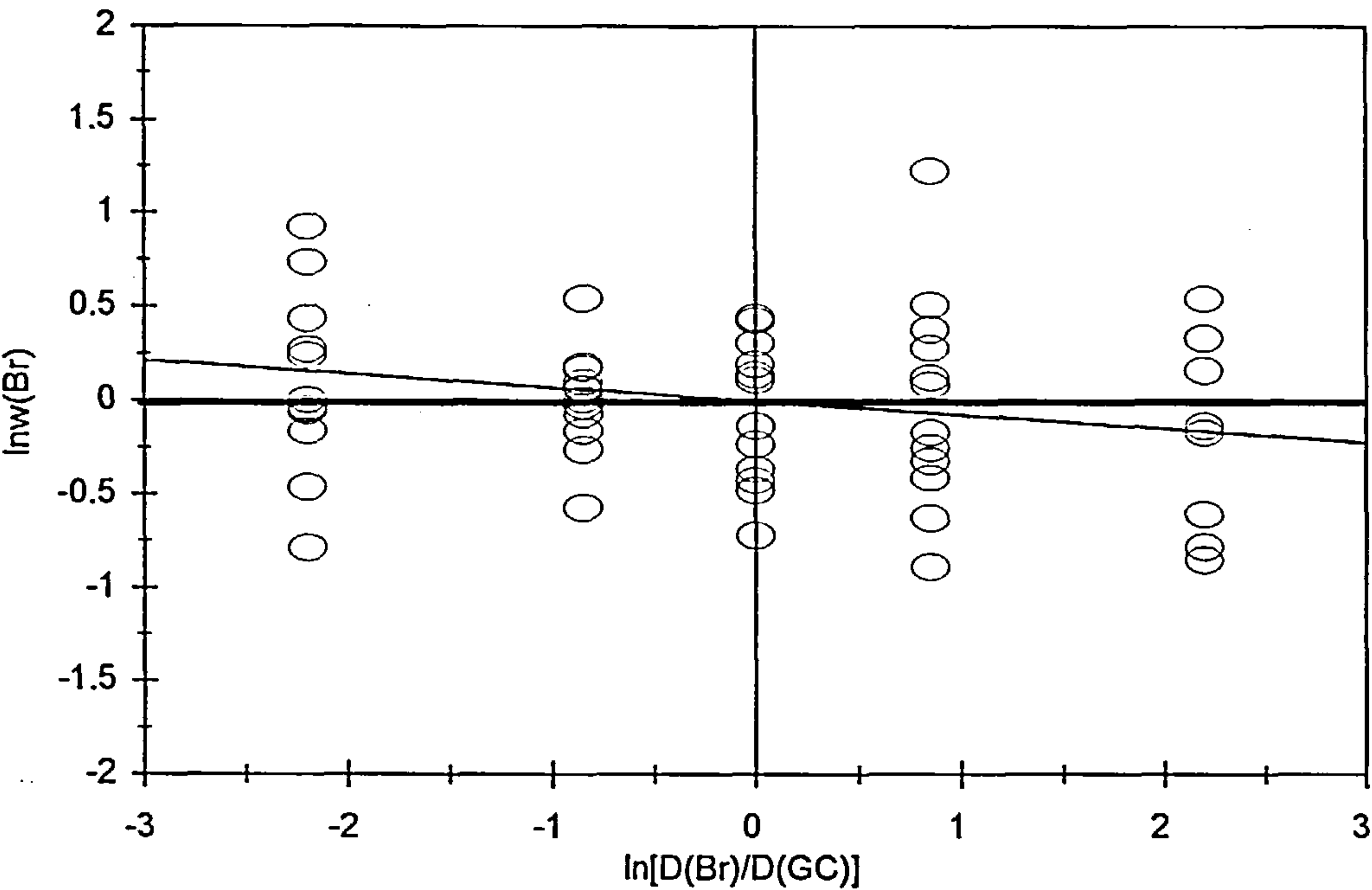


Figure 6.1. The effect of frequency ($\ln D_{Br}/\ln D_{GC}$) on selectivity ($\ln w_{Br}$) by WCPN cats in experiment 5 (low hunger treatment). The "best-fit" model is shown by the thick, solid line and the FDS trend by the thin, diagonal line.

6.2. EXPERIMENTS 6a AND 6b : TESTING FOR WITHIN-TRIAL PREFERENCE CHANGES.

6.2.1. Methods.

6.2.1.1. Experiment 6a : Rescue shelter cats.

Experimental trials were carried out between 16th and 26th September 1991 on 13 individual cats from the Southampton Blue Cross. Prior to the start of the experiment, two days of preliminary feeding trials were carried out to assess the suitability of experimental subjects (i.e. reliable feeders, but not overly friendly). All preference testing was carried out around late morning (between 1100 and 1200 hours). In each trial individual cats, as in previous experiments, received a foil dish (inner diameter 180mm) containing an evenly mixed ratio of two dry foods (Br "chicken" and GC "rabbit & liver" in this case). Each cat was tested at three different Br:GC ratios; 126:14 (90% Br), 70:70 (50%Br) and 14:126 (10% Br). These ratios were presented in a random order to each cat. At least 24 hours were allowed between each trial.

Experimental trials lasted for four minutes. To assess the effects of preference changes over time, this four-minute period was split into two preference tests; after two minutes of the trial, the initial food dish was removed and replaced with a dish of identical composition to that presented at the start of the trial. At the end of the four minute period, the numbers of each food type remaining in each dish was counted. The results of dishes from which less than 10 pieces of food were consumed were rejected. Interference from other cats during feeding was reduced by use of the "stack'n'store" basket method described in section 4.1.1. The Blue Cross cats received no dry food other than that presented during experimental trials.

6.2.1.2. Experiment 6b : Cattery cats.

This experiment was carried out between 31st March and 2nd April 1992. Subjects were nine WCPN cats (C227, C424, C429, C250, C414, H70, C566, C595, G67). The experimental protocol was identical to that of experiment 6a, with the exception that (a) the experimental foods were Br "pilchard" and GC "lamb & beef", (b) preference testing was carried out in the cats regular feeding boxes (figure 5.1).

6.2.2. Results.

6.2.1.1. Experiment 6a : Rescue shelter cats.

Three cats were removed from the analysis due to either being homed during the experiment or repeatedly failing to eat sufficient numbers of food items for reliable estimates of selectivity to be calculated.

Each two-minute period was analyzed using TTSE GLMs (Weale 1992). The analysis is summarized in table 6.2. The values of χ^2 and p refer to the improvement in the fit of model n over model $(n-1)$. In the 0-2 minute time interval there were no significant frequency-dependent or frequency-independent preferences. However, there was a significant anti-apostatic effect in the 2-4 minute time interval. This model was a good fit to the data (i.e. no extraneous variance), so the risk of type I errors is no higher than the usual 5% level (section 3.4). From GLIM parameter estimates, the best-fit models in experiment 6a were:

$$\begin{aligned} 0-2 \text{ minutes:} \quad & w_{Br} = 1 \\ & w_{GC} = 1.063 \end{aligned}$$

$$\begin{aligned} 2-4 \text{ minutes:} \quad & w_{Br} = D^{-0.13} \\ & w_{GC} = 0.862D^{-0.13} \end{aligned}$$

Model 3 (simple FDS) for the 0-2 minute interval was:

$$\begin{aligned} 0-2 \text{ minutes:} \quad & w_{Br} = D^{-0.04} \\ & w_{GC} = 1.055D^{-0.04} \end{aligned}$$

Despite obtaining significant FDS in the 2-4 minute interval, but not in the 0-2 minute interval, there was no significant difference between either overall preference between the two time intervals (improvement in model 2 fit when adding separate time interval terms: $\chi^2_{[1]}=2.507$, $p>0.1$) or the magnitude of anti-apostatic selection between the two time intervals ($\chi^2_{[1]}=0.972$, $p>0.05$).

The number of food items consumed in each trial at each frequency was consistently higher in the first two minutes of the trial than the final two minutes (table 6.3). This difference was statistically significant for $Br=50\%$ and $Br=90\%$ (paired t-test on log-transformed data), but not for $Br=10\%$.

EXPT.	TIME(mins)	MODEL 1	MODEL 2	MODEL 3
6a	0-2	deviance=12.75 df=29	deviance=12.27 df=28 $\chi^2_{[1]}=0.481$ p>0.1	deviance=11.74 df=27 $\chi^2_{[1]}=0.524$ p>0.1
	2-4	deviance=34.51 df=29	deviance=32.2 df=28 $\chi^2_{[1]}=0.14$ p>0.5	deviance=27.38 df=27 $\chi^2_{[1]}=4.82$ p<0.05
6b	0-2	deviance=51.45 df=20	deviance=27.92 df=19 $\chi^2_{[1]}=23.53$ p<0.001	deviance=27.67 df=18 $\chi^2_{[1]}=0.25$ p>0.5
	2-4	deviance=73.06 df=20	deviance=45.42 df=19 $\chi^2_{[1]}=27.64$ p<0.001	deviance=42.23 df=18 $\chi^2_{[1]}=3.19$ p>0.05

Table 6.2. Summary of GLIM analysis of experiments 6a (rescue shelter cats) and 6b (cattery cats). See text for details.

6.2.1.2. Experiment 6b : Cattery cats.

One individual (H70) was removed from the analysis for repeatedly consuming less than 10 food items per dish. GLM analysis of both the 0-2 minute and 2-4 minutes period revealed very highly significant frequency-independent preferences for GC, but no overall FDS (table 6.2). Although model 3 (simple FDS) for the 2-4 minute interval was almost significant, the significance level produced by GLIM would have been an over-estimate because of the high degree of extraneous variance. The best-fit models in experiment for experiment 6b were:

0-2 minutes:

$$\begin{aligned}w_{Br} &= 1 \\w_{GC} &= 1.72\end{aligned}$$

2-4 minutes:

$$\begin{aligned}w_{Br} &= 1 \\w_{GC} &= 1.94\end{aligned}$$

Model 3 (simple FDS) produced the following relationships:

0-2 minutes:

$$\begin{aligned}w_{Br} &= D^{-0.04} \\w_{GC} &= 1.67D^{-0.04}\end{aligned}$$

2-4 minutes:

$$w_{Br} = D^{-0.15}$$
$$w_{GC} = 1.71D^{-0.15}$$

There were no significant difference between either overall preference (improvement in model 2 fit when adding separate time interval terms: $\chi^2_{[1]}=0.527$, $p>0.1$) or the magnitude of anti-apostatic selection between the two time intervals ($\chi^2_{[1]}=1.397$, $p>0.1$).

The number of food items consumed in each trial at each frequency was always higher in the first two minutes of the trial than the final two minutes (table 6.3), with the effect being statistically significant for Br=10% (paired t-test on log-transformed data), but not for Br=50% or Br=90%.

expt	% Br	time interval	mean no. eaten (E)	mean logE	SD logE	t	df	p
6a	10	0-2	19	1.456	0.124	2.398	9	<0.05
		2-4	16	1.387	0.134			
	50	0-2	14	1.474	0.166	1.549	8	>0.05
		2-4	20	1.423	0.146			
	90	0-2	20	1.561	0.136	0.317	9	>0.1
		2-4	24	1.551	0.133			
6b	10	0-2	23.2	1.342	0.168	0.556	4	>0.1
		2-4	20.2	1.298	0.100			
	50	0-2	26.29	1.400	0.142	2.514	6	<0.05
		2-4	19.57	1.277	0.118			
	90	0-2	32.25	1.493	0.121	3.018	7	<0.01
		2-4	26.75	1.403	0.148			

Table 6.3. Comparison of numbers of food items eaten at each frequency in 0-2 and 2-4 minutes time intervals by cats in experiments 6a (rescue shelter cats) and 6b (cattery cats). Paired t-tests were carried out on the log-transformed data. All probabilities were one-tailed as there was a prior expectation that more food items would be eaten in the high hunger treatment.

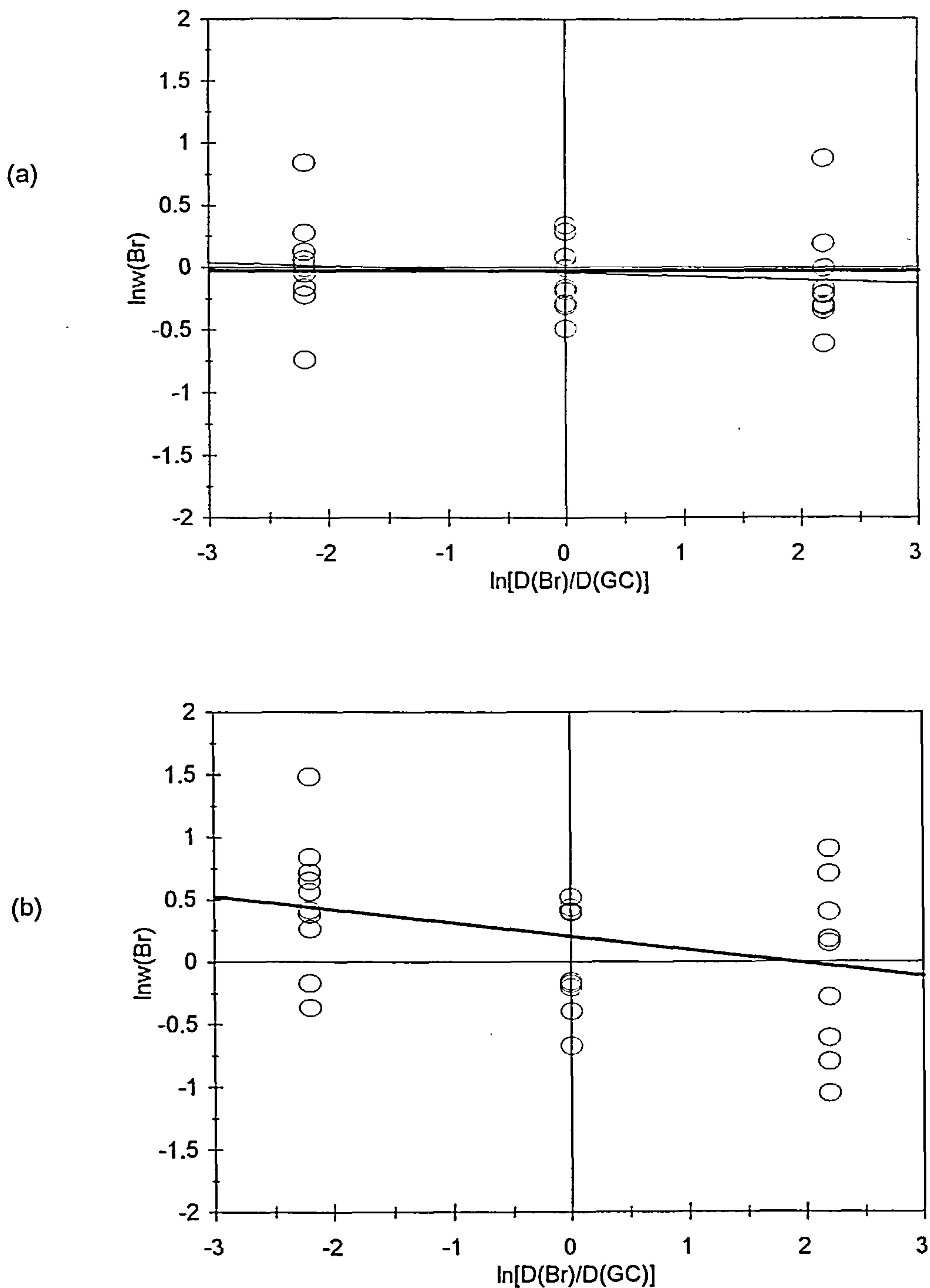


Figure 6.2. The effect of frequency, $\ln[D(\text{Br})/D(\text{GC})]$, on preference, $\ln w(\text{Br})$, in rescue shelter cats in experiment 6a. (a) 0-2 minutes time interval; solid line represents "best-fit" selection model, dashed line is FDS trend. (b) 2-4 minute time interval; solid line is "best-fit" selection model, which is frequency-dependent.

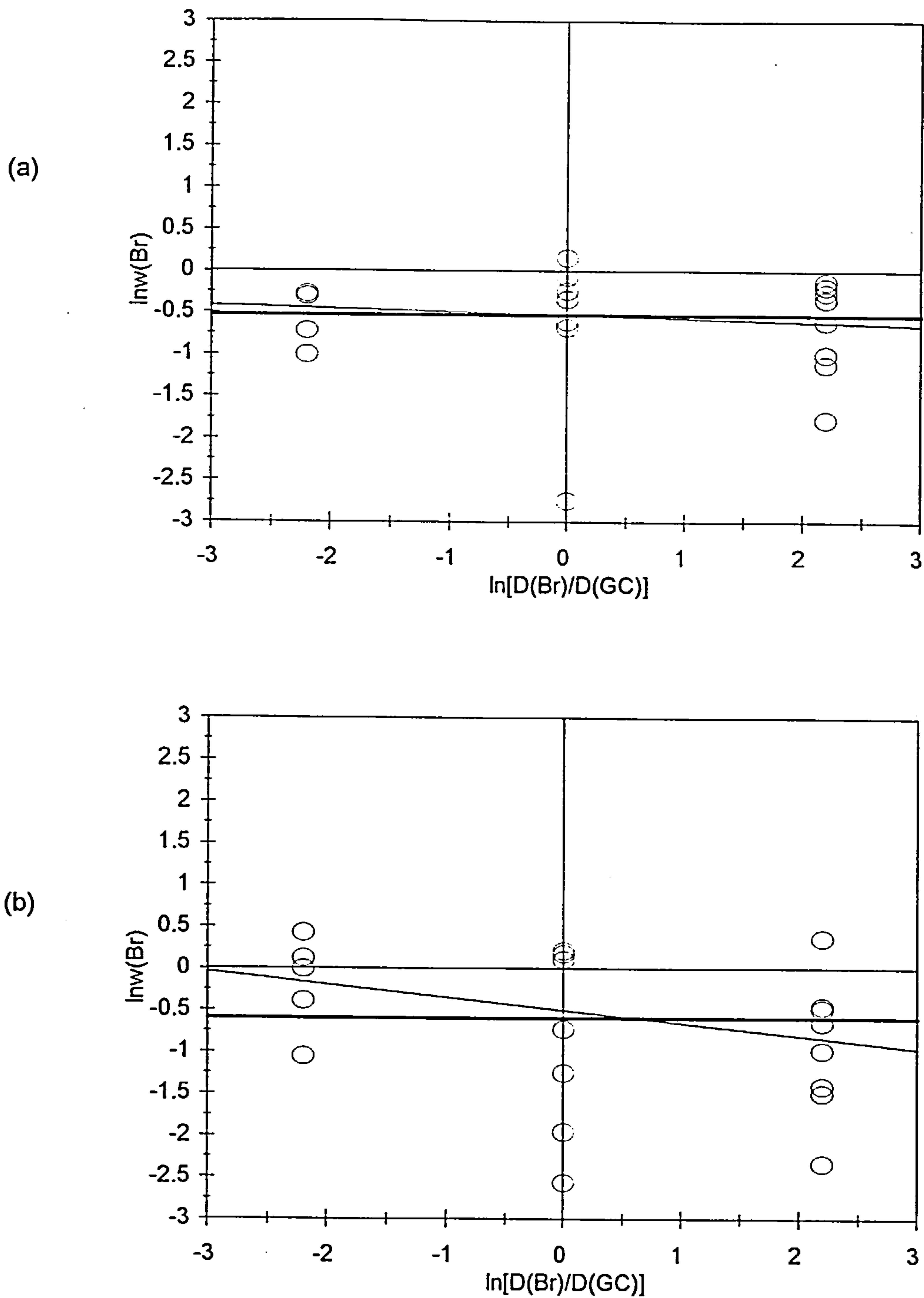


Figure 6.3. The effect of frequency, $\ln[D(\text{Br})/D(\text{GC})]$, on preference, $\ln w(\text{Br})$, in cattery cats in experiment 6b. (a) 0-2 minute time interval, (b) 2-4 minute time interval. Solid line represents "best-fit" selection model, dashed line is FDS trend.

6.3. EXPERIMENTS 7a AND 7b : TESTING THE VISUAL CONTRAST HYPOTHESIS.

6.3.1. Methods.

6.3.1.1. Preparation of visually contrasting foods.

To create experimental foods which differed in their degree of visual contrast², individual pieces of Br "chicken" (a light brown colour; plate 2.3) were dyed using one of three different food colourings; "Hexacol" brilliant black, "Hexacol" chocolate brown and "Hexacol" lemon yellow (Pointing Ltd., Prudhoe, Northumberland, U.K.). These food colourings were based on azo-dyes, which are non-toxic and easily metabolized by the domestic cat (National Research Council 1986). Solutions of the food colourings were freshly prepared by dissolving 10g of powdered food colouring in 1 litre of tap water. Pre-prepared solutions direct from the manufacturer were not used as they contained benzoic acid as a preservative which, although harmless to humans, is highly toxic to the cat (Bedford & Clarke 1972).

The surface of pieces of Br were coloured by dipping a sieve full of food (approximately 50 pieces) into the solution of food colouring for 5-10 seconds. This short time period prevented the food colour solution from saturating the pieces of food (which causes them to both expand in size and become extremely fragile). The food pieces were then laid out on paper to dry overnight. After dying, the foods retained their original size, shape and, to the human nose, odour.

6.3.1.2. Experiment 7a : Cattery cats.

Experimental trials were carried out on six consecutive days between 24th February and 1st March 1992. Subjects were 12 cats at WCPN (C403, C413, C467, C566, C592, C656, G5, G67, G586, H70, C595, C611). In each preference test, individual cats in preference boxes were presented with a foil dish (inner diam 180mm) containing an evenly-mixed ratio, either 126:14 (9:1) or 14:126 (1:9) of two of two of

²Cats cannot easily discriminate between different colours of the same subjective brightness (Bradshaw 1992). It was therefore more important that foods used to test the visual contrast hypothesis differ in brightness rather than just colour.

the three available colours of Br (black, brown or yellow). Each cat received the six possible colour/ratio combinations in a random order. These treatments were:

- 1) 126 black : 14 yellow
- 2) 14 black : 126 yellow
- 3) 126 black : 14 brown
- 4) 14 black : 126 brown
- 5) 126 brown : 14 yellow
- 6) 14 brown : 126 yellow

Preference tests were carried out in the cats' regular feeding boxes and lasted for a maximum of 5 minutes, or until approximately half of the available food had been consumed. Trials with less than ten pieces of food consumed were deemed invalid. The food remaining at the end of each trial was collected and the numbers of each food type were counted.

6.3.1.2. Experiment 7b : Rescue shelter cats.

The experimental protocol was identical to that of experiment 7a. The subjects were 10 individuals (TAB, BOB, LHBW, TAB2, SMBW, BLY, BLG, BLK, EXLH, LWB2) from the St. Francis Animal Welfare. The six treatments were presented to each cat in a random order on six consecutive days from 7th to 14th July 1993.

6.3.2. Results.

In experiment 7a, one cat (G5) failed to consume 10 food items in all six treatments and was subsequently removed from the analysis. In experiment 7b, two individuals (TAB2 and SMBW) were removed after failing to consume 10 food items in more than two trials.

The strength of selection was compared between the 9:1 and 1:9 treatments for each colour combination in each experiment using Weale's (1992) GLM TTSE models. The models were, generally, a good fit to the data from experiments 7a and 7b (i.e. deviance = d.f.). There were no significant frequency-dependent or frequency-independent effects in any of the three colour combinations in either of the experiments (table 6.4). Thus, for every colour combination in experiments 7a and

EXPT.	COLOURS	MODEL 1	MODEL 2	MODEL 3
7a	black v yellow	deviance=9.32 df=22	deviance=9.31 df=21 $\chi^2_{[1]}=0.014$ p>0.9	deviance=9.27 df=20 $\chi^2_{[1]}=0.037$ p>0.5
	black v brown	deviance=14.73 df=21	deviance=13.23 df=20 $\chi^2_{[1]}=1.49$ p>0.1	deviance=12.73 df=19 $\chi^2_{[1]}=0.5$ p>0.1
	brown v yellow	deviance=19.14 df=21	deviance=17.66 df=20 $\chi^2_{[1]}=1.478$ p>0.1	deviance=17.45 df=19 $\chi^2_{[1]}=0.22$ p>0.5
7b	black v yellow	deviance=13.52 df=16	deviance=12.23 df=15 $\chi^2_{[1]}=1.29$ p>0.1	deviance=11.96 df=14 $\chi^2_{[1]}=0.271$ p>0.5
	black v brown	deviance=9.72 df=16	deviance=7.18 df=15 $\chi^2_{[1]}=2.54$ p>0.1	deviance=7.16 df=14 $\chi^2_{[1]}=0.008$ p>0.9
	brown v yellow	deviance=15.92 df=16	deviance=14.72 df=15 $\chi^2_{[1]}=1.204$ p>0.1	deviance=12.8 df=14 $\chi^2_{[1]}=1.91$ p>0.1

Table 6.4. Summary of GLIM analysis of experiments 7a (cattery cats) and 7b (rescue shelter cats).

