Factors affecting foraging motivation in the domestic pig

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DECLARATION

I confirm that all the work in this thesis is of my own composition and all help given has been acknowledged.

(Robert John Young)
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Abstract

The welfare of farm animals is currently a topic of both scientific investigation and public concern. The aim of this thesis was to investigate motivational factors affecting the expression of foraging behaviour in domestic pigs. This topic was chosen because a number of recent scientific investigations have implicated commercial feeding regimes as being causal in reducing pig welfare.

Most of the experiments reported in this thesis used operant methodology in which pigs had to learn to perform a behavioural response to receive food reinforcement. The main aspects investigated were: the effects of social constraints on feeding behaviour; the effect of information associated with reinforcer delivery on contrafreeloading (where the same food is simultaneously offered free and contingent on an operant response); the effect of operant design on food intake and on operant choice; the effect of food level and a foraging device ('The Edinburgh Foodball') on pigs' time budget; and the effect of reinforcement rate from the Foodball on the time budget.

The results showed that: pigs are highly adaptable and flexible foragers able to overcome social constraints associated with feeding by altering the expression and temporal patterning of feeding variables (e.g., feeding rate); that information associated with reinforcer delivery had little effect on contrafreeloading and that pigs at least under these experimental conditions preferred free food over operant contingent food; that the design of an operant device can significantly influence the level of operant responding and the level of food intake; that given the opportunity food motivated pigs express their feeding motivation as complex and variable foraging behaviour; and that pigs respond to a decrease in the rate of food reinforcement by increasing both the proportion of time they forage for, and the frequency of their foraging responses.

This thesis has shown the effects of a number of factors on the expression of foraging and feeding behaviour in domestic pigs. Although it remains unclear whether or not being able to forage affects the welfare of pigs, the species-specific operant methodology developed in this thesis I believe will allow the welfare requirements of pigs to be more accurately assessed.

ACKNOWLEDGEMENTS

The work reported in this thesis has been like constructing a very large and complex jigsaw puzzle. To complete this puzzle I have required the help of many people. First and foremost in helping me put the pieces in place has been Alistair Lawrence, it was he who showed me that you start with the edge pieces and build inwards. On occasion he also pulled out some of the pieces that I'd forced into the wrong places and encouraged me when I seemed to have lost the will to put in the last few pieces. Beyond all his help with the puzzle, Alistair has become more important than a supervisor; a friend.

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Perhaps the person who has had the greatest influence on my life over the last few years has been Marion Staack. Unfortunately, words fail me to describe how I now feel, the closest I can come is to take some lines from 'Ae Fond Kiss' by Robert Burns;

Ae fond kiss, and then we sever;
Ae farewell and then for ever!

Had we never lov'd sae kindly,
Had we never lov'd sae blindly,
Never met - or never parted,
We had ne'er been broken-hearted.

Lebewohl Schatzchen.

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Finally, I would like to mention all the pigs that feature in this thesis, often as no more than numbers in the pages of the results sections, which may given them some form of immortality? But does not do justice to them as individuals who made the practical work of this thesis so enjoyable.

DEDICATION

This thesis is dedicated to the memory of my grandfather, a man who knew how to live his life in happiness, and spread that happiness to other members of his family and friends.

For, William Logan Thomson.

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NOTE TO THE READER

A point to note is that the 'Edinburgh Foodball' mentioned in Chapters 5 and 6 has been patented, and as such copies of the Foodball may not be made without permission of the Scottish Agricultural College's patent agent the British Technology Group (contact name: Hugh Stirling; Address: BTG, 101 Newington Causeway, London, SE1 6BU; Telephone: 071-403-6666).

Chapter 1

General Introduction

INTRODUCTION

'Swine utilize their muzzle, which is flattened into a tough, rounded disk, in an unending search for food on and under the substrate; this muzzle, or "rooter," gets them in a great deal of trouble when its owner is confined.'

Graves 1984

This statement implies that pigs are often hungry (highly food motivated), spend a large proportion of the day looking for food, that they use a behaviour unique to their species (species-specific) to find food and that when prevented from performing food acquiring behaviour welfare problems arise.

FORAGING BEHAVIOUR OF WILD BOAR AND FREE-RANGING PIGS

Wild boar are thought to be the genetic ancestors of the domestic pig (Spitz 1986) and are classified as the same species (Barrett 1978; *Sus scrofa*). A number of studies have shown that the behavioural repertoire of wild boar is largely indistinguishable from that of domestic pigs (e.g., Stolba and Wood-Gush 1989). It can therefore be concluded that domestication and genetic selection have mainly altered physical and not behavioural characteristics of modern pig breeds. A number of studies have been conducted using wild boar and free-ranging domestic pigs in an effort to provide information about the natural behaviour patterns of pigs (Spitz and Pepin 1984; Stolba and Wood-Gush 1989). The value of such studies is that they provide baseline information about the behaviours that pigs have evolved to express and the stimuli that elicit their expression (McBride 1984).

Members of the species *Sus scrofa* are widely distributed throughout the world, with a natural range from western Europe to Japan