7b, the "best-fit" GLIM model was:

$$w_{\text{colour1}} = w_{\text{colour2}} = 1$$

For experiment 7a (cattery cats), fitting model 3 (simple FDS) produced the following relationships:

black v yellow:

$$\begin{aligned}w_{\text{black}} &= D^{-0.009} \\w_{\text{yellow}} &= 0.99D^{-0.009}\end{aligned}$$

black v brown:

$$\begin{aligned}w_{\text{black}} &= D^{0.033} \\w_{\text{brown}} &= 0.88D^{0.033}\end{aligned}$$

brown v yellow:

$$\begin{aligned}w_{\text{brown}} &= D^{0.022} \\w_{\text{yellow}} &= 0.88D^{0.022}\end{aligned}$$

In experiment 7b (rescue shelter cats), the FDS models were:

black v yellow:

$$\begin{aligned} w_{\text{black}} &= D^{-0.028} \\ w_{\text{yellow}} &= 0.88D^{-0.028} \end{aligned}$$

black v brown:

$$\begin{aligned} w_{\text{black}} &= D^{0.005} \\ w_{\text{brown}} &= 1.21D^{0.005} \end{aligned}$$

brown v yellow:

$$\begin{aligned} w_{\text{brown}} &= D^{-0.081} \\ w_{\text{yellow}} &= 0.89D^{-0.081} \end{aligned}$$

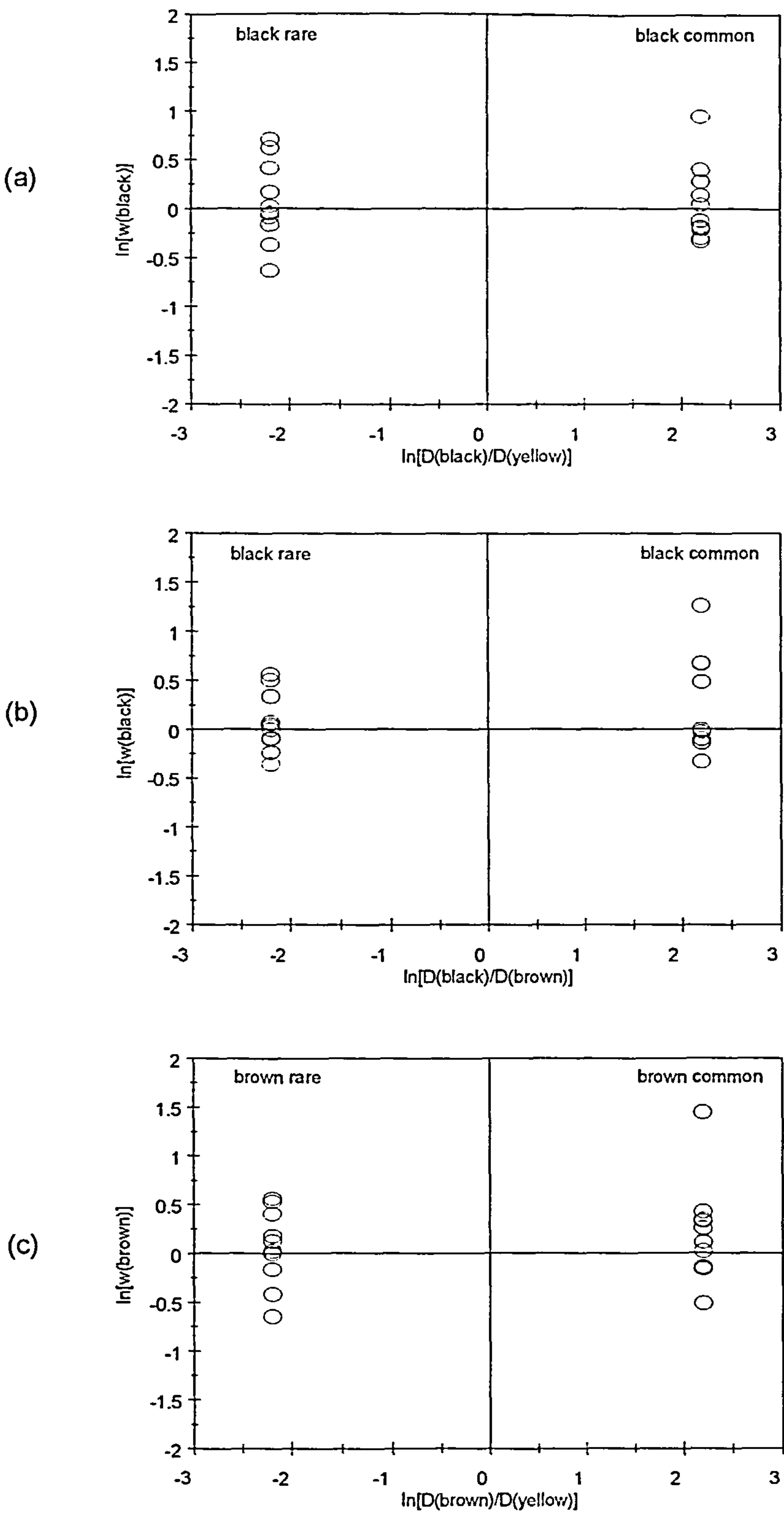
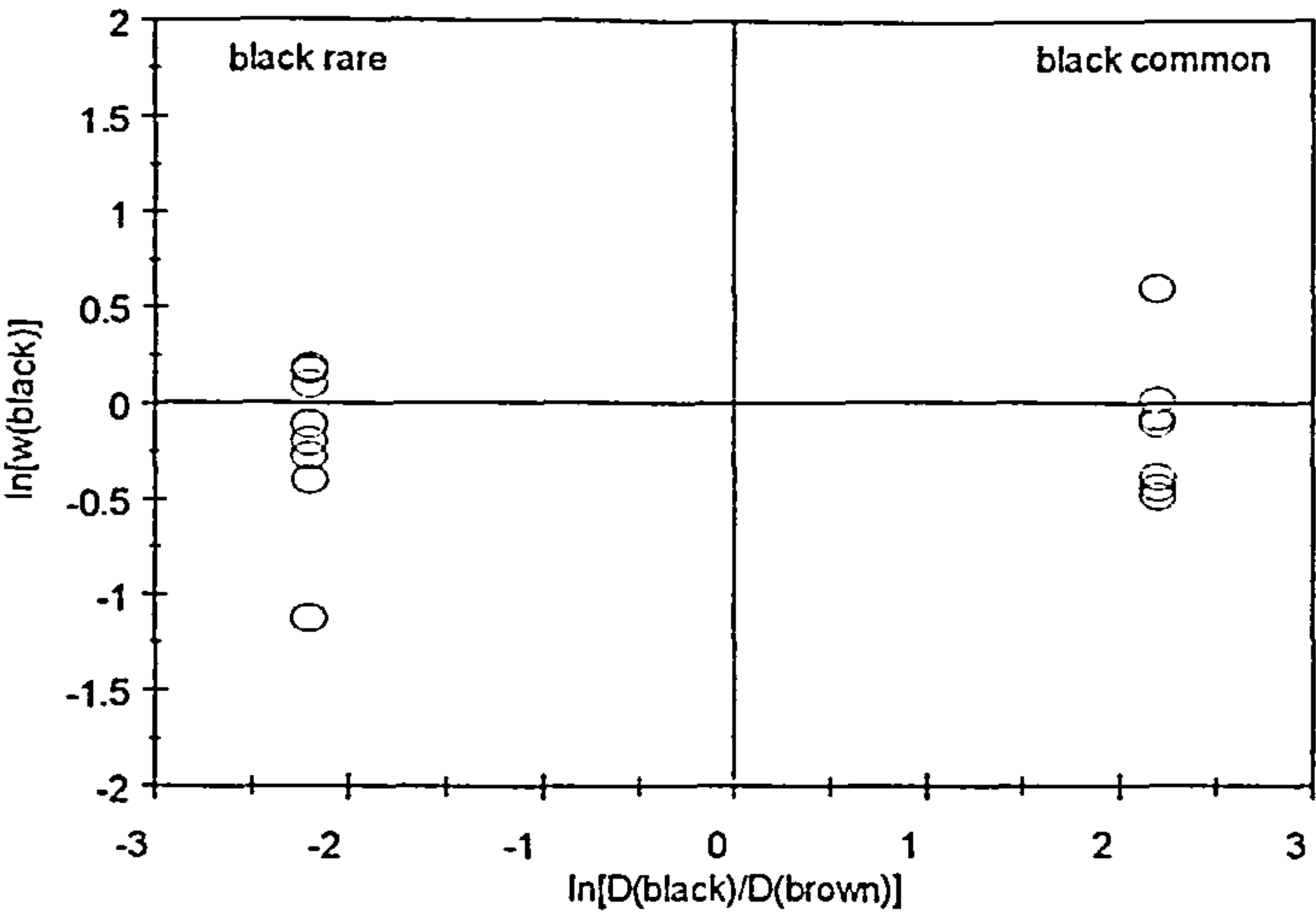
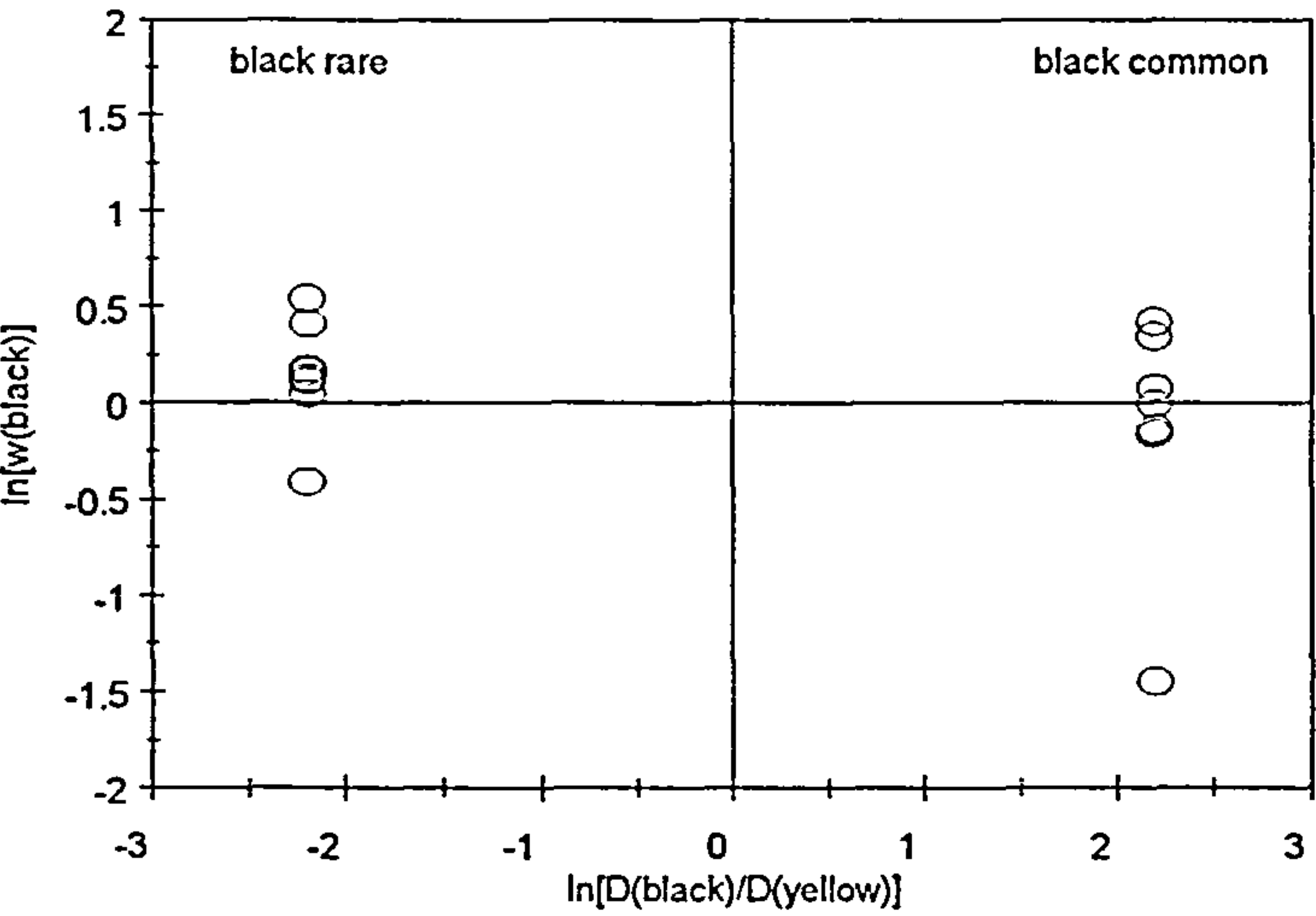


Figure 6.4. The effect of visual contrast on FDS by cattery cats in experiment 7a. (a) black versus yellow, (b) black versus brown, (c) brown versus yellow.

(a)



(b)



(c)

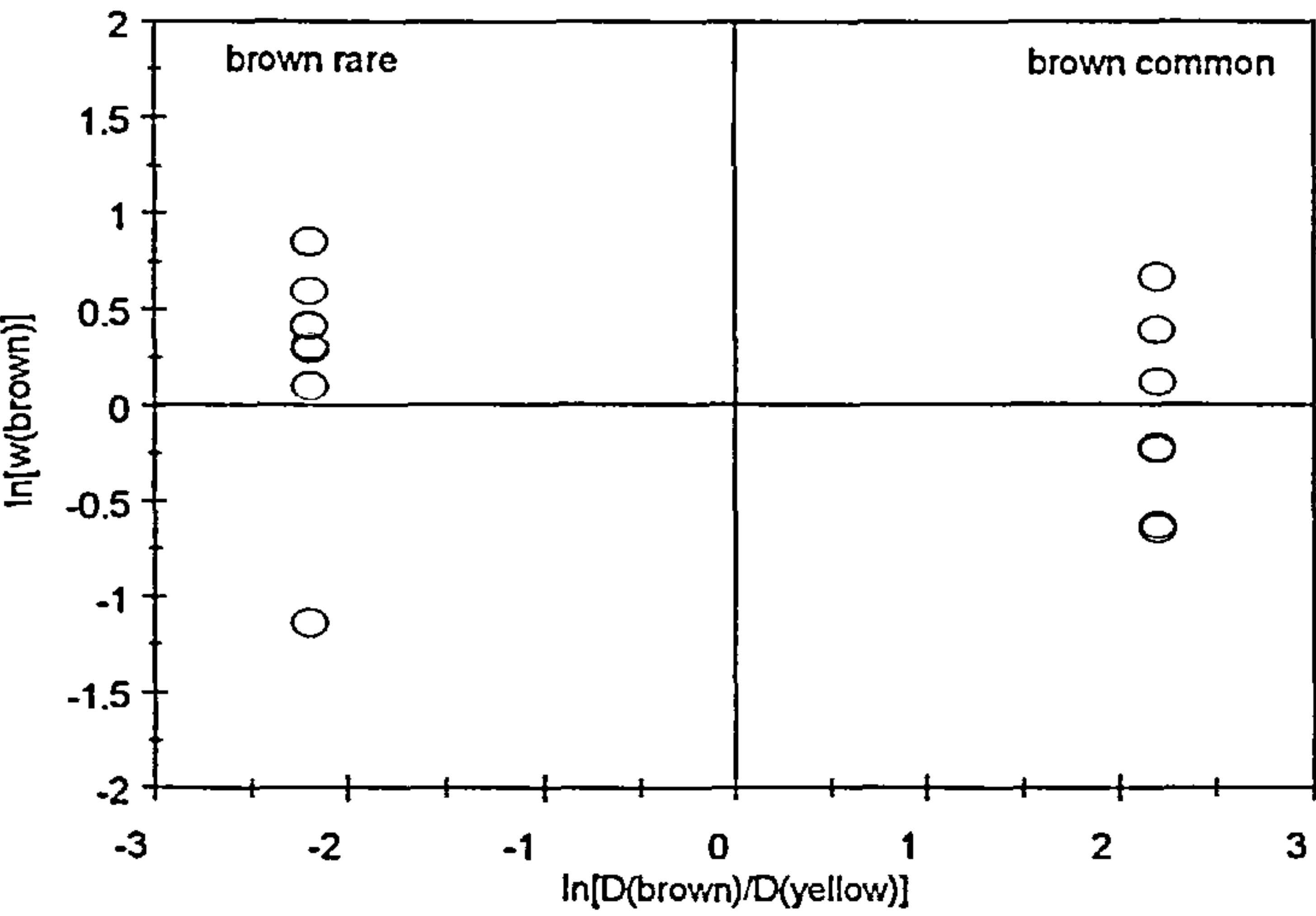


Figure 6.5. The effect of visual contrast on FDS by rescue shelter cats in experiment 7b. (a) black versus yellow, (b) black versus brown, (c) brown versus yellow.

6.4. DISCUSSION.

6.4.1. Overview.

Three main conclusions can be drawn from these experiments: (i) different hunger regimes have no effect on the magnitude of anti-apostatic selection of high-density dry foods by cattery cats, (ii) preference for rare food items tends to increase over time for both cattery and rescue shelter cats, and (iii) rescue shelter and cattery cats show no selection when foods differ only in their degree of visual contrast. Although preliminary in their nature, these results make a significant contribution towards assessing the validity of the proximate hypotheses of anti-apostatic selection outlined in the introduction (i.e. sampling, sensory-specific satiety, visual contrast, olfactory contrast). In this discussion, I consider each of these mechanisms, and the effect of hunger, and discuss the implications of the experimental findings. I also discuss possible sources of experimental error. Finally, I integrate this knowledge with the results obtained in chapter 5 in order to reassess the hypothesis that differences in the strength of anti-apostatic selection between cattery and rescue shelter cats occurred largely because of the benefits of a mixed diet, learned through foraging experiences.

6.4.2. Hunger.

No significant differences were detected between the magnitude of anti-apostatic selection by cattery cats under different hunger regimes; the models fitted to the "high hunger" and "low hunger" treatments produced very similar frequency-dependent and -independent parameter estimates. This is contrary to the conventional wisdom, that foragers are less selective when hungry (e.g. Newman et al. 1994, Schoener 1971, Snyderman 1983). One possible reason for this is that the hunger regimes imposed on the cats were not sufficiently different to reveal any change in preference. This is unlikely, however, given that there was a consistent, often significant, difference in the number of food items eaten at each frequency in the two hunger treatments. Furthermore, the numbers eaten in the high hunger treatment were far lower than those eaten by rescue shelter cats (which showed strong anti-apostatic selection) in experiments 4a-4e; it is therefore clear that hunger levels were at a level sufficiently low for any frequency-dependent preferences to be fully expressed.

An alternative explanation is that comparisons of selection were made between different experiments (as opposed to considering the effect of different hunger treatments in a single, precisely controlled experiment). As a result, all cats were subjected to the "high hunger" treatment before the "low hunger" treatment. However, it is unlikely that the effects of the high hunger treatment carried over into the low hunger treatment as there was a nine-day non-experimental period between the two experiments. In addition, previous experiments (3a and 3b in chapter 5) suggested that the selectivity of cattery cats was not modified by very recent experience (i.e. cats did not select more anti-apostatically in the second of two successive, identical experiments).

It is clear that there must be an interaction between hunger state and selectivity, but at present the physiological and/or behavioural mechanisms underlying this interaction are not well understood. Hunger is controlled by a complex suite of nervous and hormonal systems and simply initiates the process of food consumption (Castonguay et al. 1983). Food preferences, in contrast, can occur in the absence of hunger and refers to the set of signals (e.g. learned preferences and aversions, metabolic influences, specific appetites, perceptual and cognitive mechanisms) which determine selection of specific foods and nutrients. It has been proposed, however (Castonguay et al. 1983), that hunger can be considered as an aversive stimulus. It is therefore possible that lack of selectivity is predicted to occur when the predator is hungry since there is a short-term benefit to be gained purely by alleviating the effect of hunger. In these experiments on cats, hunger levels might not have been sufficiently low to produce such an aversion and its subsequent effect on selectivity.

6.4.3. Within-Trial Preference Changes : Interpretation of Mechanisms and Implications for Analysis.

In experiments 6a and 6b the preferences of both rescue shelter cats and cattery cats became increasingly anti-apostatic with time. This was consistent with the sensory-specific satiety hypothesis, but not with the sampling hypothesis. However, this interpretation appears to contradict the results of the tests for within-trial preference changes carried out in chapters 4 and 5 (i.e. by testing for correlations between $\ln w_{Br}$ and total number eaten) which suggested that preference remained approximately constant throughout trials.

How can this apparent paradox be resolved? A possible explanation is that the observed changes in preference in experiments 6a and 6b were an artifact of experimental design. This is supported by the observation that cattery cats showed a very strong anti-apostatic trend in the 2-4 min interval in experiment 6b, but exhibited only very weak anti-apostatic selection in experiments 3a to 3e in chapter 5. It is possible that either the act of replacing the food bowl after two minutes or the subsequent increase in the absolute density of food was perceived by the cat as a cue to modify its food selection behaviour. In addition, testing for preference changes by studying correlations between $\ln w_{Br}$ and number of food items eaten was likely to have produced a conservative estimate of the magnitude of preference change. This was especially likely to be the case if the development of sensory-specific satiety was dependent on time spent feeding rather than the actual amount consumed; in such a situation, the number eaten would be irrelevant³.

Despite the likelihood that experiments 6a and 6b over-estimated the magnitude of anti-apostatic selection, the very fact that there was a large increase in selectivity for rare foods suggests that preferences *may* have changed to some extent during the experimental trials in chapter 5. This has potentially important implications for statistical analysis; the GLMs used for data analysis assume that preference is constant through a trial (Weale 1992) in order for trials in which different amounts of food were consumed to be compared. If sensory-specific satiety is time-dependent, then analysis will not be affected since preferences were recorded over the same time interval. If it increases with number eaten then the magnitude of anti-apostatic selection will be under-estimated in experiments in which less food items are eaten. However, even if this were the case, it would not have affected the interpretation of chapter 5 data since roughly equal amounts of food were eaten by cats in each experiment (figure 5.7).

6.4.4. Visual Contrast.

The visual contrast hypothesis can be confidently rejected as a proximate mechanism of anti-apostatic selection by the domestic cat. In experiment 7a and 7b, there were no significant frequency-dependent or -independent preferences by either

³*It is more likely, though, that there is an interaction between the number of food items eaten and time which determines the onset of sensory-specific satiety. In this case, correlations of $\ln w_{Br}$ against number eaten would still be likely to yield conservative estimates of selection.*

rescue shelter or cattery cats. In addition, the magnitude and direction of the frequency-dependent preferences which were observed appeared to be independent of the degree of contrast between different food types. These results are consistent with our knowledge of the visual system of the cat. Although domestic cats have been shown to be able to discriminate between different visual textures (Wilkinson 1986), they do not rely upon colour discrimination when other cues are available (Meyer & Anderson 1965). Furthermore, cats cannot focus well at distances between 10 and 20 cm (Bradshaw 1992), suggesting that visual cues are virtually redundant when selecting food at close range (less than 10cm in these experiments). Indeed, it is generally accepted that odour cues are more important determinants of food selection in the domestic cat than visual cues (Rofe & Anderson 1970).

6.4.5. Olfactory Contrast.

Humans are primarily visual animals, and this is reflected in scientific research, which is undoubtedly biased towards the visual senses. Investigations into odour perception by animals, especially within an ecological context, are scarce. As a result, there is no framework within which to consider questions about olfaction. These difficulties are reflected in when attempting to assess the potential importance of the olfactory contrast hypothesis in causing anti-apostatic food selection by the domestic cat. There are four main reasons why successfully testing this hypothesis is not possible at present.

Firstly, to test the olfactory contrast hypothesis requires the use of foods which differ only in the degree of contrast between the two food types: anti-apostatic selection is predicted to be stronger when odours contrast more. Clearly, these odours must be different yet all other nutritional variables must be controlled for. However, it is virtually impossible to obtain such foods; any modification of odours may influence the cats' perception of the palatability and nutrient composition of the foods. Furthermore, there is no way to rank independently the contrast of different odours.

A second difficulty is that any odour effects are confounded by taste. It is generally accepted that taste and smell add together to produce the sensation of overall intensity (Hornung & Enns 1989). Consequently, as soon as a food item is consumed the forager may adjust its selectivity based on the taste of the food rather than its odour.

Little is also known about the manner in which odour mixtures are perceived by mammals. It has been suggested in studies of human olfactory perception (Laing 1989) that the ability of a high intensity odour⁴ to suppress a low intensity odour may depend upon the polarity of the odours and the manner in which they are adsorbed onto the olfactory mucus. However, Laing (1989) also states that: "From the limited amount of data available on the effects of mixing odours, it is still not possible to specify a single physicochemical property of odourants, or one feature of the receptor system, that will help to predict how perception of one odour will be affected by the presence of another." Unfortunately, the situation is even more complicated in the domestic cat, which possesses additional olfactory systems: the trigeminal system and the vomeronasal organ (see Bradshaw 1992). Although the vomeronasal organ is believed to be used primarily in courtship, Keverne et al. (1986) have suggested that odour perception by the cat is due to the combined effects of both the olfactory and trigeminal systems.

Finally, it is also possible that olfactory desensitization could cause anti-apostatic selection at high food density. At a behavioural level this would be indistinguishable from sensory-specific satiety. While it is not clear whether this actually occurred, it would still represent a potentially confounding mechanism when attempting to test the olfactory contrast hypothesis.

Thus, while olfactory contrast undoubtedly remains an appealing hypothesis, current knowledge about mechanisms of odour mixture perception is still far too rudimentary to be able to test for its occurrence.

6.4.6. Mechanisms of Anti-Apostatic Food Selection : A Reappraisal of Proximate and Functional Mechanisms.

The results of experiments 5, 6 and 7 can be used to reinterpret the differences in the strength of anti-apostatic selection observed between cattery and rescue shelter cats in chapter 5. With the exception of sensory-specific satiety, there was no evidence to support any of the proximate mechanisms of anti-apostatic selection outlined at the start of the chapter (although olfactory contrast was not explicitly tested for). In addition, hunger appeared to have no effect on the magnitude of anti-

⁴A high intensity odour could be considered as analogous to a common food type at high density.

apostatic selection. Although some evidence was found for sensory-specific satiety, the magnitude of this effect was similar in both cattery and rescue shelter cats. Thus, no evidence was found for direct proximate mechanisms which produce *differences* between the selective behaviour of rescue shelter and cattery cats⁵. These findings strengthen the premise that these differences in selectivity were due to the cats learning, through previous foraging experiences, that there are nutritional benefits to a mixed diet.

⁵*Although the olfactory contrast hypothesis was not tested for, there is no reason to suspect that, were it a factor, it would cause different levels of anti-apostatic selection in cattery and rescue shelter cats.*

The Effect of Temporal Availability on Food Selection by Farm Cats

Previous chapters in this thesis have investigated FDS by domestic cats feeding on high-density mixtures of two types of dry cat food. In these experiments, foods varied in their *spatial* availability. For many foragers, though, foods may also vary in their temporal availability. For example, the absolute density of prey items available to wild predators may be seasonal (see Schoener 1982 for examples), or foods may be distributed contagiously and prey patches may only be encountered relatively rarely in time. In the case of urban domestic cats, the availability of both live prey (Fitzgerald 1988) and different types of table scrap may change over time, both from day to day and from season to season. Even the temporal availability of the food of companion cats may change depending upon the whims of the owner.

In this chapter, I present the results of experiments which examine the effects of variation in temporal availability of two foods upon the food preferences of farm cats. The methods employed are similar to the training experiments outlined in chapters 1 and 2. Training experiments which have been conducted within an FDS context have usually examined selection by visual predators (Allen & Clarke 1968, Allen 1973, 1974, 1984, Allen et al. 1988, Harvey et al. 1975, Raymond 1984, 1987), although Soane & Clarke (1973) used the approach to study selection by mice using olfactory cues. These experiments have almost always resulted in an increased preference for the food on which the predator has been trained (a "training bias"). However, studies from the animal nutrition literature on laboratory or domestic

mammals have demonstrated that the effect of prior experience may result in an increased preference for "rare" food types in dogs (Griffin et al. 1984), mice (Morrison 1974) and cats (Thorne 1982, Hegsted et al. 1956, Mugford 1977). In addition, Bradshaw et al. (summarized in Bradshaw 1992), have shown that farm cats tend to prefer foods which differ from their regular diet. In this chapter, I aim to confirm Bradshaw et al.'s results under conditions in which the maintenance diet of the cats is more strictly controlled and assess the effects of different levels of temporal availability on food selection. Farm cats are ideal experimental subjects for this type of experiment since considerable control can be exerted over their maintenance diet.

7.1. EXPERIMENT 8 : ONE-DAY RARITY.

7.1.1. Methods.

Experimental trials were carried out on the Firtree Farm cats on 18 consecutive days between 9th July and 26th July 1991. All seven initial members of the colony were present at this time (see chapter 2). The experimental foods consisted of two nutritionally similar, complete commercial canned foods: Arthur's¹ (Ar) "turkey" (Spillers Ltd.) and Katkins (KK) "liver" (Pedigree Petfoods Ltd.); see table 2.1 for nutrient composition. These foods were presented to the cats in equal quantities for one week prior to the start of the experiment in order to familiarize the cats to them and to minimize the effect of long-term preferences on the experiment (the cats generally received more KK than Ar in non-experimental periods).

On each day of the experiment, the cats were presented with 1520g of one, or a combination, of the two foods as maintenance diet for 23 hours, an average of 217g per cat per day. The maintenance diets for each day of the experiment were:

- days 1-8 : Ar
- days 9-10 : Ar and KK (760g of each)
- days 11-18 : KK

¹*At the time of the experiment, this brand of food was marketed as "Kattomeat".*

During the experimental period, no other foods, either canned or dry, were fed to the cats. For one hour each day, commencing between 1000 and 1100 hours, a group dichotomous preference test was carried out. In each preference test, eight metal dishes (base diameter 85mm, depth 50mm) were presented to the cats, four of which contained Ar and four containing KK. Each dish contained 190g of food. The dishes arranged in the centre of the feeding shed as a 4x2 grid, such that each dish was just touching those dishes closest to it (figure 7.1). The choice of spatial arrangement of the food types in the array was determined randomly. The cats were allowed to feed freely on the two foods for one hour (although general observations suggested that cats usually became satiated within 15 minutes). After this period of time had elapsed, the food bowls were removed and the total amount of each food type remaining was weighed.

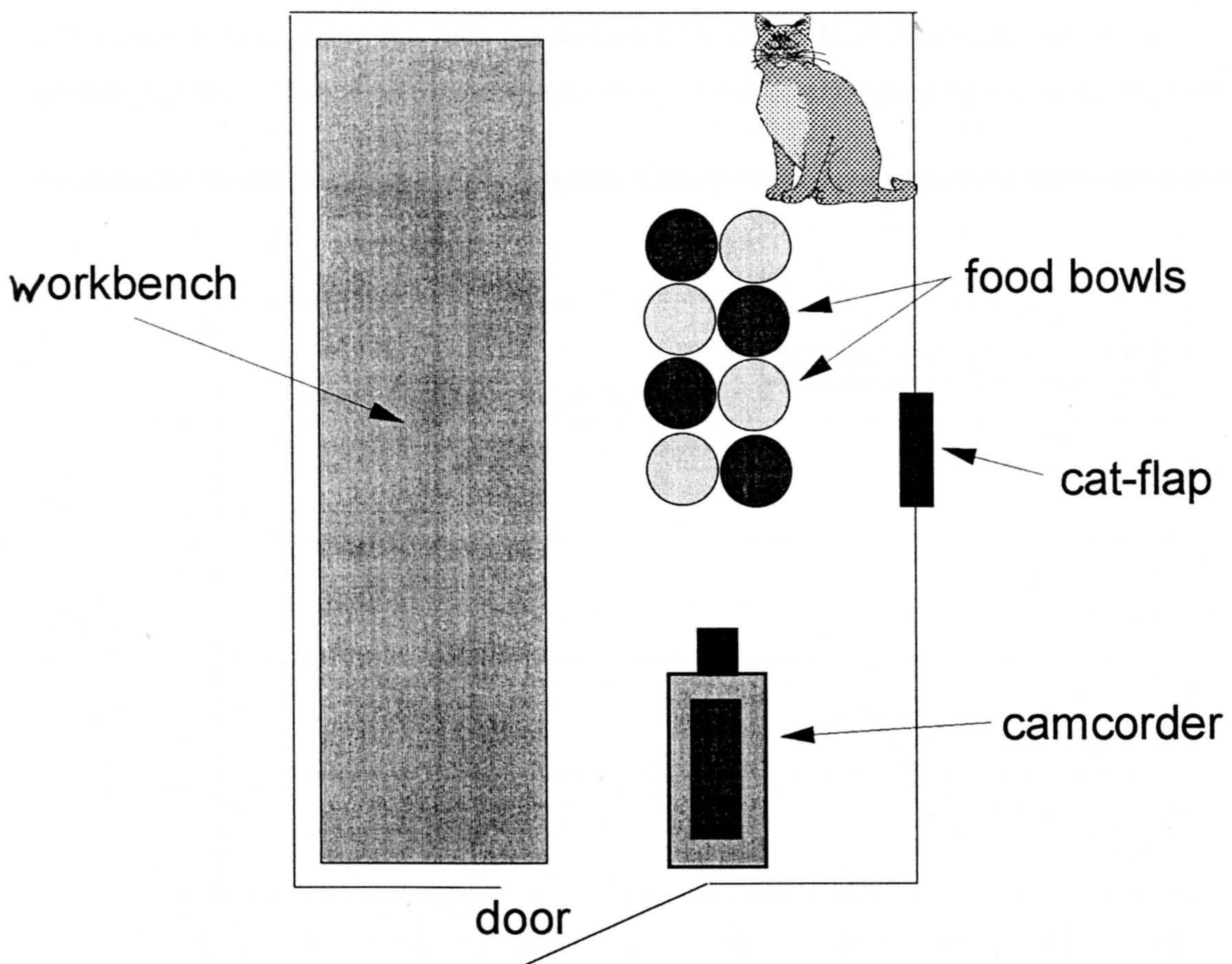


Figure 7.1. *Experimental set-up in feeding shed for group and individual dichotomous preference testing of Firtree Farm cats in experiments 8 and 9. In experiment 8, no video camera was present and the position of the food bowls were determined randomly.*

7.1.2. Results.

Group preferences for each day of the experiment were calculated using Manly's (1974) β index (equation 3.8). Although many other preference indices can be used to analyze dichotomous preference tests (see Cock 1978) Manly's β was used because (i) it is consistent with the analytical methods presented in chapter 3 for analysis of multi-frequency experiments, (ii) when multiplied by 100, β is virtually identical to a standard "percentage" measure of preference, and (iii) bias in β (see chapter 3) is not a problem in dichotomous preference tests since both foods were available in equal amounts (i.e. frequency=50%).

For the first eight days of the experiment, when the maintenance diet consisted of Ar, there was an overall preference for KK, the strength of which increased with time (figure 7.2.). When the maintenance diet was switched to KK, β_{KK} declined rapidly and resulted in a complete reversal of preference. The data point for day 6 in figure 7.2. was removed since the cats consumed 96% of the food available during the preference test. These temporal trends in β_{KK} were analyzed using linear regression.

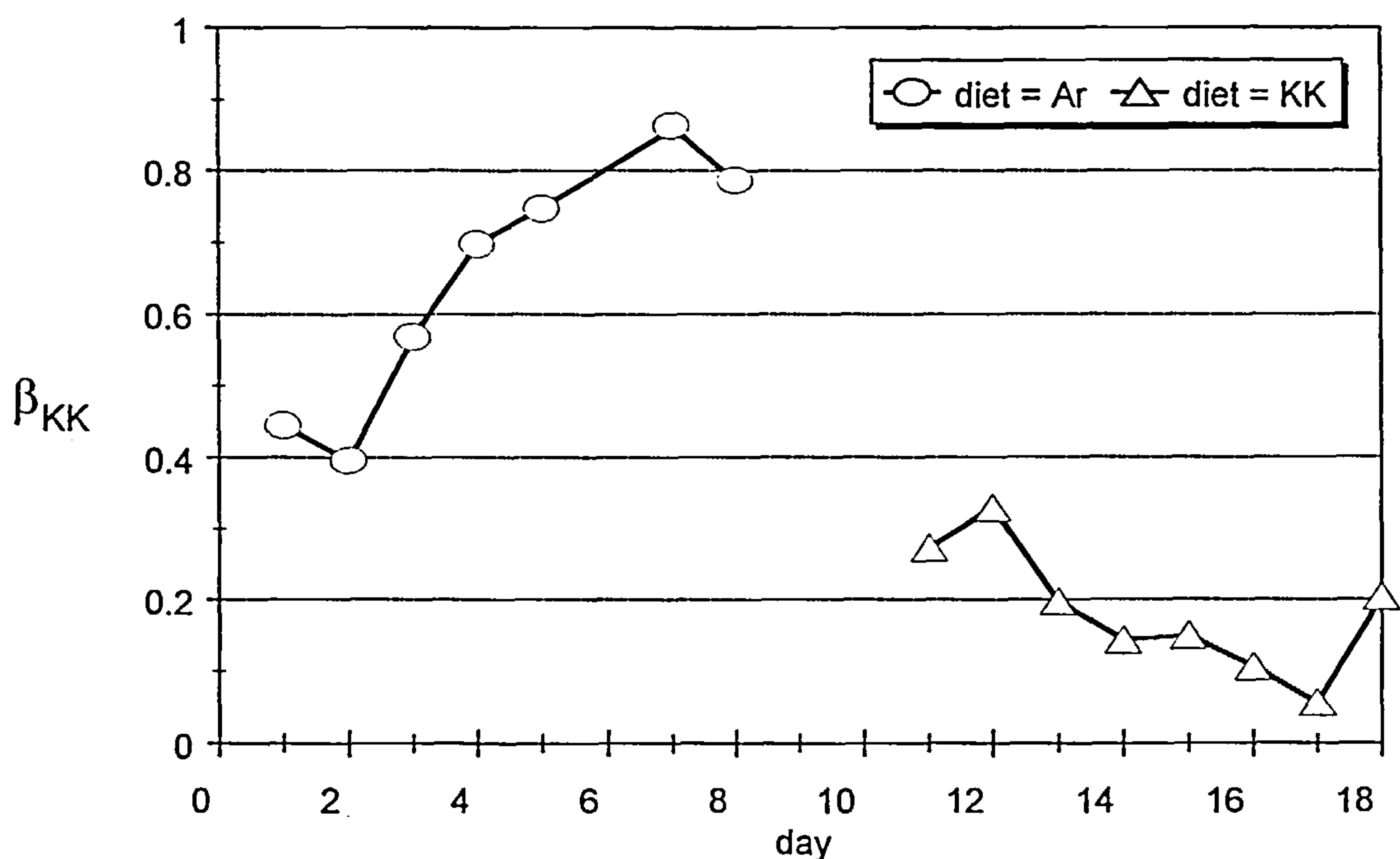


Figure 7.2. The effect of temporal availability on preference for KK (β_{KK}). Values for 1:1 maintenance diet (days 9 and 10) are omitted for clarity.

When the maintenance diet was Ar there was a significant positive relationship between β_{KK} and time (gradient=0.088, $F_{1,6}=22.59$, $p<0.01$). With KK as the maintenance diet, the slope of the regression was negative, indicating increasing preference for the temporally rare food, but statistically non-significant (gradient=-0.025, $F_{1,7}=5.62$, $p>0.05$). The y-intercept values were of no interest in this analysis.

Although more food was consumed in the preference tests when the maintenance diet was Ar (mean=953.7g, SD=286.19) than when it consisted of KK (mean=784.5g, SD=144.39), this difference was not statistically significant (one-way ANOVA: $F_{1,14}=0.098$, $p>0.5$)

7.2. EXPERIMENTS 9a-9c : SEVEN-DAY RARITY.

7.2.1. Methods.

7.2.1.1. Main experiments.

Three experiments were carried out on the Firtree Farm cats which were designed to examine the manner in which farm cats modify their preferences for canned foods after being restricted to a specific maintenance diet for seven days. As in experiment 8, the two foods used in these experiments were Ar "turkey" (Spillers Ltd.) and KK "liver" (Pedigree Petfoods Ltd.). The cats were familiar with both brands of food.

Each experiment lasted for four weeks. In the first and third week of each experiment, the maintenance diet consisted of equal proportions of the two foods. In the second and fourth weeks, the cats were restricted to a monotonous diet of a single food type. The exact amounts of maintenance diet presented, number of cats present at Firtree Farm during the experimental period², and composition of weekly maintenance diets are summarized in table 7.1.

At the end of each week, the cats were subjected to a dichotomous preference test of Ar versus KK. Since the Firtree Farm cats could not be easily handled or manipulated it was extremely difficult to obtain reliable preference data from

²Experiment 9c was carried out in 1993, just over one year after Big Ginger had died and Black-Cap had vanished.

	Experiment		
	9a	9b	9c
Date	19/9/91-17/10/91	31/10/91-28/11/91	23/6/93-21/7/93
Number of cats present	7	7	5
Group maintenance diet (per day)	1560g	1560g	1560g
Maintenance diet per cat per day	223g	223g	312g
Week 1 maintenance diet	1:1 Ar:KK	1:1 Ar:KK	1:1 Ar:KK
Week 2 maintenance diet	KK	Ar	KK
Week 3 maintenance diet	1:1 Ar:KK	1:1 Ar:KK	1:1 Ar:KK
Week 4 maintenance diet	Ar	KK	Ar

Table 7.1. Summary details of experiments 9a, 9b and 9c.

individuals. To overcome this, a remote video technique was used to record the feeding behaviour of the cats (figure 7.1). Prior to each preference test, a Philips "Explorer" autofocus video camera recorder (model VKR6859), on "macro" setting (a 9mm lens with a focal distance of 1.2m) was mounted on a tripod just inside the door of the feeding shed. The entire test was then recorded on VHS video tape.

In each preference test, as in experiment 8, eight metal dishes were presented to the cats, four containing Ar and four containing KK. Each dish contained 190g of food. The dishes were placed in the feeding shed arranged in a 4x2 grid, so that each dish was just touching those dishes closest to it. In experiment 8, the position of each food type in the 4x2 array of bowls was randomized. However, it was felt that arranging the food types in alternate food bowls (as in figure 7.1) was more

representative of a true dichotomous test since it always allowed individual cats to directly choose between two adjacent foods regardless of their position relative to the entire array of bowls. Each test lasted for approximately half an hour. Since the cats were usually hungry, they almost always appeared prior to the start of the test.

7.2.1.2. Analysis of video recordings.

The food preferences of individual cats were determined from analysis of the video recordings of the preference tests. For reasons outlined in appendix 5, it was assumed that feeding rate remained constant throughout a test. Preference measures were therefore based on the time spent feeding on each food type. The time spent feeding was defined as "the total time during which the cat was seen to be either ingesting or handling (chewing) food". Thus, pauses during which cats performed other behaviours (for example, moving to another food bowl, resting and assessment or agonistic behaviour towards other individuals) were not included in this measure.

7.2.2. Results

Preliminary analysis of videotapes revealed the amount and rate of food consumed to be far higher in experiments 9a and 9b than in 9c. In experiments 9a and 9b the first food bowls were usually emptied after approximately 5-7 minutes, with two or three bowls being emptied at after around 8-10 minutes. Virtually all available food was consumed within 15-20 minutes. Since the consumption of all of one food type in a preference test can lead to spurious estimates of preference, the preferences of individual cats were calculated from video analysis of the first *eight* minutes of each trial. In experiment 9c, the cats only consumed an average of 460g per preference test (about 30% of the amount eaten in experiments 9a and 9b) and never ate all of the food in a particular bowl. Preferences were therefore calculated for a standard 15 minute interval (see chapter 8).

The amount of time spent feeding on each food type in each trial was used to calculate a β_{KK} value (equation 3.8). For individual cats, it was difficult to judge to "true" availability, D_i , of the two foods. To overcome this, an arbitrary value of 1000 was used³.

³Since β is a ratio, the actual magnitude of D_1 and D_2 (the availabilities of food types 1 and 2) does not matter as long as $E_1 < D_1$, $E_2 < D_2$ and D_1/D_2 is constant.

The calculated values of β_{KK} (tables 7.2 to 7.4) included a large number of extreme values (i.e. close to 0 or 1), suggesting that the data was not normally distributed. Non-parametric statistical techniques were therefore adopted. There were no significant differences among the cats preferences for KK after each of the four weeks of experiment 9a (Friedman two-way analysis of variance by ranks for related samples : $\chi^2=2.46$, $df=3$, $p>0.1$). The same was true of experiment 9b ($\chi^2=0.3$, $df=3$, $p>0.9$). In experiment 9c, all five individuals showed a greater preference for KK when Ar was the maintenance diet than when KK was the maintenance diet (figure 7.5). However, possibly because of the small sample size, there was only a borderline significance between the β_{KK} values obtained for each week ($\chi^2=5.7$, $df=2$, $p=0.058$; week 3 was omitted from the analysis since incomplete data was available, thus precluding the use of a test for related values). The largest effect was due to the difference between preference in week 2 (KK maintenance diet) and week 4 (Ar maintenance diet).

Week	Maintenance diet	Sid	Honey	Dusty	Penny	Gertie
1	Ar + KK	433:10 (0.98)	0:399 (0)	406:20 (0.96)	169:191 (0.47)	94:271 (0.24)
2	KK	17:414 (0.03)	105:181 (0.36)	312:102 (0.78)	278:90 (0.78)	355:64 (0.87)
3	Ar + KK	0:471 (0)	133:257 (0.32)	211:151 (0.59)	144:236 (0.36)	424:3 (0.99)
4	Ar	42:419 (0.07)	81:166 (0.32)	164:257 (0.37)	267:102 (0.75)	8:435 (0.01)

Table 7.2. Summary table of the time, in seconds, spent feeding on each food type (KK:Ar) and preference for KK based on this time (β_{KKi} in brackets) for individual Firtree Farm cats in experiment 9a. Figures are based on analysis of 8 minutes of feeding.

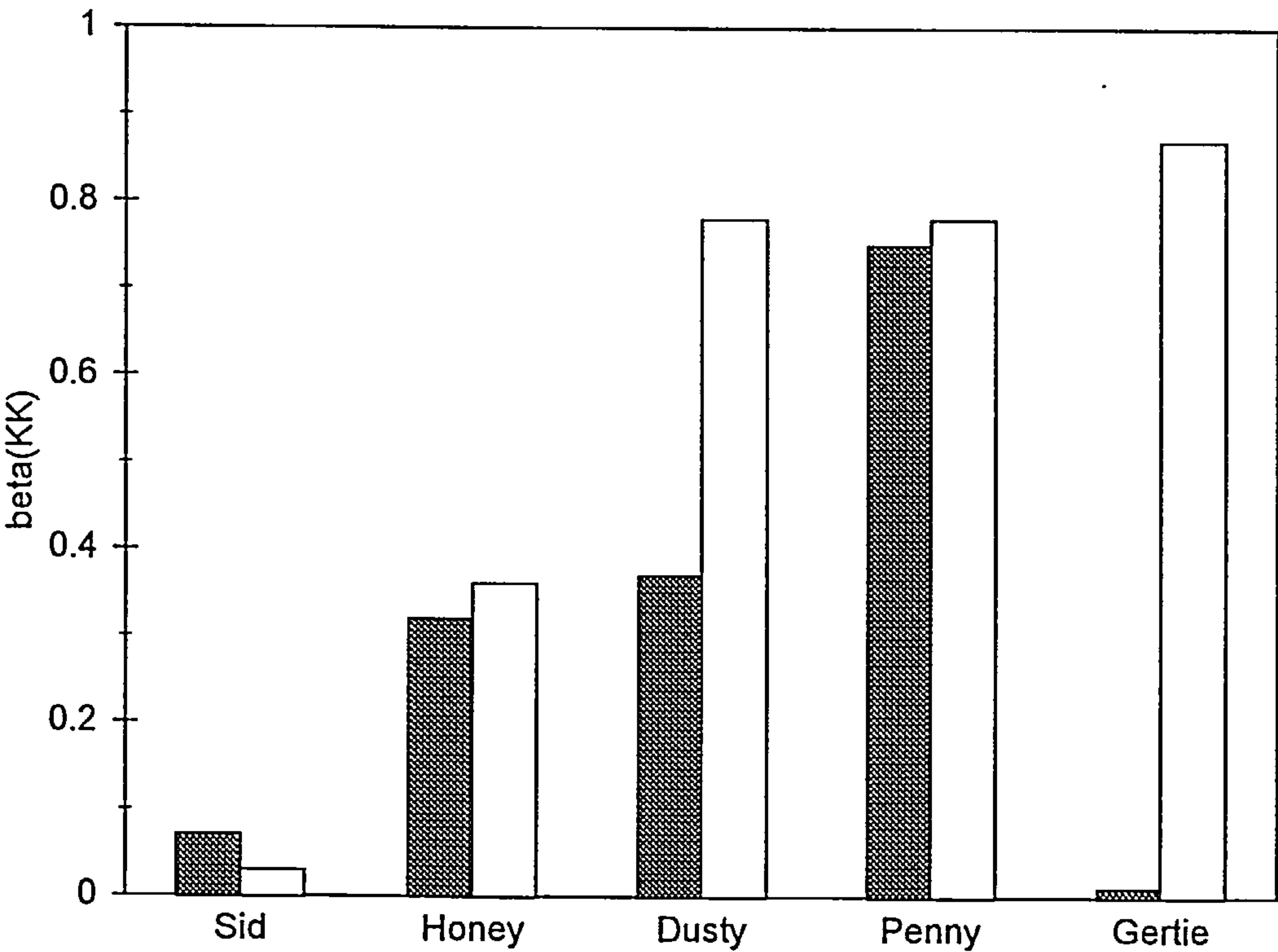


Figure 7.3. Preferences for KK (β_{KK}) by individual Firtree Farm cats under different maintenance diets in experiment 9a. Solid, black bars represent maintenance diet = Ar, white bars represent maintenance diet = KK.

Week	Maintenance diet	Sid	Honey	Dusty	Penny	Gertie
1	Ar + KK	162:286 (0.34)	149:146 (0.51)	303:106 (0.77)	258:161 (0.63)	227:162 (0.59)
2	Ar	164:288 (0.34)	172:234 (0.41)	468:0 (1)	346:95 (0.81)	0:463 (0)
3	Ar + KK	138:335 (0.26)	95:331 (0.2)	402:0 (1)	337:90 (0.82)	409:4 (0.99)
4	KK	209:250 (0.45)	177:245 (0.41)	423:0 (1)	178:240 (0.42)	268:109 (0.73)

Table 7.3. Summary table of the time, in seconds, spent feeding on each food type (KK:Ar) and preference for KK based on this time (β_{KK} ; in brackets) for individual Firtree Farm cats in experiment 9b. Figures are based on analysis of 8 minutes of feeding.

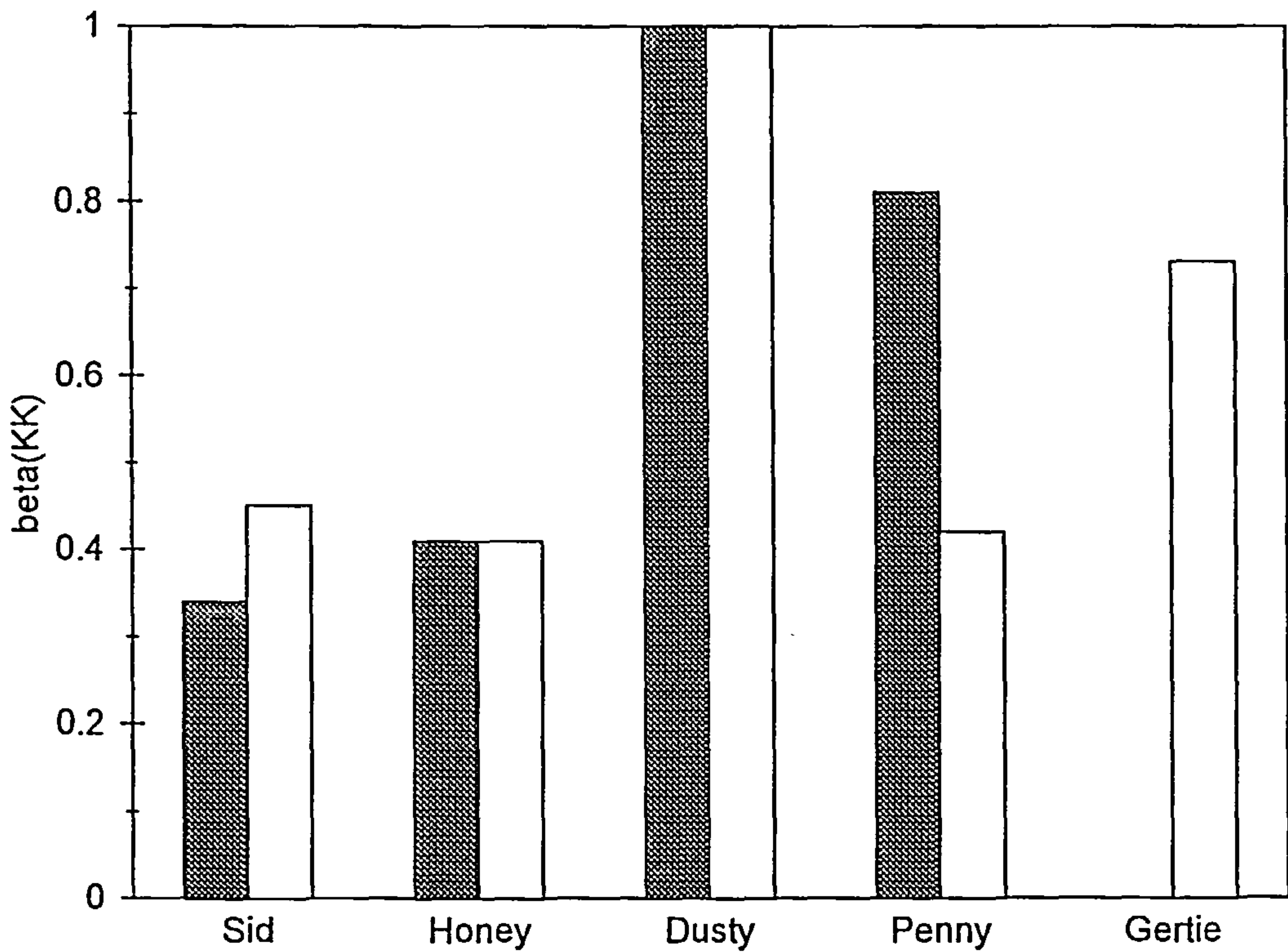


Figure 7.4. Preferences for KK (β_{KK}) by individual Firtree Farm cats under different maintenance diets in experiment 9b. Solid, black bars represent maintenance diet = Ar, white bars represent maintenance diet = KK.

Week	Maintenance diet	Sid	Honey	Dusty	Penny	Gertie
1	Ar + KK	253:213 (0.55)	33:193 (0.13)	542:0 (1)	96:138 (0.4)	274:268 (0.51)
2	KK	48:268 (0.13)	74:72 (0.51)	63:82 (0.57)	44:157 (0.21)	29:410 (0.05)
3	Ar + KK	50:392 (0.09)	174:0 (1)	- (-)	236:358 (0.37)	0:59 (0)
4	Ar	101:235 (0.28)	34:3 (0.92)	551:0 (1)	683:3 (0.99)	408:17 (0.97)

Table 7.4. Summary table of the time, in seconds, spent feeding on each food type (KK:Ar) and preference for KK based on this time (β_{KK} ; in brackets) for individual Firtree Farm cats in experiment 9c. Figures are based on analysis of 15 minutes of feeding.

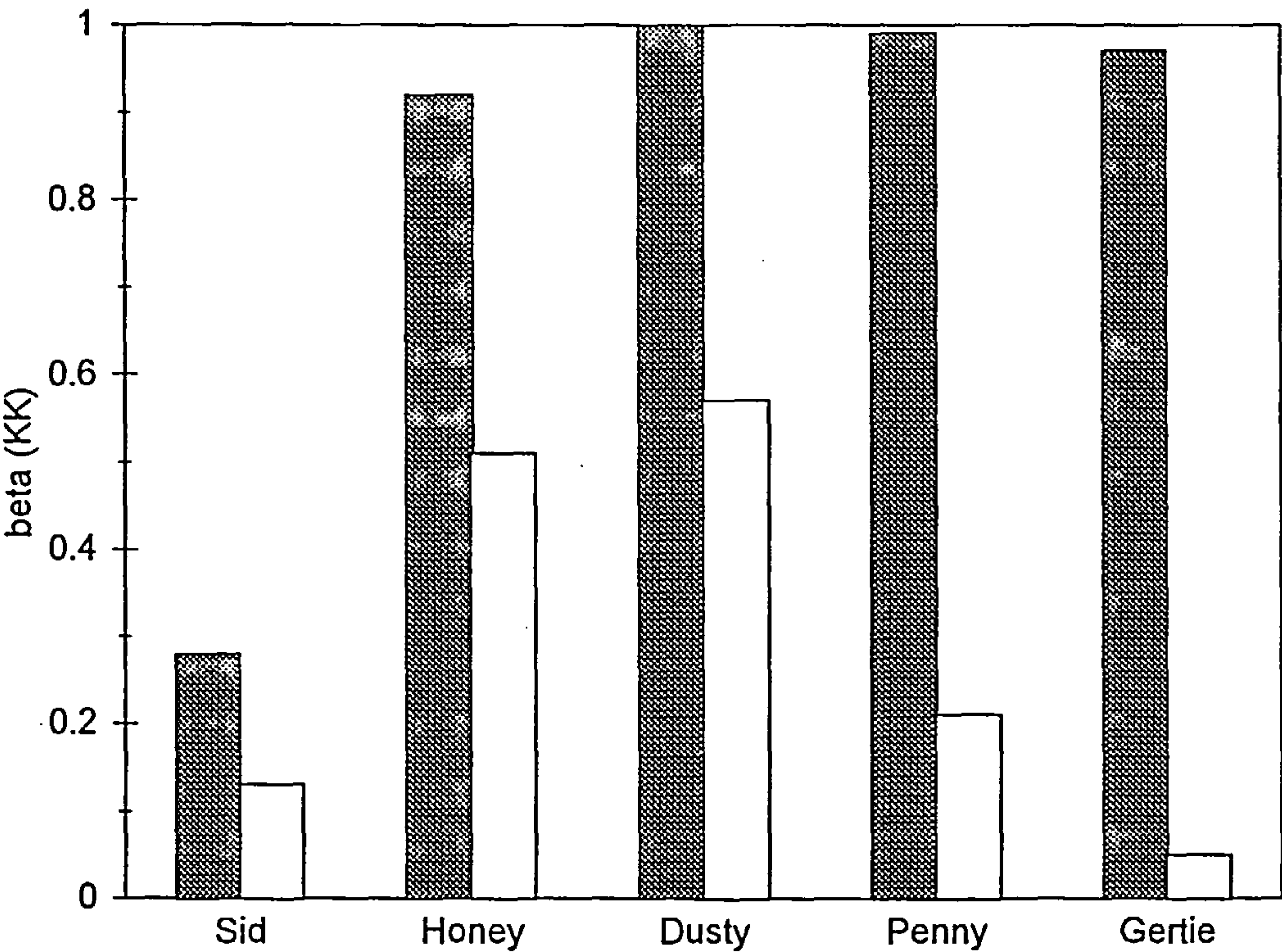


Figure 7.5. Preferences for KK (β_{KK}) by individual Firtree Farm cats under different maintenance diets in experiment 9c. Solid, black bars represent maintenance diet = Ar, white bars represent maintenance diet = KK.

7.3. DISCUSSION.

7.3.1. Overview.

The preferences of the Firtree Farm cats for foods which varied in their temporal availability appeared to be highly variable. While there was a clear tendency for the cats to select "rare" food items when preference tests were carried out daily (experiment 8), only experiment 9c revealed any such preference when testing was weekly. Experiments 9a and 9b produced highly heterogeneous data and revealed no obvious trends in preference. There were, however, clear differences between certain factors in different experiments which might help to explain these results, notably hunger levels, degree of competition and the time of year of the experiment. It is important to attempt to comprehend the factors underlying these preferences since these experiments are the first to examine the selection of major dietary components by farm cats under relatively controlled conditions (the experiments in chapters 4, 5 and 6 used dry food, which only constituted a small part of the total diet of any of the cats tested).

7.3.2. Individual Versus Group Preferences.

The preferences in experiments 8 and 9 were quantified using different techniques. Before attempting to explain differences in preference between experiments 8 and 9, it is necessary to consider whether these experiments were actually measuring different phenomena. In other words, was experiment 8 measuring a group effect, while experiment 9 was measuring an individual effect? In chapter 4, it was demonstrated that group preferences may occur entirely because of variable individual preferences. In experiment 8, though, there was an increase in group preference for temporally rare foods of such magnitude that it could only have been due to similar increases in preference for rarity by individuals. It is therefore reasonable to assume that the two experiments provide evidence for the preference changes of *individuals*.

7.3.3. Comparison of Experiments 8 and 9 : Factors Influencing Selectivity.

One of the most significant factors which differed between experiments 8 & 9c (which showed significant, or a clear trend towards, selection of rare foods) and 9a & 9b (no significant selection) was the time of year at which the experiment was conducted; the former were carried out in the summer and the latter in autumn/winter. Diet selection is known to change on a seasonal basis for many species (Schoener

1982). In winter, food availability is lower and, consequently, hunger levels are higher and these factors will lead to increased intraspecific competition. In these experiments, hunger levels were artificially raised in winter (experiments 9a and 9b) via a reduction in the average level of maintenance diet available to each individual. In addition, seasonal changes in temperature may affect the food selection of foragers which primarily use olfactory senses. These experiments can therefore be considered to mimic the effects of seasonality on food preferences.

7.3.3.2. Hunger.

The hunger levels in experiments 9a and 9b (223g per cat maintenance diet per day) were far greater than for experiments 8 and 9c (approximately 340g per cat per day, including daily intake in preference tests, and 312g per cat per day respectively). Although the cats were free to forage for other food items, the amount eaten and rate of consumption of food in experiments 9a and 9b was far higher than the other experiments, suggesting a large difference in hunger levels at the start of each test⁴. Although hunger was not shown to be an important factor in determining selectivity in multi-frequency experiments (chapter 6), the magnitude of difference between hunger levels in these experiments was extremely high. In experiment 9c, the cats consumed only about 30% of the available food (1.52kg). However, in experiments 9a and 9b, all of the food was usually consumed in around 15-20 minutes. This is consistent with the hypothesis that very high hunger levels are aversive (Castonguay et al. 1983; see chapter 6), thus making reduction of hunger, rather than selection of food the primary objective of foraging. In general, these results are consistent with the theory that foragers become more selective when approaching satiation (Schoener 1971, Snyderman 1983).

7.3.3.3. Competition.

Individuals which forage in close proximity to other conspecifics do not necessarily show the same food preferences as if they were foraging in isolation. Two mechanisms which are likely to influence selectivity in group foraging situations are social transmission of food preferences (see section 7.3.5) and competition. Foragers can compete with each other in two ways (Sih 1993); by scramble, or exploitative, competition (eating a food and thus making it unavailable to other individuals) and contest, or interference, competition (direct competitive encounters,

⁴These differences also suggest that, although free to forage for alternative foods during experimental periods, the Firtree Farm cats relied predominantly on the experimental foods.

possibly including agonistic behaviour).

It is possible that exploitative competition may have influenced the results of experiments 9a and 9b. The presence of conspecifics, in addition to high hunger levels, may have produced extremely high intake rates by the Firtree Farm cats since any cat not feeding as quickly as possible would have a lower food intake than other, faster-feeding individuals. Such effects have been documented in other vertebrate foragers. For example, Dill & Fraser (1984) showed that coho salmon increase their feeding rate and are less selective in the presence of a competitor (simulated by placing a mirror in the fishes tank), while Barnard & Stephens (1981) have demonstrated that handling times for particular prey items tend to be shorter when animals are competing for food.

Food selection may also be modified by interference competition (see Sih 1993 for review); dominant individuals may force subordinates into sub-optimal habitats. In experiments 9a and 9b this is analogous to a dominant cat displacing a subordinate for access to a preferred food item. This is conceivable, since farm cats are known to possess complex social structures (Kerby 1987, Macdonald et al. 1987, Brown 1993), often with asymmetrical aggressive encounters between individuals (Feldman 1994). Such a social structure might also cause a "subordinate" cat to choose the bowl furthest away from any potential aggressor, and this might lead to fairly extreme food preferences in some individuals. However, a study of the social behaviour of the Firtree Farm cats (Brown 1993) identified Sid as a relatively subordinate individual, yet observation of video tapes in experiment 9 suggested that he was rarely displaced for access to a particular food bowl. However, since there were four additional colony members at the time of Brown's study it is possible that the social structure of the group had changed dramatically.

There are other ways in which the presence of conspecifics may influence food selection behaviour. For example, Jaeger et al. (1983) showed that the red-backed salamander (*Plethodon cinereus*) was highly selective in the absence of competitors, but became non-selective when a competitor was present. One explanation which the authors proposed to account for this behaviour was that the foragers made "mistakes" when attempting to assess both competitor and prey availability (i.e. there was an information processing constraint). However, it is unlikely that such constraints applied to the Firtree Farm cats in experiments 9a and 9b since the information processing required in a dichotomous preference test must be virtually

negligible⁵.

7.3.3.3. Temperature.

Food temperature may have contributed to the lowered selectivity in experiments 9a and 9b. Although experimental foods were stored in the laboratory prior to preference testing, they were, upon transportation, subjected to ambient temperature⁶ for approximately half an hour before testing. They also cooled further upon opening when placed in cold metal food bowls. It is known that cats prefer foods at a temperature of around 35°C (Robinson & Thorne 1990). However, since both foods were treated in exactly the same way prior to testing it is not clear whether this would result in a change of preference. Given that cats primarily use olfactory cues to select food (Rofe & Anderson 1970), it might be that foods are perceived as more similar when cold since less volatile compounds are released. Behaviourally, this would tend to cause the cats to become unselective.

7.3.3.4. Experimental Design.

The Firtree Farm cats were the only group of farm cats available for experimentation. This placed some constraints upon the design of experiments and, although unlikely, it is possible that these constraints may have influenced the experimental results. Firstly, it was not possible to control fully for the effects of different sequences of maintenance diet (the group could not be split into two, each presented with maintenance diets in a different order). Experiments 9a and 9b attempted to overcome this to some extent by switching the position of the KK and Ar maintenance diets in the presentation sequence. There were no obvious differences in selectivity, suggesting that sequence effects were not important (although this is a slightly weak argument given that there was no selection anyway).

Another potential source of error was the spatial arrangement of the two foods in the 4 x 2 array of bowls presented in preference tests. These bowls were randomly arranged in experiment 8 but arranged alternately in experiments 9a-9c. However, since the random arrangement was more likely to produce heterogeneous preferences (for example, some individuals might be forced to feed where there are two or three

⁵*In a high-density, dichotomous preference test the forager always possesses complete information about the available choices and there are no recognition constraints*

⁶*Average maximum monthly temperatures for Southampton in 1991 : September 21.1°C, October 14.7°C, November 11.0°C. Source: Meteorological Office, Bracknell.*

bowls of similar composition) yet experiment 8 produced the most consistent and strongest selection for rare foods⁷, this effect must be considered to be negligible.

7.3.4. Learning and Temporal Availability.

The lack of selectivity in experiments 9a and 9b could be related to high hunger and high competition. However, these processes reveal little about the underlying mechanisms which might have caused the increased preferences for temporally rare foods observed in experiments 8 and 9c (in which hunger levels and intraspecific competition were at relatively low levels). In experiment 8, it is probable that, by presenting the same maintenance diet and preference test for eight consecutive days, the cats were able to learn that one food was available only for a short period of time each day. This is consistent with the concept of monotony (Siegel & Pilgrim 1958), a form of cognitive satiety (Rolls 1986). This mechanism, though, simply predicts that foragers will learn that a food is rare and will adjust their intake accordingly; it offers no explanation of why this selection should occur. The most convincing interpretation is that there are nutritional benefits to be gained from consuming a mixed diet (Greenwood 1984). This explanation was invoked to explain anti-apostatic selection by rescue shelter cats in multi-frequency experiments (chapters 5 and 6). Since the Firtree Farm cats were experienced at foraging on a variety of nutritionally variable foods, they might be expected to select in a manner broadly similar to rescue shelter cats (i.e. anti-apostatically).

Cognitive satiety can also be proposed as an explanation for the selection observed in experiment 9c. However, since the cats did not have the opportunity to predict the availability of different foods the form of learning may have been subtly different from that found in experiment 8. The cats must have based their food selection only on foods eaten prior to preference testing since there was no predictable sequence of availability.

⁷Experiment 8, if anything, tended to underestimate the magnitude of β_{KK} in preference tests. This was because preferences can be affected once more than half of the total food available has been removed, especially if there is a strong preference for one food type over the other, as in this experiment. However, such a situation will generally produce an underestimate the magnitude of the preference for the rare food. Consider an extreme case where there is exclusive preference for one food (i.e. $\beta=1$) of a pair of equally-available foods. If more than half of the total food available is consumed (all of the preferred food), the forager will be forced to eat the less preferred food, resulting in the measured preference being greater than the true preference.

7.3.5. Social Transmission of Food Preferences.

There is strong evidence that social effects influence diet selection in groups of animals (Heyes 1993, Galef 1991, Davis 1973). For example, after interacting with a recently fed "demonstrator" rat, an "observer" rat will show an increased preference for the food just eaten by the demonstrator (Galef & Wigmore 1983, Posadas-Andrews & Roper 1983). Presumably, the observer learns that the food is nutritious without having to risk sampling it itself. Since cats can learn behavioural tasks through observation (e.g. John et al. 1968), it might be expected that the Firtree Farm cats learned about the different foods from each other. If so, individual preferences would be predicted to converge. However, the fairly extreme variation between the preferences of the individuals in experiments 9a-9c suggests that this was not the case. This may have been due to the fact that both experimental foods were nutritionally complete and individuals may have learned that there were no aversive side effects.

7.3.6. Nutrient Effects.

The two foods used in experiments 8 and 9, Ar and KK, were very similar in terms of their macronutrient composition and were considered to be nutritionally complete. While preferences for temporally rare foods could be ascribed primarily to cognitive effects (i.e. learning that a palatable food was rare and would only be encountered on certain occasions), it is possible that they may have been due to subtle differences in nutrient composition, particularly micronutrients. The direct response of cats to nutrient composition is of fundamental importance to the arguments put forth in this thesis. The nutritional benefits which mixed diets offer has been proposed as an explanation for anti-apostatic selection by the domestic cat throughout this thesis. Yet this interpretation would be undermined if cats were found not to respond to actual nutritional differences in experimental foods. In the next chapter, I therefore examine the selectivity of cats for canned foods which vary not only in their temporal availability, but also in their nutritional composition.

The Effect of Macronutrient Composition on Food Selectivity

The nutritional composition of foods is known, or has been suggested, to influence diet selection by many species of foragers, both vertebrate and invertebrate (e.g. Belovsky 1978, 1981, 1990, Ackroff 1992, Borges 1992, Sourd & Gautier-Hion 1986, Lundberg et al. 1990, Stamps et al. 1981, Greenstone 1979, Bernays et al. 1992, Simpson & White 1991, Karasov 1985, Geissler & Rollo 1988). In general, omnivorous foragers are likely to be more sensitive to differences in the caloric and nutritive properties of available foods than herbivores or carnivores (Hirsch et al. 1978, Rogers & Blundell 1991). Carnivores, including all *Felis* species, have evolved to feed primarily on live prey and these food items are likely to be fairly constant in their caloric and macronutrient composition (Hirsch et al. 1978). *Bulk* is therefore a good indicator of nutrient intake. In an urban environment, though, the domestic cat must select its diet from a wide variety of human food waste (see chapter 1). In these foods, bulk is no longer a reliable indicator of nutrient composition. In other words, cats must make diet choice decisions similar to those of omnivores if they are to select a nutritionally adequate diet. However, the task of meeting nutritional demands by scavenging is likely to be more difficult for cats than omnivores because of their more precise dietary requirements.

The experiments presented in chapters 4 to 7 demonstrated that cats with experience of foraging on nutritionally variable resources show stronger anti-apostatic selection than cats which lack such experience. These results provided indirect

evidence to support the hypothesis that there are nutritional benefits to be gained from eating a mixed diet. This interpretation was aided by a lack of evidence for other mechanisms of anti-apostatic selection, both proximate and functional. However, all the foods in these experiments were nutritionally complete. It is therefore essential to carry out experiments on nutritionally variable foods to test whether the domestic cat actually does modify its food selection on the basis of the nutrient content.

In this chapter, I describe an experimental study which investigates the effect of macronutrient composition on food selection when the foods vary in their temporal availability. The primary aim of the study was to test the prediction that selection for temporally rare foods is greater when the available foods differ in their macronutrient content (i.e. the foods are complementary to some extent and so there are benefits to be gained from the consumption of a mixed diet) than when the foods are nutritionally very similar.

8.1. METHODS.

8.1.1. Experiment 10a : Selection of Nutritionally Similar Foods by Cattery Cats.

The aim of this experiment was to examine the effect of temporal availability on selection by WCPN cats for two canned foods of similar macronutrient composition. The experiment was carried out on 12 WCPN cats over the four-week period from 1st February to 28th February 1992. The two experimental foods were Arthur's (formerly Kattomeat) "turkey" (Ar) and Kit-e-kat "rabbit" (KEK). These foods were very similar in macronutrient composition (see table 2.1. in Chapter 2). Both were considered by their manufacturers to be nutritionally complete.

The 12 subjects (C227, C688, H71, C250, C424, C425, C432, C470, C431, C443, C463, C704) were arbitrarily divided into two groups of six. Each group was housed in a small panel room for the duration of the experiment (see chapter 2 for description). During each of the four weeks of the experiment, the cats were presented with a maintenance diet consisting of one or both of the two experimental foods (table 8.1). The two groups received the Ar and KEK maintenance diets in opposite orders to control for sequence effects. The maintenance diet was

presented to the cats overnight (from 1600 to 0800 hours) in large communal food bowls for five consecutive days each week. Each cat received an average of 200g of maintenance diet prior to each preference test. This quantity provided the cats with approximately two-thirds of their daily energy requirement. Equal quantities of Ar and KEK were fed ad-lib to the cats on the 2 days each week on which preference tests were not conducted (days 1-2, 8-9, 15-16 and 22-23). However, the quantity of the maintenance diet had to be increased slightly (from 200g to 232g per cat per day) from day 17 as some cats were showing a small weight loss.

Day	Group 1 Maintenance Diet	Group 2 Maintenance Diet
3-7	100g Ar + 100g KEK	100g Ar + 100g KEK
10-14	200g KEK	200g Ar
17-21	116g Ar + 116g KEK	116g Ar + 116g KEK
24-28	232g Ar	232g KEK

Table 8.1. Maintenance diet (average per cat) for WCPN cats in experiment 10a (level increased after day 17 because of loss of weight in some cats).

Preference tests were carried out on five consecutive days during each of the four weeks of the experiment. Each test was carried out at 1300 hours and followed the overnight presentation of the maintenance diet (table 8.1). Each cat was assigned to its regular feeding box for all preference testing (figure 5.1). Both food types were offered at room temperature and handled in the same way prior to feeding. Individual cats were presented with 180g of each food, in two small foil dishes. Each preference test lasted for a standard duration of 15 minutes, by which time most cats had become satiated. After the test, the amount of each food type remaining was weighed and recorded.

To minimize errors in preference measurement from "side-bias"¹ the relative position of the two foods in preference tests was alternated over the time course of the experiment. On each day, half of the cats received one food in the left bowl and the other half received the same food in the right bowl. During repeated testing on individuals, the position of each food type during presentation was alternated daily.

¹Some individual cats may possess an innate "handedness" and will tend to prefer a food because of its relative position (left or right) relative to the cat (C.J. Thorne, personal communication; see also Trivers 1985).

8.1.2. Experiment 10b : Selection of Nutritionally Dissimilar Foods by Cattery Cats.

In this experiment, the effect of temporal availability on the selection of nutritionally different foods by cattery cats was examined. The experiment adopted the same experimental design as experiment 10a and was carried out over the four-week period from 14th March to 10th April 1992. The two foods used in the experiment were specially prepared by Pedigree Petfoods. Food "HP" was a high protein, low fat formulation, while food "LP" was low in protein and high in fat (see table 2.1 for nutritional composition). The foods were manipulated (see chapter 2) such that their caloric density was identical (there is evidence that cats select foods on the basis of their energy content; Castonguay 1981, Kane et al. 1987). The two foods were presented to the cats in equal quantities for several days prior to the start of the experiment to allow the cats (a) to become familiarized with their nutritional composition, and (b) to overcome any neophobic effects (Bradshaw 1986).

Experimental subjects were the 12 heaviest cats in the group of 24 WCPN cats which were available for testing at the time of the experiment (C432, C425, C424, C470, C431, C403, C467, D318, C443, C611, C656, C704; 7 of which were used in experiment 10). The weights of these individuals ranged from 3.6kg to 5.51kg at the beginning of the experiment (mean weight=4.68kg, SD=0.64kg). The heaviest individuals were chosen since cats above 3.5kg have very similar daily energy requirements (K. Earle, *personal communication*; see figure 8.1). Since the 12 experimental subjects had similar energy requirements, it was reasonable to assume that their macronutrient requirements were also similar.

As in experiment 10a, the cats were divided into two groups of six to control for sequence effects. The maintenance diets which individuals in these groups received are shown in table 8.2.

The amount of maintenance diet available to each cat (on average) was precisely calculated. The fat content of foods HP and LP was largely irrelevant since the minimum requirement of this macronutrient was very small (0.41g/400kcal ME/day; National Research Council 1986) and easily satisfied by 280g per day of either food. However, the minimum protein requirement for cats was much higher (19.2g/400kcal ME/day; National Research Council 1986). While this level was attained by consuming 280g of HP per day, 280g of LP was not enough. Therefore, individual cats were presented with the opportunity (during each preference test) to meet their protein requirements. The cats were fed ad-lib on equal quantities of the two foods prior to the two days each week in which preference testing was not carried out.

All other experimental details were the same as experiment 10a

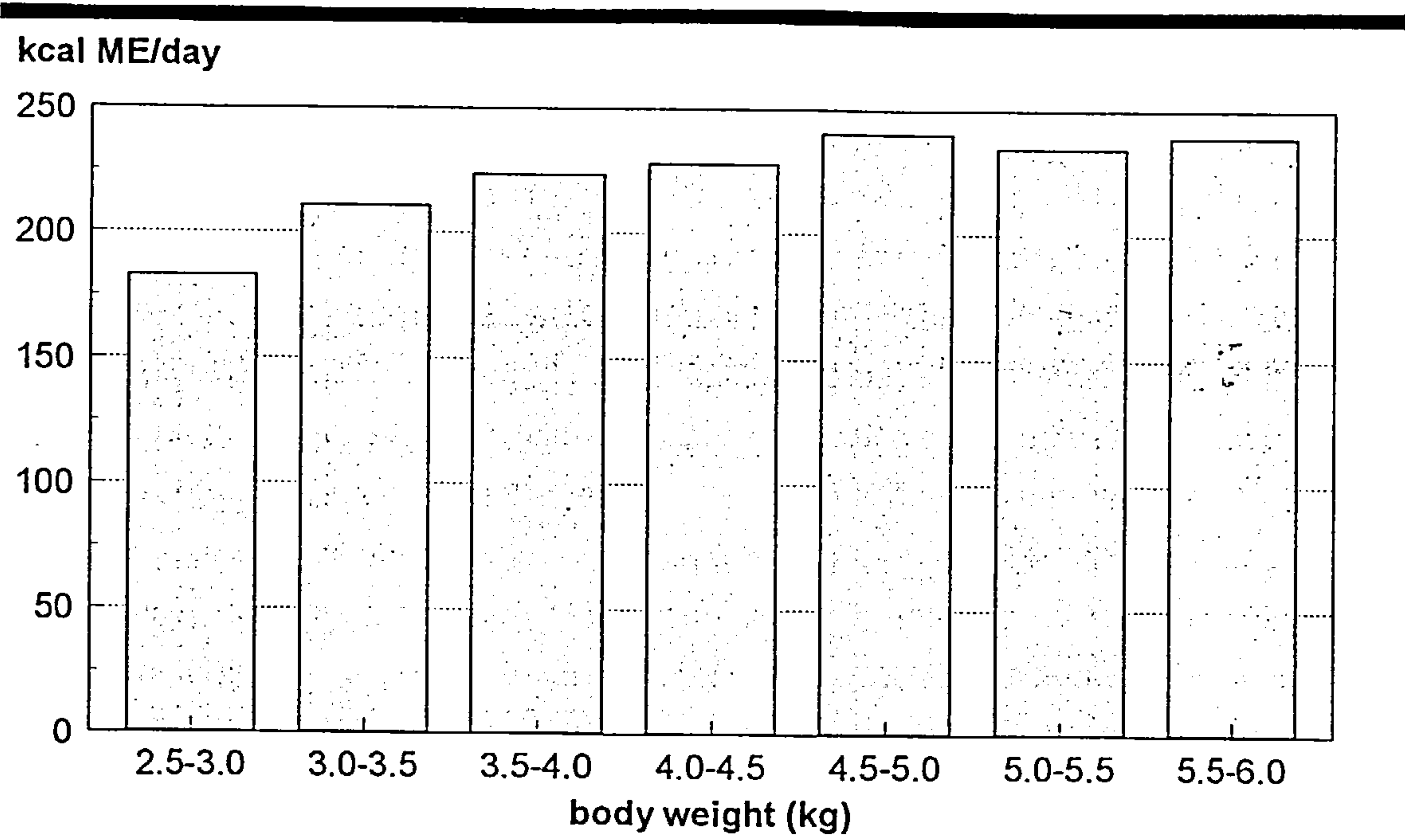


Figure 8.1. The effect of body weight on the daily energy requirements of WCPN cats (ME = metabolizable energy). (Source : WCPN).

Day	Group 1 Maintenance Diet	Group 2 Maintenance Diet
3-7	280g HP + 280g LP	280g HP + 280g LP
10-14	280g HP	280g LP
17-21	280g HP + 280g LP	280g HP + 280g LP
24-28	280g LP	280g HP

Table 8.2. Maintenance diets (average per cat) for WCPN cats in experiment 10b.

8.2. RESULTS.

Manly's β (equation 3.8) was used as an index of selectivity. Since both foods in each experiment were presented in equal quantities during the preference test, β was not subject to bias (Weale 1992; see also chapter 3). The results of preference tests in which less than 20g of food was consumed were rejected, in line with the standard preference testing procedures of Pedigree Petfoods (C.J. Thorne, *personal communication*).

8.2.1. Experiment 10a : Nutritionally similar foods.

β_{Ar} values were calculated for each preference test in which more than 20g of food was eaten. One cat in group 1 (C250) fulfilled this criteria in only three out of 20 preference tests and was subsequently removed from all statistical analysis.

Inspection of the β_{Ar} values obtained for each cat revealed no obvious trends in preference within any of the experimental maintenance diets. The temporal changes in preference shown by individual cats in groups 1 and 2 during the Ar and KEK maintenance diets are shown in figures 8.2 and 8.3. To quantify these trends, linear regression of individuals cats' β_{Ar} values against time (day) was carried out for the five days during which each maintenance diet was presented. No significant deviations of the estimated slope of the regression from zero were found for any individual during the Ar and KEK maintenance diets (tables 8.3 and 8.4).

Preference is a dynamic process; each preference test only reveals a "window" on to a range of preferences which are constantly modified by experience. It is therefore possible that within-maintenance diet effects might have obscured any trends in the data. For example, in addition to the maintenance diet, the previous days' preference test might have influenced preference. Consequently, to test for more general changes in preference, a five-day β_{Ar} value was calculated, based on the total availability and consumption of KEK and Ar in *all* preference tests over the 5-days for which each of the four maintenance diets was presented². These data are summarized for groups 1 and 2 in table 8.5 and 8.6.

Within each group, there were no significant differences among the five-day β_{Ar} values in any of the four weeks of the experiment (Friedman two-way analysis of variance by ranks for related samples; group 1: $\chi^2=6.66$, $df=3$, $p>0.05$; group 2: $\chi^2=6.55$, $df=3$, $p>0.05$). Contrary to expectation (given that the cats were arbitrarily divided into the two experimental groups) the β_{Ar} values obtained in group 1 were significantly higher than those of group two when the maintenance diet consisted of Ar ($t=4.57$, $df=9$, $p<0.01$), KEK ($t=2.92$, $df=9$, $p<0.05$) and during week 3 (the second week of Ar + KEK) of the experiment ($t=3.46$, $df=9$, $p<0.01$). There was no significant difference between the two groups in the first week (Ar + KEK) of the experiment ($t=1.14$, $df=9$, $p>0.1$), although there was still an overall preference for Ar.

²Including tests in which <20g was consumed; although these tests could not be used reliably to generate single beta values, they are still important when one is interested in total food intake over a series of preference tests.

Data from group 1 and group 2 were pooled in order to examine the overall effects of different maintenance diets on preference changes. Despite the differences between the overall preference of the two groups, pooling was justified since *changes* in preference are likely to be largely independent of the degree of overall preference.

To test for systematic preference changes during the experiment, the β_{Ar} values for each cat were compared between the first and third weeks of the experiment (i.e. between the two Ar+KEK maintenance diets). There was no significant difference (paired t-test: $t=0.36$, $df=10$, $p>0.5$)

In terms of assessing the effects of temporal availability on selectivity, the most important comparisons were between selection during (i) the Ar only and KEK only maintenance diets, (ii) the Ar only diet and the Ar+KEK diet in the week prior to it, and (iii), the KEK only diet and the Ar+KEK diet in the week prior to it³. To examine these effects, data from the two groups were pooled in the following manner:

- POOL 1 : KEK (week 2 for group 1 plus week 4 for group 2).
 POOL 2 : Ar+KEK in the week prior to KEK maintenance diet (week 1 for group 1 plus week 3 for group 2)
 POOL 3 : Ar (week 4 for group 1 plus week 2 for group 2)
 POOL 4 : Ar+KEK in the week prior to the Ar maintenance diet (week 3 for group 1 plus week 1 for group 2)

There were significant differences in the preferences of the cats among the four pools (Friedman two-way analysis of variance by ranks: $\chi^2=11.209$, $df=3$, $p<0.05$). To determine which treatments were significantly different, pairwise comparisons between treatments were carried out according to the method described by Siegel & Castellan (1988). Significance was tested using the inequality:

$$|\bar{R}_u - \bar{R}_v| \geq z_{\alpha/k(k-1)} \sqrt{\frac{k(k+1)}{6N}} \quad (8.1)$$

where R_u and R_v are the mean ranks within each condition, z is the test statistic, α is the required significance level, k is the total number of classes and N is the number of observations within each class. The estimated significance levels were adjusted for the effects of multiple comparisons between treatments (pools) (Siegel &

³The beta values obtained in the Ar+KEK diet prior to each Ar only or KEK only maintenance can act as a "baseline" preference. From this preference it is possible to see how preferences change during the Ar only and KEK only maintenance diets.

Castellan 1988). The significant difference between pools was due to a difference in β_{Ar} values between the two Ar+KEK maintenance diets (pools 2 and 4 above; $p < 0.05$). All other pairwise comparisons were non-significant ($p > 0.05$). The changes in β_{Ar} between (i) the Ar only and KEK only diets, (ii) the Ar only and Ar+KEK diet in the preceding week, and (iii) the KEK only and Ar+KEK diet in the preceding week are shown in figure 8.4.

There were no significant differences between the total amount of food consumed by individuals in group 2 between any of the four weeks of the experiment (Friedman two-way analysis of variance by ranks for related samples : $\chi^2 = 5.6$, $df = 3$, $p > 0.1$). However, there was a significant difference between the amount eaten by group 1 cats under the four periods of maintenance diets ($\chi^2 = 10.38$, $df = 3$, $p < 0.05$). Using equation 8.1 revealed that the total intake in week 1 (maintenance diet = Ar+KEK) was significantly lower than that of week 3 (maintenance diet = Ar+KEK, $p < 0.01$). All other pair-wise comparisons were non-significant ($p > 0.05$).

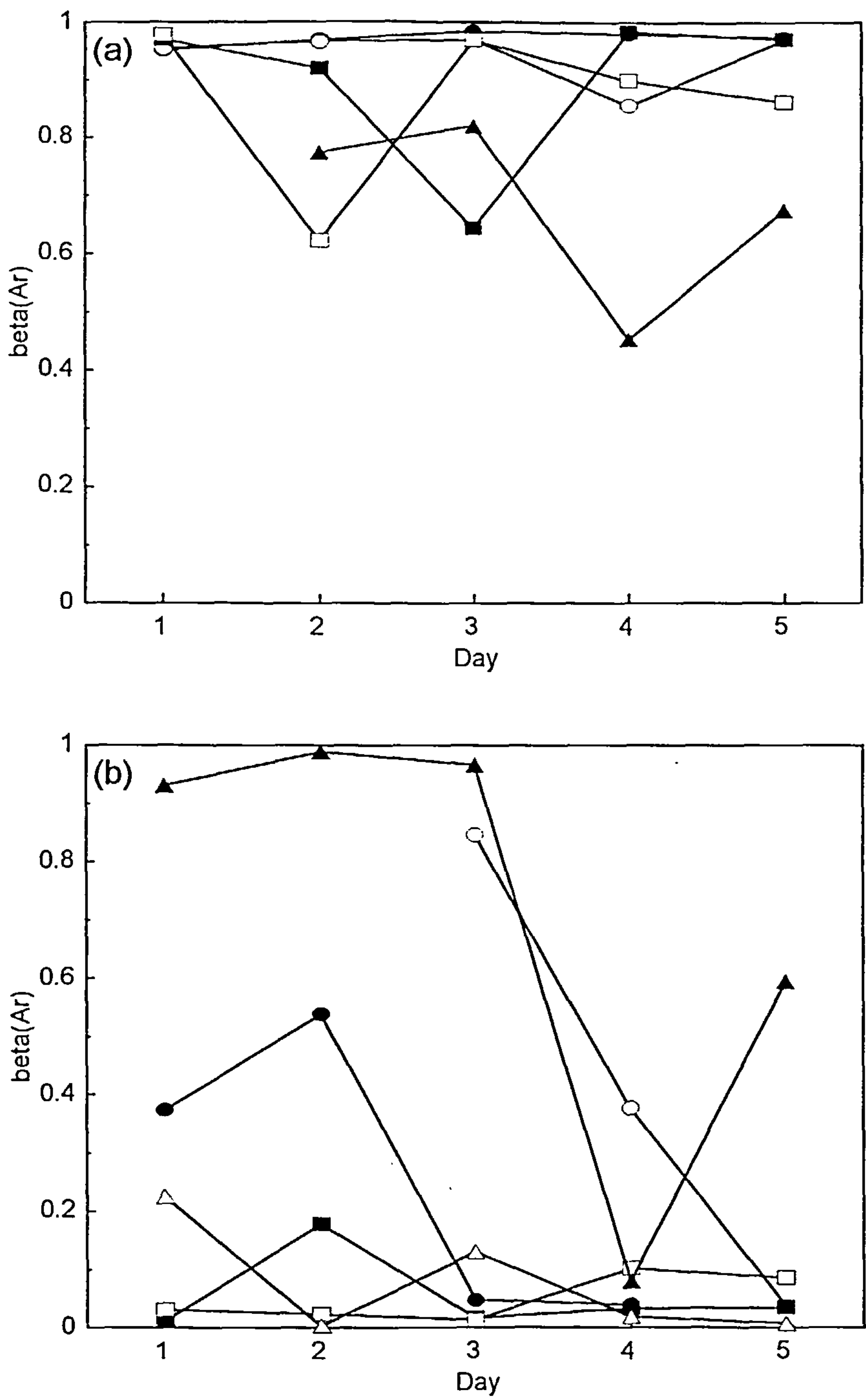


Figure 8.2. Trends in preference for Ar (β_{Ar}) for individual cats in (a) group 1 and (b) group 2 over the five days during which the maintenance diet consisted of Ar in experiment 10a. Each symbol represents a different individual.

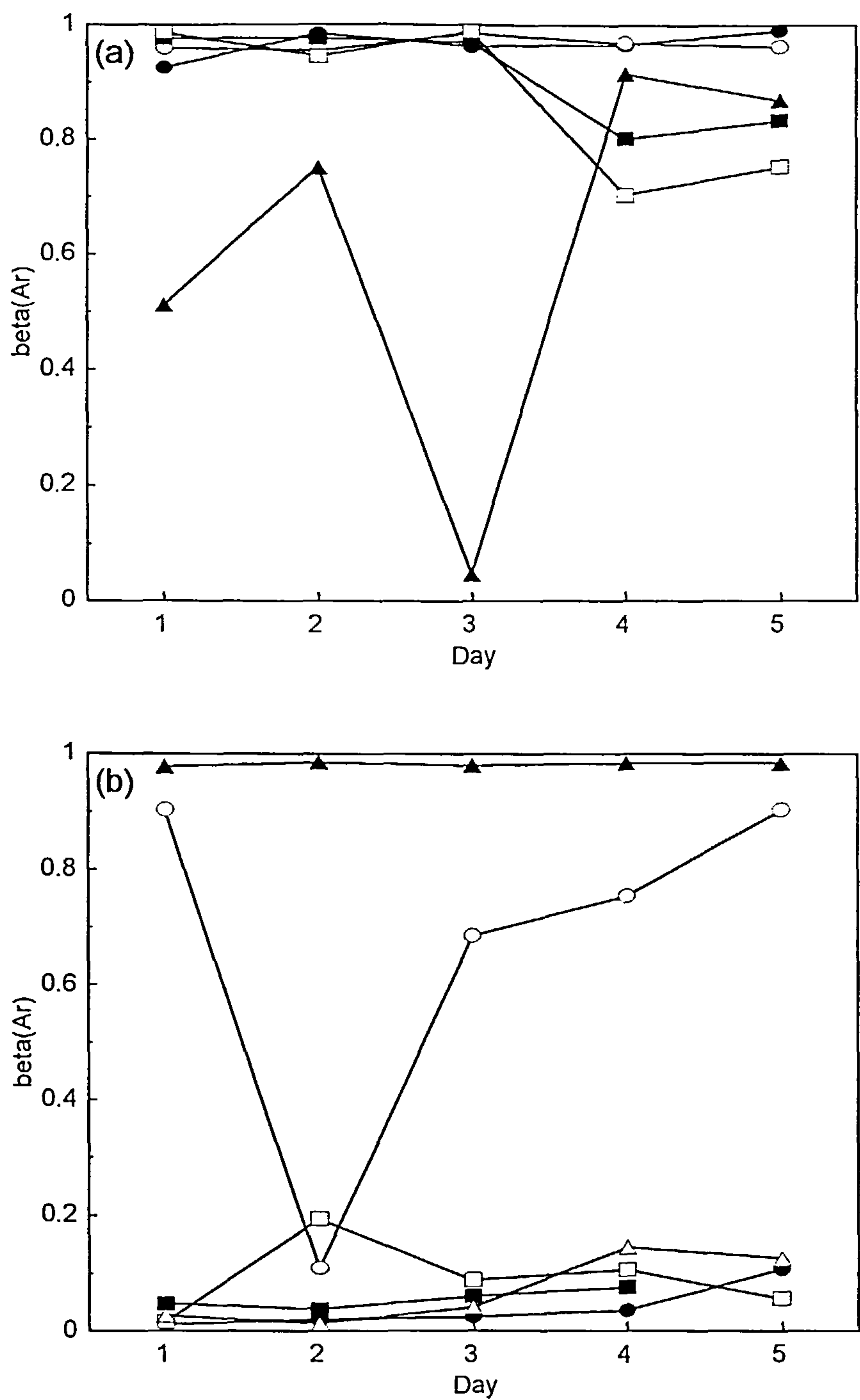


Figure 8.3. Trends in preference for Ar (β_{Ar}) for individual cats in (a) group 1 and (b) group 2 over the five days during which the maintenance diet consisted of KEK in experiment 10a. Each symbol represents a different individual.

Group	Cat	b	a	df	F	p
1	C704	0.005	0.956	1,3	2.328	>0.1
	C431	-0.008	0.968	1,3	0.226	>0.5
	C463	0.006	0.879	1,3	0.014	>0.9
	C227	0.004	0.855	1,3	0.006	>0.9
	C432	-0.067	0.915	1,2	0.767	>0.1
2	C424	-0.149	0.624	1,2	3.081	>0.1
	C470	-0.405	2.04	1,1	116.468	>0.05
	C688	-0.01	0.085	1,3	0.162	>0.5
	C425	0.019	-0.005	1,3	3.616	>0.1
	C443	-0.158	1.187	1,3	2.125	>0.1
	H71	-0.042	0.204	1,3	2.579	>0.1

Table 8.3. Regression of β_{Ar} against time for individual cats in experiment 10a during "Ar only" maintenance diet. *F* and *p* values refer to deviation of slope from zero.

Group	Cat	b	a	df	F	p
1	C704	0.011	0.932	1,3	2.819	>0.1
	C431	0.002	0.961	1,3	0.19	>0.5
	C463	-0.046	1.05	1,3	7.377	>0.05
	C227	-0.071	1.088	1,3	6.17	>0.05
	C432	0.088	0.356	1,3	0.536	>0.5
2	C424	0.021	-0.023	1,3	7.89	>0.05
	C470	0.064	0.478	1,3	0.319	>0.5
	C688	0.011	0.029	1,2	4.658	>0.1
	C425	-0.001	0.095	1,3	0.001	>0.9
	C443	0.001	0.979	1,3	1.034	>0.1
	H71	0.033	-0.029	1,3	8.51	>0.05

Table 8.4. Regression of β_{Ar} against time for individual cats in experiment 10a during "KEK only" maintenance diet. *F* and *p* values refer to deviation of slope from zero.

	Maintenance Diet			
Cat	Ar+KEK (week 1)	KEK (week 2)	Ar+KEK (week 3)	Ar (week 4)
C704	0.863	0.965	0.976	0.972
C431	0.955	0.965	0.947	0.947
C463	0.779	0.891	0.898	0.875
C227	0.817	0.861	0.884	0.878
C432	0.214	0.653	0.874	0.698

Table 8.5. Five-day β_{Ar} values for group 1 cats in experiment 10a.

	Maintenance Diet			
Cat	Ar+KEK (week 1)	Ar (week 2)	Ar+KEK (week 3)	KEK (week 4)
C424	0.709	0.275	0.160	0.050
C470	0.617	0.371	0.617	0.661
C688	0.318	0.047	0.081	0.059
C425	0.481	0.055	0.038	0.097
C443	0.900	0.767	0.954	0.974
H71	0.191	0.082	0.031	0.089

Table 8.6. Five-day β_{Ar} values for group 2 cats in experiment 10a.

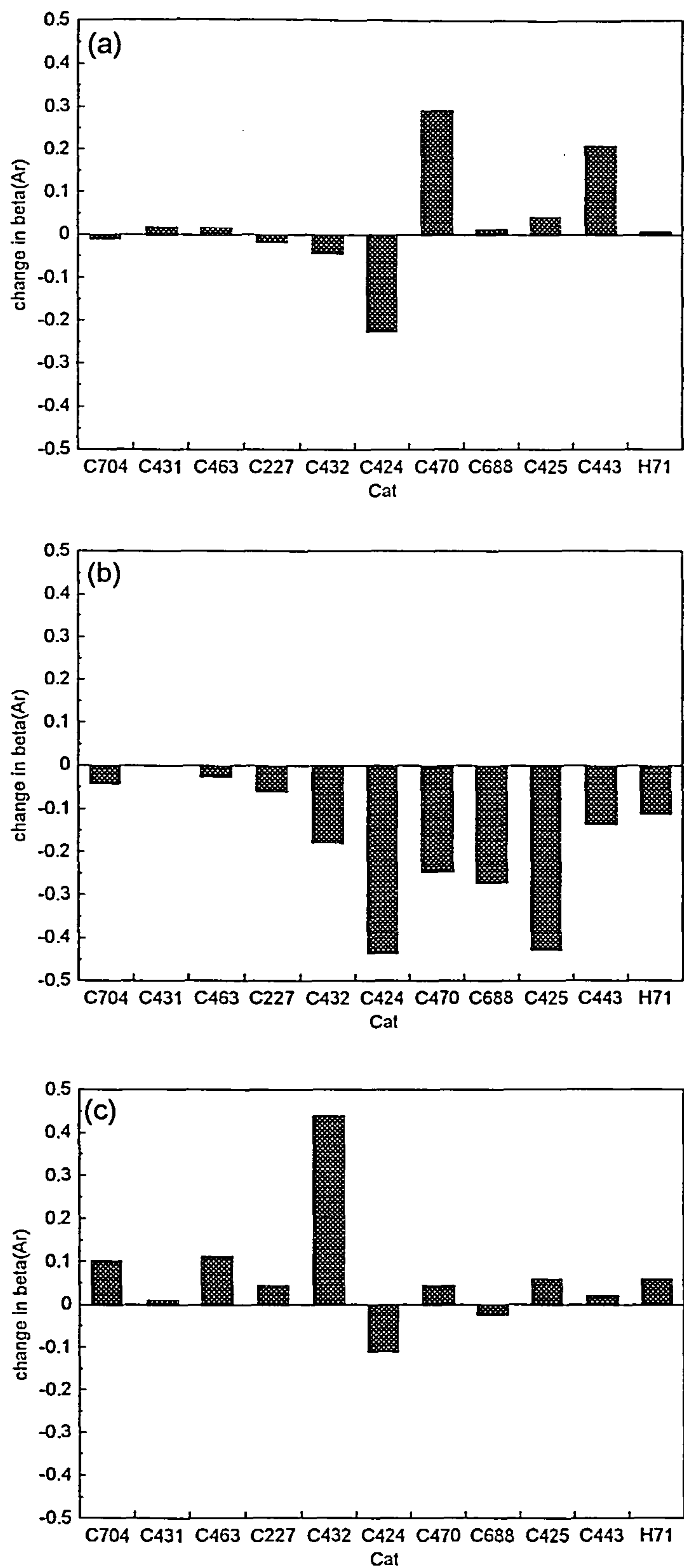


Figure 8.4. Preference changes (five-day β_{Ar} values) for individual cats in experiment 10a between (a) Ar and KEK maintenance diets (positive value indicates increased preference for temporally rare food), (b) Ar diet and Ar+KEK diet in the preceding week, (c) KEK diet and Ar+KEK diet in the preceding week.

8.2.2. Experiment 10b : Nutritionally Dissimilar Foods.

8.2.2.1. Analysis of preference changes.

Two cats, one from each experimental group, were excluded from the statistical analysis. One (C424) consistently consumed less than 20g of food in preference tests, while the other (D318) often appeared stressed⁴ and frequently consumed well over half of the food presented in the preference tests.

As in experiment 10a, there were no obvious preference trends over the five day duration of each maintenance diet (see figures 8.5 and 8.6 for trends within HP and LP maintenance diets), although in both groups there appeared to be an overall preference for HP. Linear regression of β_{HP} against time (day) for individual cats during the HP only and LP only maintenance diets revealed only one (out of 20) significant departure of the estimated slope from zero (tables 8.7 and 8.8).

As in experiment 10a, five-day β_{HP} values were calculated from the total amount of each food presented and consumed each week (tables 8.9 and 8.10). There were no significant differences between the preferences of individuals among the four weeks of the experiment in group 1 (Friedman two-way analysis of variance by ranks: $\chi^2=4.22$, $df=3$, $p>0.1$). In group 2, though, the effect was of borderline significance ($\chi^2=7.8$, $df=3$, $p=0.05$), with the largest difference in mean rank being between preferences in the HP and LP diets (all individuals had a greater preference for HP under the LP maintenance diet than under the HP maintenance diet).

There were no significant differences in five-day β_{HP} values between experimental groups, either during the HP ($t=1.085$, $df=8$, $p>0.1$) or LP ($t=1.126$, $df=8$, $p>0.1$) maintenance diets, or during the HP+LP diets presented in the first ($t=0.411$, $df=8$, $p>0.5$) and third ($t=0.603$, $df=8$, $p>0.5$) weeks of the experiment.

The five-day β_{HP} values from weeks 1 and 3 (i.e. the two HP+LP maintenance diets) were pooled to test for *changes* in overall preference during the experiment. No significant differences were detected (paired t-test : $t=0.746$, $df=9$, $p>0.1$). Although 8 out of 10 individuals demonstrated a preference for HP in both week 1 and week 3, the overall preference for HP was not significantly different from the "no preference" β_{HP} value of 0.5 (week 1 : $t=0.837$, $df=9$, $p>0.1$; week 3 : $t=0.637$, $df=9$, $p>0.1$).

⁴Cat D318 did not appear to be socially integrated with other individuals in the experimental group. At the time of these experiments he was particularly stressed, having recently been moved from another panel of cats at WCPN.

To analyze preference changes based on temporal availability, data from the two groups were pooled in a similar manner to experiment 10a:

- POOL 1 : HP (week 2 for group 1 plus week 4 for group 2)
- POOL 2 : HP+LP in the week prior to HP maintenance diet (week 1 for group 1 plus week 3 for group 2)
- POOL 3 : LP (week 4 for group 1 plus week 2 for group 2)
- POOL 4 : HP+LP in the week prior to LP maintenance diet (week 3 for group 1 plus week 1 for group 2).

Comparison of the five-day β_{HP} values for each cat revealed a highly significant difference among pools (Friedman two-way analysis of variance for related samples: $\chi^2=11.64$, $df=3$, $p<0.01$). Between-pool comparisons, using equation 8.1, showed that β_{HP} values were significantly higher under the LP maintenance diet (pool 3) than the HP maintenance diet (pool 1; $p<0.05$). All other pairwise comparisons were non-significant ($p>0.05$). Differences in preference during the HP and LP maintenance diets and during these two diets and the HP+LP maintenance diets preceding them are shown in figure 8.7. Although non-significant, it is clear that there was a general trend to increase preference for whichever food was temporally rare.

There were no significant differences between the total amount of food eaten by each cat under each maintenance diet (Friedman two-way analysis of variance for group 1: $\chi^2=0.12$, $df=3$, $p>0.9$; group 2: $\chi^2=7.08$, $df=3$, $p>0.05$)

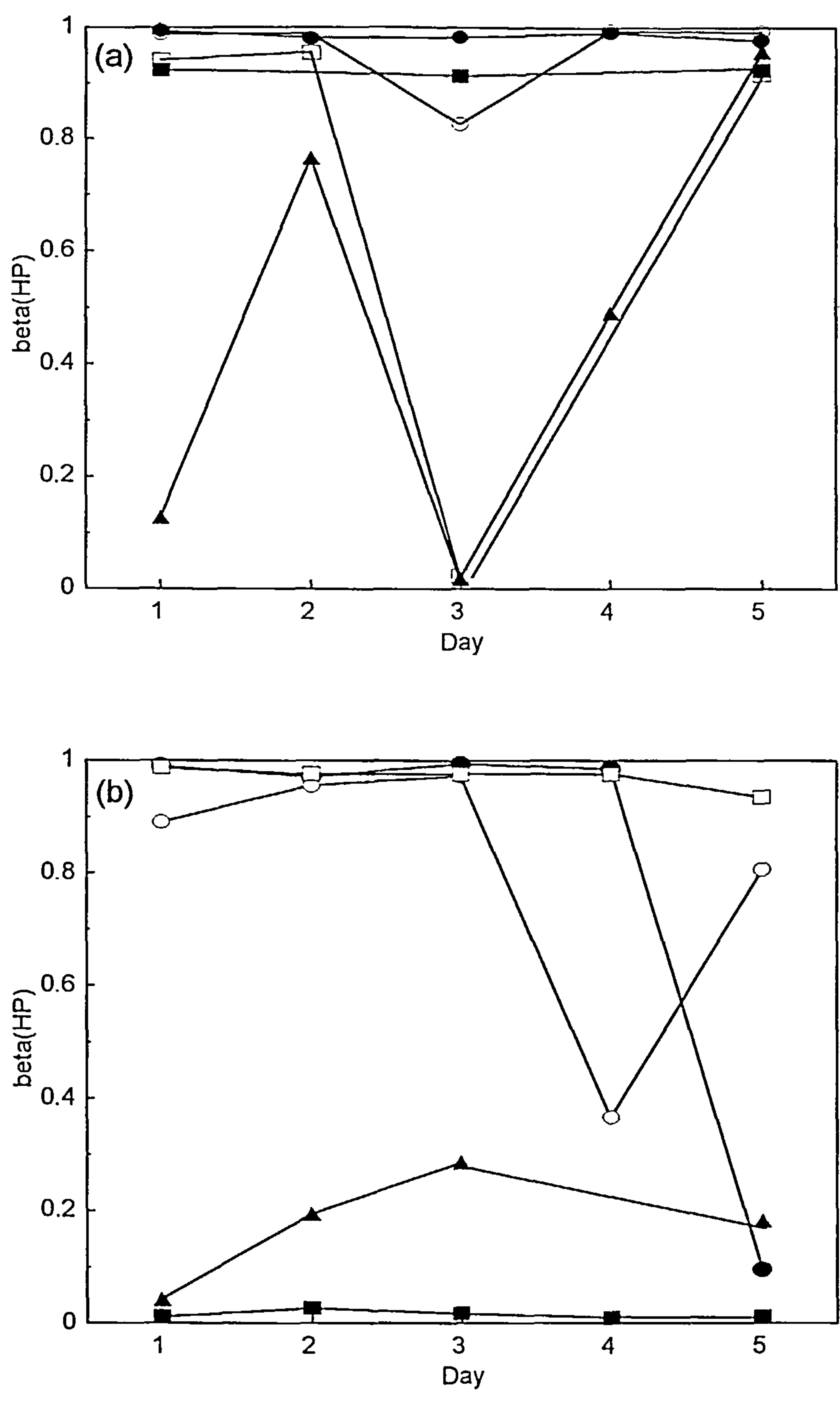


Figure 8.5. Trends in preference for HP (β_{HP}) for individual cats in (a) group 1 and (b) group 2 over the five days during which the maintenance diet consisted of HP in experiment 10b. Each symbol represents a different individual.

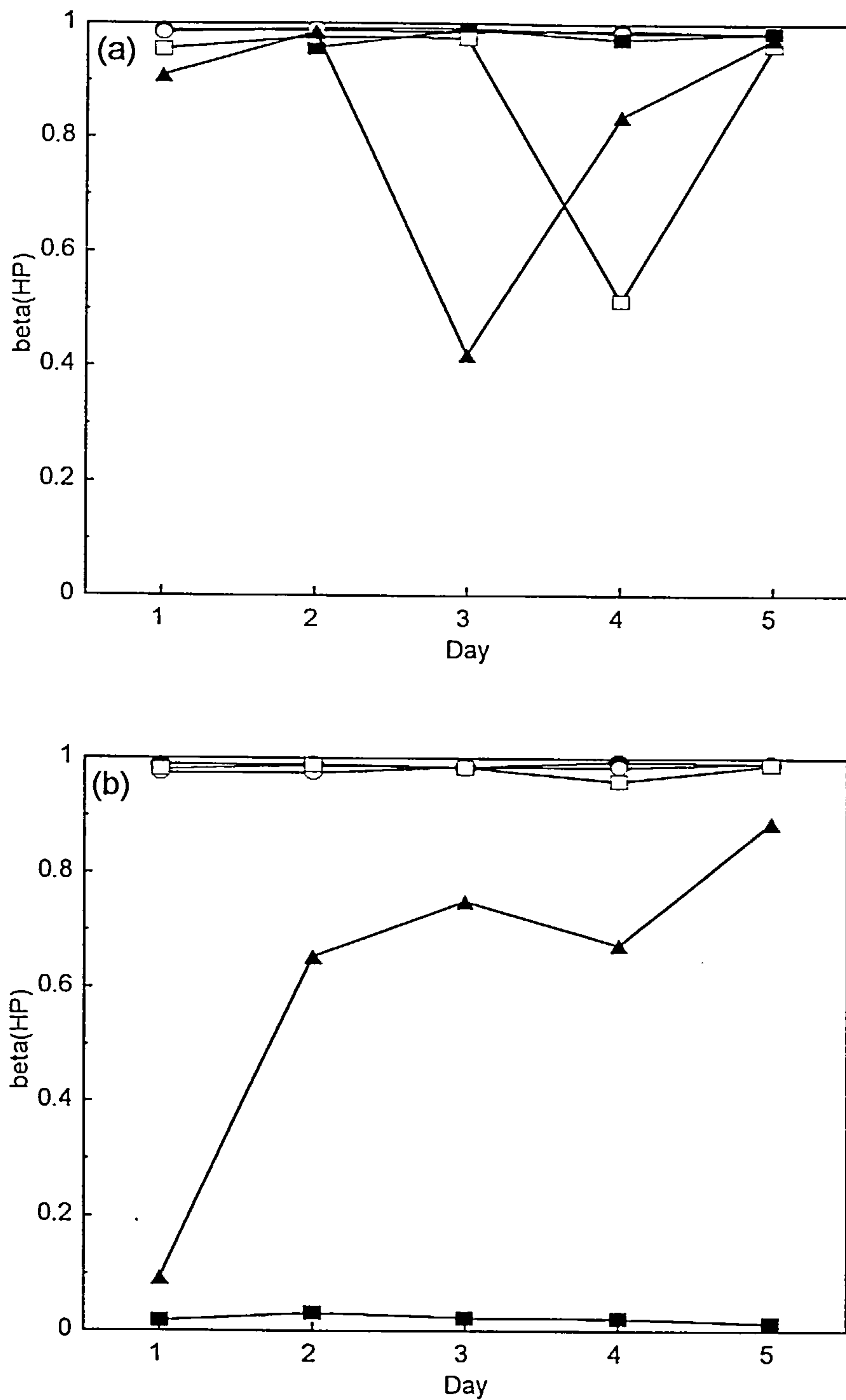


Figure 8.6. Trends in preference for HP (β_{HP}) for individual cats in (a) group 1 and (b) group 2 over the five days during which the maintenance diet consisted of LP in experiment 10b. Each symbol represents a different individual.

Group	Cat	b	a	df	F	p
1	C704	-0.003	0.993	1,3	1.29	>0.1
	C431	0.001	0.955	1,3	0.002	>0.9
	C432	0.00	0.92	1,1	0.00	1.0
	C470	-0.033	0.802	1,2	0.032	>0.5
	C425	0.138	0.057	1,3	1.262	>0.1
2	C443	-0.177	1.339	1,3	2.964	>0.1
	C656	-0.076	1.026	1,3	0.885	>0.1
	C403	-0.002	0.02	1,3	0.493	>0.5
	C467	-0.011	1.002	1,3	6.659	>0.05
	C611	0.029	0.095	1,2	0.684	>0.1

Table 8.7. Regression of β_{HP} against time for individual cats in experiment 10b during the "HP only" maintenance diet. F and p values refer to deviation of slope from zero.

Group	Cat	b	a	df	F	p
1	C704	-0.001	0.991	1,3	1.77	>0.1
	C431	-0.001	0.989	1,3	0.214	>0.5
	C432	-0.192	1.356	1,2	2.798	>0.1
	C470	-0.045	1.01	1,3	0.413	>0.5
	C425	-0.002	0.830	1,3	0.0003	>0.9
2	C443	0.0009	0.987	1,3	0.692	>0.1
	C656	0.005	0.969	1,3	24.796	<0.05
	C403	-0.0018	0.027	1,3	0.655	>0.1
	C467	-0.001	0.983	1,3	0.054	>0.5
	C611	0.161	0.129	1,3	7.01	>0.05

Table 8.8. Regression of β_{HP} against time for individual cats in experiment 10b during the "LP only" maintenance diet. F and p values refer to deviation of slope from zero.

	Maintenance Diet			
Cat	HP+LP (week 1)	HP (week 2)	HP+LP (week 3)	LP (week 4)
C704	0.991	0.984	0.988	0.985
C431	0.954	0.952	0.987	0.986
C432	0.922	0.890	0.556	0.975
C470	0.937	0.650	0.601	0.862
C425	0.312	0.435	0.786	0.83

Table 8.9. Five-day β_{HP} values for group 1 cats in experiment 10b.

	Maintenance Diet			
Cat	HP+LP (week 1)	LP (week 2)	HP+LP (week 3)	HP (week 4)
C443	0.984	0.986	0.980	0.780
C656	0.952	0.979	0.965	0.793
C403	0.042	0.024	0.025	0.015
C467	0.963	0.976	0.974	0.973
C611	0.722	0.602	0.302	0.177

Table 8.10. Five-day β_{HP} values for group 2 cats in experiment 10b.

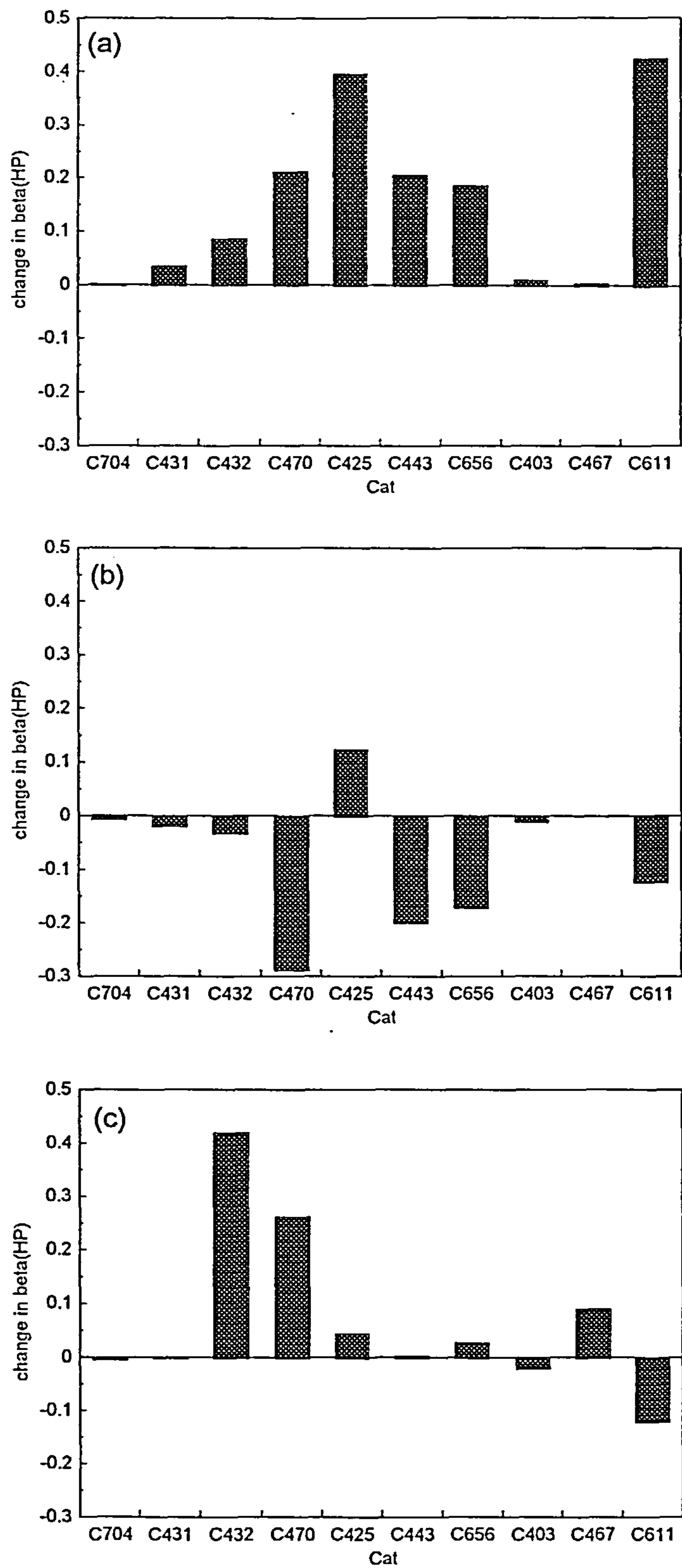


Figure 8.7. Preference changes (five-day β_{HP} values) for individual cats in experiment 10b between (a) HP and LP maintenance diets (positive value indicates increased preference for temporally rare food), (b) HP diet and HP+LP diet in the preceding week, (c) LP diet and HP+LP diet in the preceding week.

8.2.2.2. Analysis of total intake.

A full understanding of nutrient selection can only be gained by considering both the preference changes and the actual amount consumed of particular food items. Figure 8.8 shows the 5-day absolute intakes during the preference tests for individual cats during the HP and LP maintenance diets. Individual cats did not attain their daily protein requirements when presented with a limited maintenance diet of food LP only (during the 5 days of the LP maintenance diet, the cats received only 84g of their 96g minimum protein requirement). The daily preference test was the only opportunity which cats had to select adequate protein. The most direct route to attaining the minimum protein requirement in this case was to direct selection towards food HP (high protein). Indeed, it appears that this was the strategy which most of the cats adopted; intake was biased strongly towards HP (closed squares in figure 8.8) when LP was the background diet. When the maintenance diet consisted solely of HP, the cat had no pressing macronutrient requirements and the points (open circles in figure 8.8) became more scattered. Significantly more LP was

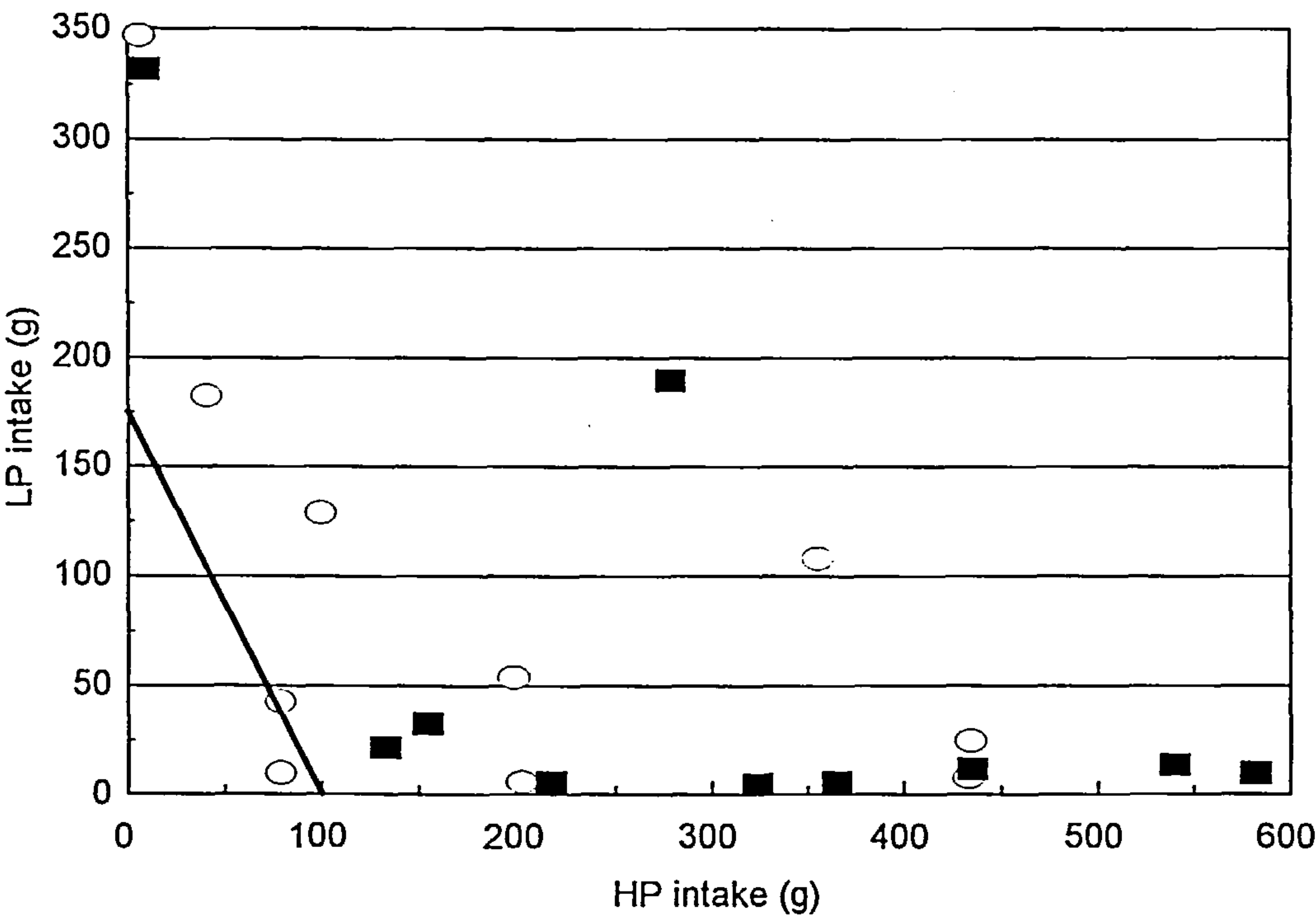


Figure 8.8. Five-day intake of foods HP and LP in preference tests. Solid line represents isocline for minimum protein requirements when food LP is the maintenance diet. Data points represent intake of individual cats during LP (■) and HP (○) maintenance diets.

consumed by each cat during presentation of the HP maintenance diet than the LP diet (paired t-test : $t=2.304$, $df=9$, $p<0.05$). Similarly, significantly more HP was consumed during the LP maintenance diet than the HP diet (paired t-test : $t=2.37$, $df=9$, $p<0.05$).

8.3. DISCUSSION.

8.3.1. Overview.

The results of experiments 10a and 10b are broadly consistent with the prediction that cattery cats should demonstrate greater increases in preference for temporally rare foods when the foods are nutritionally dissimilar (10b) than when they have similar nutritional composition (10a). The only (relevant) significant preference change (based on five-day β values) in the two experiments was between selection during the HP and LP maintenance diets in experiment 10b, in which cats showed an increased preference for whichever food was temporally rare. Analysis based on absolute food intake also demonstrated that individual cats selected more of the LP diet when there was no protein deficit (i.e. when the maintenance diet consisted of HP), yet avoided this diet more when there was a protein deficit. There was, however, a non-significant trend in *both* experiments (figures 8.4 (b) and (c) and 8.7 (b) and (c)) for cats to increase their preferences for a temporally rare food relative to the baseline preference for that food obtained during the preceding week (in which foods were presented in equal amounts). While these results suggest that diet selection was driven largely by the protein requirements of individual cats, some caution must be exercised since (a) there were experimental inconsistencies which had the potential to produce spurious results, and (b), there may be alternative, yet equally plausible, explanations for the behaviour.

8.3.2. Methodological Difficulties & Confounding Factors.

8.3.2.1. Maintenance diets.

In experiment 10a, it was necessary to raise the level of the maintenance diet after two weeks of the experiment (from 200g per cat per day to 232g) because some subjects were losing weight. This may have slightly reduced the hunger levels of the cats at the time of testing. However, no obvious preference changes were apparent between the two halves of the experiment. In addition, the magnitude of the increase in maintenance diet was minor compared to that used in experiment 5

(chapter 6), where I showed that moderate changes in hunger levels were insufficient to produce changes in preference. It is therefore unlikely that the small reduction in hunger level imposed by the increase in maintenance diet was sufficient to influence preference.

The difference in the quantity of maintenance diet presented in experiments 10a and 10b (200/232g and 280g respectively) presents, at first glance, a problem when attempting to compare directly the two experiments. However, such comparisons are likely to be valid when we take into account (i) the energy requirements of individual cats in each experiment (the cats in experiment 10a were, on average, 0.837kg lighter than those in experiment 10b⁵), and (ii) the energy content of the experimental foods. Simple calculation based on these values demonstrate that the energy requirements of the cats in experiment 10a were, on average, 15-19% lower than those in 10b (compared to the 18-29% reduction in the weight of the maintenance diet). Thus, differences in the weight of the maintenance diet were likely to have had a negligible effect on preference.

8.3.2.2. Systematic changes in preference.

The foods used in experiment 10b, HP and LP, were both relatively novel to the WCPN cats, having been first encountered only a few days prior to the start of the experiment. It is therefore possible that the cats were still learning about the nutritional composition of the foods in the first week of the experiment. Under these conditions, the overall preference for HP might have systematically changed over the experiment as the subjects became more familiar with the nutritional composition of the two experimental foods (we might expect a "conditioned satiety", *sensu* Booth (1972), to be formed whereby foragers modify their intake of a food item as they learn about its nutritional content). There was, however, no evidence for such a preference change; there were no significant differences between the preferences of individuals for HP between the first and third weeks of the experiment.

No systematic changes in preference were detected in experiment 10a. However, there was a surprising difference between the overall preferences of the two groups in this experiment; group 1 had a significantly greater preference for Ar than group 2 for the final three weeks of the experiment. There is no obvious behavioural explanation for this effect; the most likely explanation is that the polarity of

⁵Experiment 10a: mean weight = 3843.33g, SD = 850.12g. Experiment 10b: mean weight = 4680.5g, SD = 641.446g.

preferences in the two groups was merely due to chance.

Despite the lack of evidence for systematic changes in preference, there is some evidence that temporal effects did influence the results of experiment 10a. In this experiment, there appeared to be an increase in preference for temporally rare foods relative to a baseline preference established during the previous week⁶. Yet comparison of selectivity during the Ar and KEK maintenance diets revealed no trend in preference whatsoever. The reason for this may have been related to the significant difference between selection in pools 2 and 4 which would have obscured any comparison. Although it is difficult to explain these changes in preference, it could be argued that preferences might be expected to "wander" more when foods are nutritionally similar than when they differ.

8.3.2.3. Repeated use of individuals.

Interpretation of these experimental data are confounded by the (unavoidable) use of six individual subjects in both experiments⁷. It might therefore be argued that the data were biased towards the selective behaviour of these few individuals. However, this appears not to have been the case since the behaviour of these six cats in each experiment was consistent with that of the subjects which were used in only one experiment. In experiment 10a, four of the six cats showed an increase in preference for Ar when it was temporally rare compared to when it was common. Three out of the six cats which were only used in this experiment showed such an increase. In experiment 10b, all six cats increased their preference for HP when it was rare (compared to when it was common). All four of the single-experiment cats behaved in a similar manner.

8.3.3. Alternative Explanations.

Despite the congruence of the experimental results with the *a priori* predictions, it is possible that the observed preferences were not due to the effect of protein availability, but to some unanticipated alternative explanation. Here I consider two possibilities; (i) unforeseen nutritional deficits and (ii) the effect of contrast between experimental foods.

⁶*Comparison of preferences to a baseline preference may be a more sensitive measure since the two tests are temporally closer.*

⁷*Seven individuals actually started both experiments, but one individual (C424) was removed from analysis of both experiments.*

8.3.3.1. Unforeseen nutritional deficits.

Interpretation of experiments 10a and 10b was based largely on the protein content of the experimental foods since it is this nutrient which was deliberately manipulated. However, it is possible that there were other, unforeseen, nutritional differences between the experimental foods. Such possible differences were unlikely to be macronutrient-based since the fat content of foods has little effect on the dietary preferences of the cat (Kane et al. 1987) and the caloric densities of foods, although suspected to influence selectivity (Castonguay 1981, Thorne 1982; but see Kanarek 1975, Hirsch et al. 1978), were largely controlled in these experiments. It is possible, though, that selectivity may have been influenced by differences in the micronutrient composition of the experimental foods (for which only the macronutrient composition was known). For example, a scenario in which the foods KEK, Ar and HP contained a complete complement of micronutrients while food LP was deficient in some respect could have produced similar results to those observed. However, it seems unlikely that such deficiencies would occur in the experimental foods in a manner which coincided precisely with the prediction made at the start of the chapter.

8.3.3.2. Contrast Effects.

In addition to differences in their relative protein content, the pairs of experimental foods used in experiments 10a and 10b also differed along other contrast dimensions (smell, taste, colour, texture). In particular, foods HP and LP showed greater contrast in their textural and visual properties than did foods Ar and KEK (although even the latter pair could still be easily identified solely on the basis of either of these contrasts). While the visual properties of the food may not be important (see chapter 6), it is known that food textures influence diet selection by the domestic cat (Kane 1989, Robinson & Thorne 1990). Indeed, Thorne (1985) has warned that overlooking textural differences may lead to misinterpretation of preference data. It is therefore possible that the observed results may have been due to innate or learned preferences for contrasting foods by the WCPN cats. Since foods HP and LP appeared to contrast more than Ar and KEK, larger increases in preference for rare foods would have been expected in the former. At functional level, though, it is still necessary to invoke some sort of explanation based on nutritional requirements in order to explain *why* contrasting foods should be preferred. It is reasonable to assume that a foods with a high level of contrast will tend to differ more in their nutritional composition than two foods which are sensorily similar.

8.3.4. Mechanisms of Nutrient Selection: Some Hypotheses.

The food preferences of the domestic cat are known to be influenced by the nutritional composition of available foods (Kane 1989, Bradshaw 1991, National Research Council 1986). Following Rogers & Blundell (1991) I propose two types of hypothesis based on the proximate mechanisms which may result in increased preference for rare foods when the available foods differ in their nutritional composition: (i) the effect of endogenous regulatory systems, and (ii) learned responses to nutritional factors. Although these hypotheses are directed primarily at possible mechanisms of protein selection in relation to experiments 10a and 10b, they can be generalized to other foragers.

8.3.4.1. Endogenous regulatory systems.

Omnivorous mammals, such as rats and humans, may adjust their macronutrient intake in response to fluctuating availability via endogenous regulatory systems. For example, Rogers & Blundell (1991) suggest that selection of macronutrients by humans may be driven by changes in the synaptic activity of the brain neurotransmitter serotonin, activated by changes in the metabolite composition of the blood plasma. However, it has been suggested that such regulation does not occur in the domestic cat in response to changes in the level of protein in the diet (Kane 1989). The best evidence for this is the study of Cook et al. (1985) who demonstrated that kittens do not develop avoidance of protein-free diets. The reason for this apparent lack of regulation may be that the live prey of the ancestors of the domestic cat contained roughly constant levels of protein and so no regulation was needed. Indeed, Kane (1989) states: "Perhaps, during the evolution of the cat, there has been no selective pressure on control systems to ensure an adequate protein intake, since presumably, cats have always ingested relatively constant and greater than adequate levels of protein." It is therefore unlikely that such a mechanism was responsible for the results of experiments 10a and 10b.

8.3.4.2. Learned responses to nutritional factors.

Nutrient-based preferences might also occur as a result of foragers learning to avoid less nutritious foods (Rozin 1976). Foragers may learn an association between the sensory stimuli of the food (taste and odour in particular) and the physiological consequences of consumption. They can then "...avoid the most relevant stimuli associated with disadvantageous gastrointestinal consequences" (Bradshaw 1992, p. 122). However, little is known about the actual nature of these internal cues

(McFarland 1993). An important aspect of this process is that a forager does not necessarily have to become deficient in a particular nutrient for learning to occur. For example, Baker et al. (1987) have demonstrated that rats can develop a "learned hunger" for protein, whereby the protein content of foods can be learned even when there is no protein deficit. Only when protein is required are high protein foods preferred. It is possible that this might explain the preferences obtained in experiment 10b; the cats had the opportunity to learn the protein content of foods HP and LP both during their initial presentation and during the early stages of the experiment. The low protein levels imposed during the presentation of the LP maintenance diet might then have resulted in the expression of a preference for the HP (high protein) food. This hypothesis is unlikely to be relevant to experiment 10a, however, since protein availability was probably not sufficiently low to influence selectivity.

8.3.5. The Role Of Monotony.

Interpretation of experiments 10a and 10b to date has concentrated primarily on the nutritional composition of the available foods. However, it is also possible that monotony (cognitive satiety) was occurring independently of any nutritional effects (Siegel & Pilgrim 1958). Although there were no significant preference changes in experiment 10a based on the temporal availability of foods, there was some evidence that individuals increased their preference for rare foods relative to the baseline established in the previous week. A similar effect was found in experiment 10b. While the changes in experiment 10a might have been due to nutritional differences between the foods, it is also possible that they were due to the early effects of monotony. In other words, in addition to the possible effects of nutrients, the cats may have simply learned that foods were rare and selected them on this basis. If it occurred, monotony would act in tandem with any mechanisms based purely on the selection of specific nutrients. Teasing apart the effects of monotony and those of nutrient selection experimentally is likely to prove extremely difficult.

8.3.6. Broader Implications For Diet Selection in Cats.

The experiments are broadly consistent with the hypothesis that preference for rare foods increases when there are nutritional benefits to be gained from the consumption of a mixed diet (Greenwood 1984). This is despite the fact that the nutritional benefits were relatively minor. The cats could have attained their protein requirement in experiment 10b simply by consuming a greater quantity of the low protein food. However, the fact that the nutritional composition of foods appeared to

influence selectivity has important implications for the interpretation of the experiments presented in previous chapters. In these chapters, I suggested that consistent differences between the strength of anti-apostatic selection in rescue shelter and cattery cats could be attributed to learning the nutritional benefits of a mixed diet. The results presented here tend to reinforce this argument.

General Discussion

In this thesis, I have demonstrated that, in general, domestic cats preferentially select spatially or temporally *rare* food items. Anti-apostatic food selection was detected, albeit to different degrees, in cats from a variety of experiential backgrounds using both multi-frequency and training experiments. The variety and number of these experiments suggest that selection of rare foods is a robust phenomenon in *F.s. catus*.

It is also clear, though, that anti-apostatic food selection by the domestic cat is a highly complex process which may be caused by a plethora of behavioural mechanisms, both proximate and ultimate. In this discussion, I initially attempt to synthesize the knowledge gained from this study, both in terms of the selection of cats from different backgrounds and the behavioural mechanisms underlying the observed selection. I then examine the broader implications of these findings for studies of foraging behaviour and ecology. After assessing the potential future role of the domestic cat in studies of food selection, I finally outline possible avenues for future research.

9.1. FDS BY THE DOMESTIC CAT : A COMPARATIVE VIEW.

There were remarkably consistent differences between the strength of anti-apostatic

selection exhibited by cats from the different experiential backgrounds. In the high-density, multi-frequency experiments in chapters 5 and 6, selection by rescue shelter cats was always stronger than that of cattery cats in comparable experiments. The magnitude of this difference also depended upon the sequence (random or sequential) in which food ratios were presented to the subjects. The results from the training experiments on farm and cattery cats in chapters 7 and 8 may also be compared in a similar manner. In chapter 7, farm cats showed strong preferences for temporally rare foods when hunger levels were not excessively high, while cattery cats (chapter 8) only displayed a weak (non-significant) trend towards the preference of rare foods in similar experiments. A stronger effect was only observed in cattery cats when the experimental foods differed to an appreciable extent in their nutritional composition, as predicted by the "mixed diet" hypothesis.

It is reasonable to speculate that there was some fundamental difference between the cats from the different experiential backgrounds (i.e. rescue shelter and farm cats versus cattery cats). Although there may be an innate component to food selection in the cat (Bradshaw 1992), it is more likely that the observed differences reflect learned foraging behaviour. Although learning may be considered as a proximate mechanism of behaviour, it is most valuable in the present context to consider it in terms of ontogeny.

There were two major sources of ontogenetic change in food selection which may have differed between cattery and farm/rescue shelter cats. The first possible source, and one which I have largely overlooked until now, is that food preferences were culturally transmitted to the experimental subjects from their mothers during weaning. Certainly, adult predatory behaviour in cats is determined by the types of live prey encountered as a kitten (Caro 1980). It has also been reported (Kuo 1967, Hart 1974) that kittens which are reared on a restricted diet tend to be more "finicky" as adults, although Thorne (1982) states that studies on cattery cats do not support this view. However, the possibility of a "sensitive phase" (e.g. see McFarland 1993) during the development of the kittens, during which some of the adult food preferences and foraging tactics develop, cannot be ruled out. It is not clear, though, how important such effects were in this study since little information about the early feeding experiences of the experimental subjects in the rescue shelters and at Firtree Farm was available. However, it is reasonable to suppose that the cattery cats were reared on foods which were less variable in their nutritional content than those of the

shelter and farm cats, and this difference might have influenced the foraging behaviour of the adults.

A second potential source of ontogenetic change was the development of foraging tactics during the post-weaning lifetime of the cat. In the multi-frequency experiments of chapter 5 (section 5.3.4.2), I suggested that there were differences between the learning abilities of rescue shelter cats and cattery cats by virtue of their differential exposure to what can be broadly classified as "problem-solving opportunities"¹. In chapters 7 and 8 there were also differences between the preferences for *temporally* rare foods observed in the Firtree Farm cats and the cattery cats. As with the shelter cats, the farm cats were likely to have been exposed to a greater environmental complexity and unpredictability than cattery cats. Thus, broadly speaking, nutritionally "experienced" cats (i.e. those which had been required to select their diet from a nutritionally diverse, constantly changing array of foods) may have responded to changes in food availability more rapidly than "inexperienced" individuals. In addition, farm cats and rescue shelter cats were more experienced at foraging on nutritionally variable foods than were the cattery cats. There were therefore likely to be greater benefits associated with the selection of a mixed diet in the rescue shelter and farm cats, and individuals from these locations may have learned that there were deleterious effects associated with the consumption of a monotonous diet. Anti-apostatic selection may have arisen as a natural consequence of avoiding this situation. I therefore propose that the combination of (i) differences in speed of learning, and (ii) differences in the benefits which a mixed diet had offered, in the development of the experimental subjects represents the most plausible hypothesis to account for the consistent differences in the strength of anti-apostatic selection between cats from different backgrounds.

It may be tempting to interpret the results of these experiments purely in terms of ontogenetic factors. However, it is possible that there were components of anti-apostatic selection that were similar in all of the study subjects. In particular, results consistent with the occurrence of sensory-specific satiety were obtained for both rescue shelter and cattery cats. Sensory-specific satiety is a physiological

¹Kamil (1983) has outlined how previous experience can affect the shape of the learning curve in animals by considering the theory of learning sets. The basic learning set paradigm consists of presenting an animal with a series of many different two-choice discrimination problems, correct responses being rewarded with food. Although each problem in the series is different, later problems are solved much more rapidly than early problems.

mechanism of selection and can be therefore be considered to be largely innate. Rolls (1986) has suggested that the function of sensory-specific satiety is to cause an animal to select a mixed diet. However, it is by no means clear what selection pressures might have acted on the ancestors of the domestic cat to cause such a mechanism to evolve. The wild ancestors of the cat almost certainly fed primarily on "nutritionally exchangeable" (Rozin 1976) live prey items. It can be speculated, though, that sensory-specific satiety was selected for because of the fitness benefits (obtained via nutritional benefits) associated with eating different tissues of a live prey item. Animal tissues and organs differ greatly in their nutritional composition. For example, liver is rich in vitamin A while muscle is virtually devoid of it. Thus, any felid unable to consume the entire prey item (e.g. if it was large, or there was competition between individuals for access to parts of the carcass) would need to eat a variety of tissues to satisfy its nutritional requirements. This possible origin of sensory-specific satiety may have "pre-adapted" (an ugly term, but one which is widely understood) contemporary urban feral cats to be able to forage successfully on nutritionally variable resources.

9.2. BROADER IMPLICATIONS OF THE STUDY.

Some of the issues which have arisen from the experiments reported in this thesis may be important on a much broader scale. Although the experiments were performed using artificial foods in a contrived environment, some of the points raised are likely to have interesting implications for behaviour and ecology in general. Here I briefly consider some of these implications.

9.2.1. Foraging Theory.

The cat is an obligate carnivore (MacDonald et al. 1984), yet the results obtained in chapter 8 suggest that its diet selection decisions were influenced to some extent by nutritional factors. This perhaps illustrates a shortcoming of the application of optimal foraging theory: optimality models rarely consider nutritional factors as the optimization "currency" (see Stephens & Krebs 1986). While it is true that the level of food availability had to be relatively low in order to produce a nutrient constraint (experiment 10b), it is clear that unneutered colonies of urban feral cats are likely to face such food shortages (colony growth tends to lead to food shortages), as well as

being faced with the option of eating even less ideal foods than those used in the experiments. In general, though, it may be that nutritional factors are more important in influencing food preferences than previously thought. Although Stephens & Krebs (1986) considered nutrient constraints as a possible reason why energy-maximizing foraging models (e.g. the classic optimal diet model) are subject to errors, little research has been carried out on nutrients in an optimal foraging context².

A second issue raised by this study is that of the role of ontogenetic factors in determining food preferences and foraging strategies. Such factors are known to influence the foraging behaviour of many wild animals (e.g. see Partridge & Green 1985, Desrochers 1992). This suggests that considerable care must be taken when attempting to equate the results of foraging studies on laboratory-reared animals with those of wild conspecifics (although such care is rarely taken).

9.2.2. Individual Variation in Ecological Processes.

Variation between individuals is fundamental to biology; the universal acceptance of the neo-Darwinian synthesis is testimony to this. In chapter 4, I discussed the importance of considering the effect which variation among individuals has at the population level, and demonstrated that fairly unremarkable variation among the preferences of individuals could produce substantial anti-apostatic selection at the group (or population) level. Although I do not intend to reiterate this argument, it is worth emphasizing the potential importance of these processes in ecology and population dynamics. During the next 10 years we may see a revolution in population dynamics as individual effects are explored in greater detail.

9.3. THE DOMESTIC CAT AS A "MODEL" FORAGER.

Prior to this study, the foraging decisions of domestic cats in urban areas had rarely been contemplated within the context of foraging behaviour in general. As domestic animals, cats were, perhaps understandably, largely overlooked as subjects for investigations of diet selection. As a result of this study, we are now in a position to

²*Applications of linear programming (e.g. Belovsky 1978, 1981) are perhaps an exception, but these only predict the behaviour of predators on a coarse-grained time scale.*

assess the validity and future potential of the domestic cat as a model for studies of diet selection.

At a superficial level, the domestic cat might seem an ideal subject; much is known about its nutritional requirements and it is ubiquitous and easy to handle. However, upon further contemplation, difficulties emerge which I believe preclude the use of the domestic cat as a model mammalian forager. Firstly, it is not entirely clear what the domestic cat can be considered as a model of. In urban areas the cat certainly cannot be considered as a general model of a mammalian *carnivore* since wild carnivores primarily feed on live prey items. These prey are (i) encountered sequentially, (ii) virtually nutritionally complete (or "nutritionally exchangeable"; Rozin 1976) and (iii) non-sedentary. Since the food items scavenged by urban feral cats tends to be (i) encountered simultaneously, (ii) nutritionally variable and (iii) sedentary, it is hard to imagine how any insight could be obtained into the foraging behaviour of wild carnivores (the only possible exception to this might be other carnivores which have successfully exploited urban areas, such as foxes and raccoons).

It is clear that urban cats are required to select food in a manner which has more in common with omnivorous mammalian scavengers (e.g. rats, mice). Yet the cat is not likely to be a good model for these organisms either, since it possesses fairly precise nutritional requirements (National Research Council 1986) and must therefore select its food from a relatively small subset of the available food items. This effectively limits the scope of experimental studies since it will be difficult to manipulate the nutritional composition of foods over a wide range. In addition, the current supremacy of OFT as a conceptual framework for investigating diet choice decisions dictates that a domesticated animal would not be a good subject because of the difficulties of applying optimality arguments. Even were this not a problem, the prevalence of energy maximizing models in OFT also presents a problem. I have suggested that cats appear to be limited by nutrients rather than energy, yet a good model forager should allow both energy and nutrient-based hypotheses to be tested. Unfortunately, cats tend to find high-energy foods unpalatable (Sean O'Malley, *personal communication*), so energy-based models will be difficult to apply.

It is likely that a generalist mammalian forager such as a wild rat would make a far better general model for investigations of diet selection than the domestic cat.

Although studies of food selection by the domestic cat may reveal some general insights into foraging behaviour, it lacks the true flexibility to be used on a regular basis. I suggest that the real interest of the domestic cat is as a unique and successful forager in its own right.

9.4. FUTURE WORK.

Two main avenues of research are suggested by the work presented in this thesis. The first is to continue to explore the foraging decisions of the domestic cat; that is to extend, clarify and, hopefully, confirm the results of this study. The second is to pursue some of the ideas about foraging and FDS generated here, using other organisms and computer models. Here, I discuss possibilities about the nature of this research.

9.4.1. Studies on Cats.

9.4.1.1. The effect of nutritional differences on anti-apostatic selection.

In this thesis, the effects of nutritional requirements on FDS were only studied at a relatively superficial level. Future experiments should investigate the effect of nutrient deficiencies on selectivity in greater detail. The best approach may be to use nutritionally defined³ foods to make precise predictions about selection. For example, pairs of experimental foods could be chosen such that both foods were deficient in a *different* micro- or macro-nutrient (but as similar as possible with respect to all other nutrients). In this case, anti-apostatic selection and a complete reversal of overall preference would be predicted if nutritional factors were the sole determinants of selectivity. It might also prove illuminating to study selection on foods in which the magnitude of the deficiency is manipulated. It can be predicted that anti-apostatic selection will increase in strength as the size of the deficiency in each food increases (since each food will, presumably, become more "profitable" as it becomes rarer by virtue of containing the nutrient which is deficient in the common food). However, there might be a threshold of nutrient deficiency, above which

³*Ideally, the precise macro- and micro-nutrient composition of the foods should be known; these could be either specially formulated artificial diets or more "natural" foods such as liver or red meat.*

deficient foods may be excluded from the diet altogether.

9.4.1.2. The ontogeny of FDS.

The hypothesis that differences in the selection of cats from different backgrounds is due primarily to ontogenetic factors is testable, although a series of long-term experiments is required. Different groups of cattery kittens could be reared from birth on either (i) a monotonous but nutritionally complete diet or (ii) a nutritionally variable diet but containing enough nutrients for a balanced diet to be selected. FDS could then be tested for in multi-frequency and training experiments after 1 or 2 years. It is predicted that those cats raised on a nutritionally variable diet will exhibit stronger anti-apostatic selection than those raised on a monotonous diet. If necessary, the study could be extended to look for sensitive phases in development. This could be done by restricting the kittens to a monotonous diet for only a limited, specified periods of, say, one or two months during their development.

These experiments would also provide very useful information about the actual benefits of a mixed diet via the growth rates of individual kittens raised on the different diets.

9.4.1.3. Diet selection of urban feral cats.

A comparative approach to diet selection and FDS by the domestic cat is likely to be the most fruitful approach to considering food selection. To date, though, no studies have addressed the diet selection of "true" urban feral cats within a framework of contemporary foraging theory. Most have merely catalogued the foods which these cats consume (for example, see table 1.1). Although such a study would undoubtedly be difficult (urban feral cats are virtually impossible to manipulate and it would be very difficult to keep track of all their nutritional intake), it might also provide, of all the potential studies which could be carried out on cats, the most interesting insights into the phenomenal success of the domestic cat in urban areas.

9.4.2. Studies on Natural Predator-Prey Systems.

The ultimate aim of FDS experiments is surely to enhance our understanding of the processes which operate in natural systems. Yet remarkably few studies have been

performed on such systems (see chapter 1). Although relatively few researchers have studied FDS by mammalian foragers (notable exceptions being Soane & Clarke 1973, Greenwood et al. 1984ab, Ostfield 1982), wild omnivorous mammalian foragers such as rats and mice offer perhaps the greatest scope for new insights into foraging behaviour.

I suggest that there are two main areas where advances may be made. The first is in the area of olfactory prey detection. As outlined in chapter 6, this is a vastly under-explored area of research (although justifiably so, since it is very difficult to study). It is clear that olfactory mechanisms have the potential to produce frequency-dependent detection rates in wild predators, possibly due to the effect of olfactory mechanisms analogous to search image formation in visual predators (Nams 1991). If so, there exists the potential to identify a new source of stabilizing selection in many predator-prey systems. Since mammals rely to a large extent on olfaction to detect food items, they represent ideal models for such a study. Although, a neurophysiological study would be required to uncover fully the mechanisms of olfactory prey detection, great progress can still be made at the organismal level by considering behaviour in a similar way to present studies of visual search (e.g. Getty 1993).

The second area of research is to examine the effects of nutritional composition on FDS by wild mammalian foragers. This may be studied in a similar manner to that proposed for cats (section 9.4.1.1.). As with cats, there is an enormous literature concerning the nutritional requirements of rodents. This must be considered as a pre-requisite for any nutrient-based foraging study. Plesner Jensen (1993) has demonstrated that, among wild mammals, the wood mouse (*Apodemus* sp.), which feeds on a wide variety of seeds and fruits, may be a suitable model for nutrient-based experimental studies. Deer mice (*Peromyscus* sp.), used by Holling (1965) in his classic studies of functional response, and, more recently, by Vickery et al. (1994), are another alternative.

The major benefit of experiments on natural predator-prey systems is that the ecological consequences of FDS on the population dynamics and community structure of the natural prey species may be directly inferred (or, preferably, studied experimentally). A potentially useful model system for examining the effects of FDS at the population/community level may be a rodent-seed system. Rodents are

known to be a major source of post-dispersal seed predation (Crawley 1992), yet FDS has never been explicitly demonstrated in such a system. By integrating ecological and behavioural approaches to such a system, it may be possible to shed new light on the processes which govern plant population dynamics.

Acknowledgements

I owe a huge debt of thanks to many people for their assistance and advice over the past three-and-a-half years. Biggest thanks must go to my friends and supervisors John Allen and John Bradshaw for helping me when I needed it and for not hassling me when I didn't! I don't think you could ask for any more from a supervisor.

I'm also very grateful to Tom Sherratt, Mike Weale and Rory Putman for invaluable discussions about the joys of FDS. Special thanks to Tom in particular - my fieldwork in Trinidad in 1992 was undoubtedly the high point of my "PhD".

My research at the Waltham Centre for Pet Nutrition was made considerably easier as a result of the friendship and assistance of Chris Thorne, Sean O'Malley, Nicky Metcalf and Chris Pegg.

I also thank Ann Hillman and the staff of the St. Francis Animal Welfare, Richard the Farmer at Firtree Farm and Southampton Blue Cross for allowing me to work with their cats.

Finally, I indebted to my friends in Southampton for keeping me sane during the past three and a half years, especially Liz Butler, 'Becca Knill, Steve Wickens, Phil Heneghan, Ed Pilling and Phil Ridley. Thanks also to the sad sherry drinkers of 5 Oaktree Road (James and Leigh especially) for doing their best to reverse this trend.

This research was supported by a SERC CASE award with the Waltham Centre for Pet Nutrition.

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```

program egttse;

{compares FDS between TOSEs and TTSEs using Elton-Greenwood model}

uses crt;

const
    iterations      =      100;      {total number of iterations}
    etot            =      50;      {total number eaten}
    b               =      1.5;      {freq-dep strength (1=null)}
    i               =      1;      {0=TOSE, 1=TTSE}

var
    meanloge        :      array [1..100] of real;
    loge            :      array [1..iterations] of real;
    p1              :      real;
    e1av,e2av       :      real;
    e2tot,e1tot     :      integer;
    q,m             :      integer;
    a1,a2,e1,e2     :      integer;
    logesum         :      real;
    data            :      text;
    loga            :      real;
    d1,d2,density   :      integer;
    w,w1,w2         :      real;

procedure eat1;      {adjusts prey 1 density upon predation}
begin
    d1:=d1-i; e1:=e1+1;
end;

procedure eat2;      {adjusts prey 2 density upon predation}
begin
    d2:=d2-i; e2:=e2+1;
end;

procedure d1zero;    {stops no. of prey 1 eaten becoming <0}
begin
    e1:=5*density; e2:=etot-e1;
end;

procedure d2zero;    {stops no. of prey 2 eaten becoming <0}
begin
    e2:=100-(5*density);e1:=etot-e2;
end;

procedure randompredation; {uses equation 3.1. to calculate}
var rng, f1, f2 : real; {probability of predation}

begin
    e1:=0;e2:=0;
    d1:=(5*density); d2:=100-d1;
    repeat
        rng := random;
        f1:=w*d1; f2:=(1-w)*d2;

```

```

        p1 := f1/(f1+f2);
        if rng <= p1 then eat1;
        if rng > p1 then eat2;
        if d1=0 then d1zero;
        if d2=0 then d2zero;
    until e1+e2 = etot;
end;

procedure egcalc;                                {calculates log(e1/e2) for each trial}
begin
    loge[q] := 0.4343*ln(e1av/e2av);
    logesum := logesum + loge[q]
end;

procedure savedata;                              {saves data to an ASCII file}
begin
    assign(data, 'a:\type2b1.txt');
    rewrite(data);
    for density := 1 to 19 do begin
        loga := (0.4343*ln(5*density/(100-(5*density))));
        writeln(data, loga, ", meanloge[density]);
    end;
    close(data);
end;

begin                                            {main program}
    clrscr;
    randomize;
    for density := 1 to 19 do begin
        logesum:=0;
        d1:=5*density; d2:=100-d1;
        w1:=exp((b-1)*(ln(d1))); w2:=exp((b-1)*(ln(d2)));
        w:=w1/(w1+w2);                        {calculates w value for each density from eqn 3.5}
        for q:=1 to iterations do begin
            e1tot := 0; e2tot := 0;
            for m:= 1 to 10 do begin
                randompredation;
                e1tot := e1tot + e1; e2tot := e2tot + e2;
            end;
            e1av := e1tot/10; e2av := e2tot/10;
            egcalc;
        end;
        clrscr;
        writeln(5*density, '% complete');
        meanloge[density]:=logesum/iterations;
    end;
    savedata;
    clrscr;
    writeln('done - press <ENTER> to continue');
    readln;
end.

```

```
program beta;
```

```
{Monte Carlo simulation to estimate bias and variance in Manly's beta for a TTSE with a  
random predator and randomly dispersed prey}
```

```
uses crt, graph;
```

```
const
```

```
    iterations      =      1000;           {total number of iterations}  
    e                =      10;           {total number eaten}
```

```
var
```

```
    preyid           :      array [1..10, 1..10] of integer;  
    meanbeta         :      array [1..49] of real;  
    beta             :      array [1..1000] of real;  
    betavar          :      array [1..49] of real;  
    q, i             :      integer;  
    a1,a2,e1,e2      :      integer;  
    r1, r2, betasum  :      real;  
    data             :      text;  
    number           :      integer;  
    freq, sigma      :      real;
```

```
procedure setupprey;
```

```
{set up random prey positions}
```

```
var
```

```
    i,j,k,c          :      integer;  
    ranx, rany       :      integer;
```

```
begin
```

```
    for i:= 1 to 10 do begin  
        for j := 1 to 10 do begin  
            preyid[i, j] := 1;  
        end;  
    end;  
    c := 0;  
    repeat  
        ranx := round(random(10)+1);  
        rany := round(random(10)+1);  
        if preyid[ranx, rany] = 2 then c := c-1;  
        preyid[ranx, rany] := 2;  
        c := c+1;  
    until c = a2;
```

```
end;
```

```
procedure randompredation;
```

```
{random predation on prey}
```

```
var
```

```
    i,c              :      integer;  
    ranx, rany       :      integer;
```

```
begin
```

```
    c:=0;  
    repeat  
        ranx := round(random(10)+1);  
        rany := round(random(10)+1);  
        if preyid[ranx, rany] = 11 then c:=c-1;  
        if preyid[ranx, rany] = 12 then c:=c-1;
```

```

        if preyid[ranx, rany] = 1 then preyid[ranx, rany] := 11;
        if preyid[ranx, rany] = 2 then preyid[ranx, rany] := 12;
        c:=c+1;
    until c=e;
end;

procedure adduptotals;                                {count numbers of each prey left}
var                                                    {after random predation}
    i,j          :      integer;

begin
    e1 := 0; e2 :=0;
    for i:= 1 to 10 do begin
        for j:= 1 to 10 do begin
            if Preyid[i,j] = 11 then e1:=e1+1;
            if preyid[i,j] = 12 then e2:=e2+1;
        end;
    end;
end;

procedure betacalc;                                    {calculates beta values from numbers left}
begin
    r1 := a1-e1; r2:= a2-e2;
    if r1 <= 0 then r1 := 0.001;
    if r2 <= 0 then r2 := 0.001;
    beta[q] := ((ln(a1/r1))/((ln(a1/r1))+ln(a2/r2))));
    betasum := betasum + beta[q];
end;

begin                                                    {main program}
    clrscr;
    randomize;
    for number := 1 to 49 do begin
        a1 := (2*number); a2 := 100-a1; betasum := 0;
        for q := 1 to iterations do begin
            setupprey;
            randompredation;
            adduptotals;
            betacalc;
        end;
        clrscr;
        writeln ((2*number), '% complete');
        meanbeta[number] := betasum/iterations;
        sigma := 0;
        for i := 1 to iterations do begin
            sigma := sigma + (sqr(beta[i] - meanbeta[number]));
        end;
        betavar[number] := sigma/(iterations-1);
    end;
    clrscr;
    assign(data, 'a:\bet1e10v.dat');
    rewrite(data);
    for number := 1 to 49 do begin
        freq := ((2*number)/100);
        writeln(data, freq, ", meanbeta[number], ", betavar[number]);
    end;
    close(data);
end.

```

[o] GLIM 3.77 update 0 (copyright)1985 Royal Statistical Society, London
[o]
[i] ! Define number of data points, or "units"..
[i] ? \$units 40\$
[i] ! Define factors/classification variables..
[i] ? \$fac trial 20 food 2\$
[i] ! State variables for input....
[i] ? \$data trial food d e\$
[i] ? \$din 20\$
[i] File name? a:\fir90.dat
[i] 1 1 972 264
[i] 1 2 108 49
[i] 2 1 972 658
[i] 2 2 108 78
.....values omitted.....
[i] 19 1 972 731
[i] 19 2 108 92
[i] 20 1 972 715
[i] 20 2 108 91
[i] ! Define y variable..
[i] ? \$yvar e\$
[i] ! Binomial error in terms of density..
[i] ? \$error b d\$
[i] ! Use complementary log-log link..
[i] ? \$link c\$
[i] ? \$offset\$
[i] ? \$scal lnd=%log(d)\$
[i] ! Fit model 1 (null model)...
[i] ? \$fit trial\$
[o] scaled deviance = 111.57 at cycle 3
[o] d.f. = 20
[o]
[i] ! Fit model 2 (simple preference)...
[i] \$fit +food\$
[o] scaled deviance = 109.50 (change = -2.073) at cycle 3
[o] d.f. = 19 (change = -1)
[o]
[i] ! Fit model 3 (simple FDS)...
[i] \$fit +lnd\$
[o] scaled deviance = 63.333 (change = -46.16) at cycle 3
[o] d.f. = 18 (change = -1)
[o]
[i] ! Display parameter estimates..
[i] ? \$dis e\$
[o] estimate s.e. parameter
[o] 1 -0.3941 0.1119 1
[o] 2 1.206 0.06883 TRIA(2)
.....values omitted.....
[o] 19 1.435 0.06828 TRIA(19)
[o] 20 1.389 0.06835 TRIA(20)
[o] 21 -0.07406 0.03178 FOOD(2)
[o] 22 -0.1006 0.01446 LND
[o] scale parameter taken as 1.000
[i] ? \$stop\$

```

program indvar;

{ examines the effect of between/within individual preference variation on group FDS }

uses crt;

const
  toteat      = 337;           {total number eaten per trial}
  iterations  = 100;
  prey1d      = 108;           {total number of prey 1 available}
  prey2d      = 972;           {total number of prey 2 available}

var
  a1, a2      : real;
  rbeta       : array [1..5,1..150] of real;
  i,k,q,u     : integer;
  indata      : text;
  outdata     : text;
  prob1, ran   : real;
  betares     : array [1..100] of real;

procedure getranddata;
begin
  assign(indata, 'c:\statg\data\norbetr2.dat');    {set up to read text file}

  {file norbetr2.dat contains normally-distributed random data from Statgraphics}

  reset(indata);
  for u:= 1 to 150 do begin
    readln(indata, rbeta[1,u], rbeta [2,u], rbeta [3,u], rbeta [4,u], rbeta [5,u]);
  end;
  close(indata);
end;

procedure a1lesszero;           {adjust parameters when a1<0}
begin
  a1 := 0; q:=q-1; k:=k-1;
end;

procedure a2lesszero;           {adjust parameters when a2<0}
begin
  a2 := 0; q:=q-1; k:=k-1;
end;

procedure eatprey;              {eat prey based on random probabilities}
begin
  k:=0;
  repeat
    q:=1;
    repeat
      prob1 := (rbeta[q,i]*a1)/((rbeta[q,i]*a1)+((1-rbeta[q,i])*a2));
      ran := random(100);
      if ran <= (prob1*100) then a1 := a1-1 else a2:=a2-1;
      if a1 <= 0 then a1lesszero;
      if a2 <= 0 then a2lesszero;
      k := k+1;
    until k=100;
  until k=100;
end;

```

```

                if k = toteat then q:=6;
                q:=q+1;
            until q > 5;
        until k = toteat;
    end;

    procedure betacalc;                                {calculate  $\beta$  values at end of trial}
    begin
        if a1 = 0 then a1 := 0.001;
        if a2 = 0 then a2 := 0.001;
        betares[i] := ((0.4343*ln(preylD/a1))/((0.4343*ln(preylD/a1))+(0.4343*ln(preyl2D/a2))));
    end;

    begin                                              {main program}
        clrscr;
        randomize;
        getranddata;
        for i:= 1 to iterations do begin
            a1 := preyl1d;
            a2 := preyl2d;
            eatprey;
            betacalc;
        end;
        clrscr;
        assign(outdata, 'a:\norcom2.dat');
        rewrite(outdata);                             {save results data}
        for i := 1 to iterations do begin
            writeln(outdata, betares[i]);
        end;
        close(outdata);
    end.

```

The Use Of Gain Functions In Video Analysis Of Preference

Estimating the food preferences of an individual forager requires that the quantities of available foods consumed by that forager are precisely measured (either via the weight of foods or the number of discrete food items eaten). For wild animals, such as the farm cats used in chapter 7, it is often difficult to directly measure the preferences of individuals because other individuals often interfere with the test subject. In such cases, using video to record behaviour is often a useful alternative. The *time* spent feeding on each food type can then be easily obtained from analysis of the videotapes. However, the use of "time spent feeding" presents a problem of its own: during a single feeding bout, intake rate tends to decline exponentially with time as satiation sets in (McCleery 1977, Bousfield 1933). It is therefore possible that using "time spent feeding" rather than actual intake may not yield good estimates of preference since this method contains the implicit assumption that intake remains constant throughout a feeding bout. Here, though, I attempt to justify the use of this method as the basis for the measures of preference obtained in chapter 7.

To assess the magnitude of satiety effects in the Firtree Farm cats, "gain functions" were calculated for Ar and KK at hunger levels similar to those encountered in experiments 8 and 9 (320g of food per cat per day on average). The experimental subjects were the two Firtree Farm cats which were least disturbed by human presence; Sid and Honey. To determine intake rate, for seven days prior to each test the farm cats were fed only the test food in the required quantity. On the seventh day, feeding rate was measured. The two cats were sequentially presented with three foil dishes, each containing 200g of the food. Each tray was presented for two minutes. During this time, the other cats were dissuaded from going near to the test food. The total amount consumed by the two cats was weighed for each two minute period. The whole six minute period was recorded on videotape (see chapter 7 for further details of video technique).

Videotapes were analyzed to determine the time spent feeding ("the total time during

which the cat was seen to be either handling or consuming food") during each two-minute period (there were, in fact, few pauses by either cat). Measurements of the total time spent feeding and the total intake during each two minute period were used to calculate a standardized value based on the amount of food which one cat would have consumed were it feeding constantly throughout the trial (a standard satiety curve includes all pauses, which can be extremely variable). The gain functions determined by this method are shown in figure A5.1. The curves obtained suggest that feeding rate declines slowly during a feeding bout, and the level of this decline appeared to differ between the two foods.

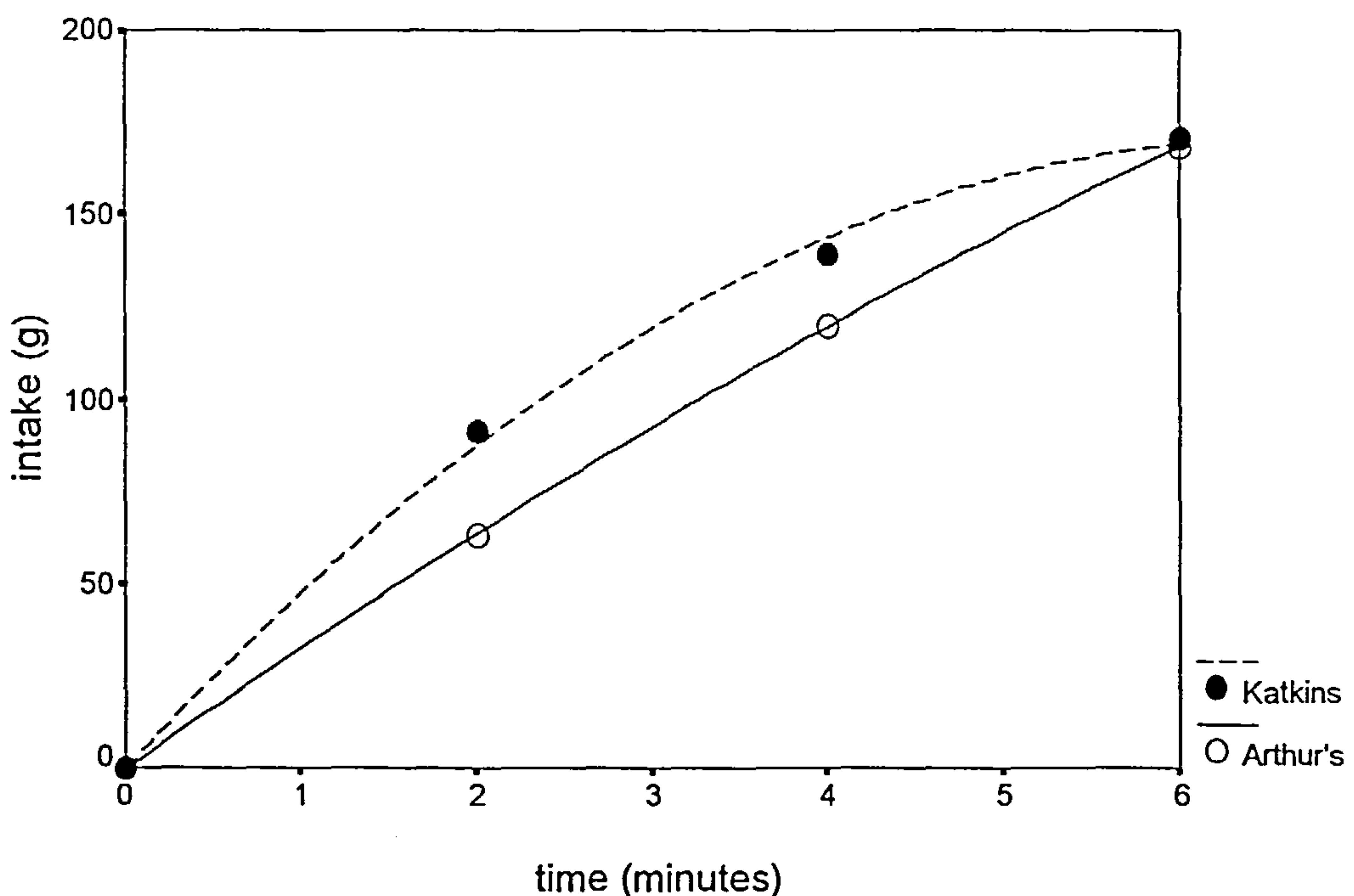


Figure A5.1. Gain functions for Arthur's and Kit-e-kat for Firtree Farm cats.

Despite the observed decline in feeding rate, I believe that the use of gain functions to transform time spent feeding in preference tests into actual intake cannot be fully justified. This is because, although gain functions are theoretically the correct way to proceed, there are, in reality, several practical difficulties which preclude their use.

Firstly, it is not practical to measure gain functions for more than six minutes since the individuals used rarely fed non-stop for longer than this period. This makes it difficult to extrapolate the function to periods longer than this time (all group preference tests were at least 15 minutes). Furthermore, casual observations of

preference tests suggested that cats often divided their foraging time into short bouts. It is difficult to relate a single gain function to several short bursts of feeding.

Second, gain functions can only be measured for one food at a time, yet preference must be measured when two foods are simultaneously present. It is unlikely to be reasonable to assume that subjects behave in exactly the same way towards a particular food when it is presented alone as when it is presented with another food as part of preference test.

Third, the gain functions were necessarily derived from the feeding behaviour of Sid and Honey, the two Firtree Farm cats which were least wary of humans. However, it is possible that the feeding rate in the other farm cats was more constant since (a) observations of preference tests suggest that these cats spent more time in vigilant activities than Sid and Honey during a foraging bout, and (b) their overall intake *rate* appeared lower (although the other cats were a similar size to Sid and Honey, they generally spent more time feeding).

Finally, there are experimental considerations. Assuming constant intake rate makes data extraction from videotapes far easier. It also allows longer foraging periods to be analyzed, and there are no problems with pauses in feeding. Furthermore, studies at WCPN have demonstrated that "time spent feeding" is a good approximation to preference based on true intake (C.J. Thorne, *personal communication*).

Anim. Behav., 1994, 48, 747-749

Anti-apostatic food selection by the domestic cat

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(Received 14 January 1994; initial acceptance 23 February 1994; final acceptance 13 April 1994; MS. number: SC-974)

It is estimated that there are between 1 and 2 million feral domestic cats, *Felis silvestris catus*, in the U.K. that obtain food primarily by hunting and scavenging around human settlements (Bradshaw 1992). In urban areas feral cats select a large proportion of their diet from the nutritionally diverse spectrum of food types that humans discard as household waste (Rees 1981). Domestic cats are obligate carnivores (MacDonald et al. 1984), and few of the food items discarded by humans will meet all their nutritional demands. As a result, the fitness of (unneutered) feral individuals will depend on their ability to select a nutritionally adequate mixture of foods. One factor that may influence the choice of food is the relative availability of different food types. Such frequency-dependent food selection has been widely documented among vertebrates (see Allen 1988 for review) and can be caused by a variety of behavioural mechanisms (Greenwood 1984, 1985). We report here that domestic cats show increased preferences for rare foods ('anti-apostatic selection') when presented with high-density mixtures of two food types.

We used 16 cats, housed in four communal pens, at the St Francis Animal Welfare, a private animal rescue shelter at Horton Heath, near Southampton, U.K. The cats were either strays, unwanted pets or trapped feral cats and were likely to have had some experience of scavenging for food. They were maintained primarily on proprietary tinned foods, although a variety of household scraps were also available. This food was presented to the cats twice daily, at approximately 0900 and 1500 hours. We carried out experimental trials on 12 consecutive days at 1200 hours each day. In each trial, we allowed individual cats to select from a mixture of 140 pieces of two types of nutritionally complete proprietary dry catfoods, 'A' and 'B'. Although nutritionally similar (Table I), the two foods had very different sensory properties. Individual pieces of food A

were light brown, three-pointed stars while pieces of food B were dark brown, four-pointed stars. Both foods produced characteristic meaty odours which could be easily discriminated by the human nose. For the entire period of the experiment, these foods were encountered by the cats only during experimental trials. The two foods were mixed together as a single layer in the bottom of a foil dish (180 mm diameter). We divided the experimental subjects into two groups of eight individuals. The frequency of A relative to B was gradually changed over the course of the experiment from 90 (126:14) to 10% (14:126) in group 1, and, in the reverse order, from 10 to 90% in group 2 (Table II).

We allowed each cat to feed on the mixture for 5 min, although they usually stopped before this time had elapsed. At the end of each trial, we counted the numbers of each food type remaining. Trials in which fewer than 10 pieces of food were eaten were rejected since these were likely to have produced poor estimates of selectivity (Murdoch et al. 1975). Three cats in group 1 did not complete at least one trial at each frequency and were subsequently removed from the analysis of the experiment.

Data were analysed using Manly's β index (Manly 1974) for experiments where food items are not replaced as they are eaten. β lies in the range 0-1, with $\beta_A=1$ representing exclusive preference for food A, and $\beta_A=0$ total rejection of A. $\beta_A=0.5$ represents no selection.

Table I. The nutritional composition of the experimental foods

	Food A	Food B
Protein (%)	30.0	30.0
Oil (%)	7.5	8.0
Ash (%)	9.0	7.5
Fibre (%)	2.5	3.0

Table II. The ratio of foods (A:B) presented to individual cats on each day of the experiment

	Day					
	1-2	3-4	5-6	7-8	9-10	11-12
Group 1	126:14 (90%)	112:28 (80%)	84:56 (60%)	56:84 (40%)	28:112 (20%)	14:126 (10%)
Group 2	14:126 (10%)	28:112 (20%)	56:84 (40%)	84:56 (60%)	112:28 (80%)	126:14 (90%)

The corresponding frequency of food A is shown in parentheses.

The preference changes of the cats within each group were analysed by analysis of covariance (Sokal & Rohlf 1981). We found no significant differences between the slopes of the regression lines for individual cats in group 1 ($F_{4,38}=1.69$, $P>0.1$, common slope = -0.0012) and group 2 ($F_{7,79}=1.03$, $P>0.1$, common slope = -0.0016). The negative values of the common slopes indicated that selection was anti-apostatic in both groups. There were, however, significant differences between the frequency-independent component of selection of individual cats in both group 1 (test for homogeneity of Y -intercepts: $F_{4,42}=9.78$, $P<0.001$) and group 2 ($F_{7,86}=9.32$, $P<0.001$).

We found no significant difference between the common slopes of the two groups ($t=0.574$, $df=139$, $P>0.5$), suggesting that the order in which the frequencies were presented to each group did not influence the magnitude of anti-apostatic selection. Linear regression on the pooled data revealed a highly significant anti-apostatic effect ($Y=0.685-0.0014X$, $t=3.322$, $df=141$, $P=0.001$; Fig. 1). Note that the regression line does not cross the 'no selection' line, owing to a very highly significant overall preference for food A (departure of regression line from $\beta_A=0.5$ at 50% frequency: $t=9.12$, $df=141$, $P<0.001$).

Other studies of frequency-dependent selection by vertebrates when prey are at a high density have generally shown anti-apostatic selection (Horsley et al. 1979; Allen & Anderson 1984; Greenwood et al. 1984a, b, in press). In their demonstration of anti-apostatic food selection by mice, Greenwood et al. (1984b) suggested three types of explanation for the behaviour: (1) rare forms stand out among common forms (either by olfactory or visual cues) and are therefore easier

to locate; (2) initial sampling of food leads to disproportionately more rare types being taken; and (3) there are learned and/or innate preferences for rare food items, based upon the nutritional benefits which a mixed diet may offer. Explanation (2) is unlikely in the present experiment since the cats were both extremely familiar with the experimental foods and, because of the high density, were easily able to assess which foods were present. While we cannot rule out explanation (1), we suggest that explanation (3), particularly with respect to learned preferences, is most likely since anti-apostatic selection has been observed in cats from different experiential backgrounds but tends to be stronger in cats that are more experienced at foraging on nutritionally variable foods (Church 1994). Although the foods

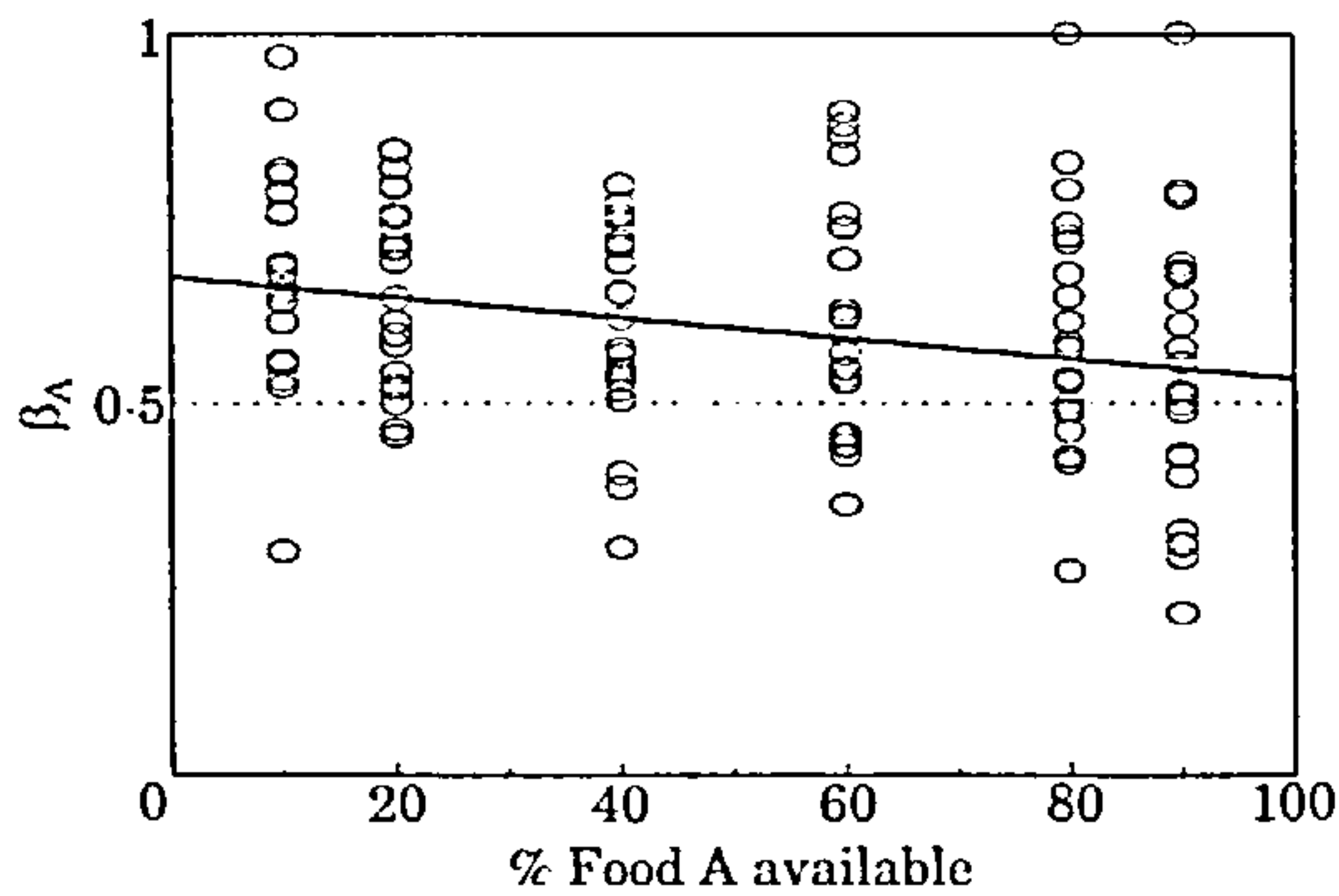


Figure 1. Frequency-dependent preferences of the domestic cat feeding on high-density mixtures of two commercially available dry cat foods, A and B. The solid line is the fitted linear regression line. The dashed line ($\beta_A=0.5$) represents no selection. Individual data points represent the preference of a single individual in one preference test.

in our experiment were nutritionally complete, foods with different sensory attributes will, in general, have different nutritional composition. Increased preference for rare foods appears to be a general phenomenon in domestic cats that primarily scavenge for food; for example, J. W. S. Bradshaw, D. W. Macdonald and co-workers (summarized in Bradshaw 1992) have shown that farm cats, in dichotomous preference tests, prefer foods that are rarely encountered over foods that form a major part of their regular diet. In summary, anti-apostatic selection makes sense as a foraging strategy when foragers are required to select their diet from a nutritionally diverse array of food types, as urban feral cats are.

We thank Tom Sherratt, Sean O'Malley, Chris Thorne, Rebecca Knill, Jeremy Greenwood and an anonymous referee for helpful comments on the manuscript and Anne Hillman for allowing us to work with the cats at the St Francis Animal Welfare. The research was supported by a SERC CASE award with the Waltham Centre for Pet Nutrition.

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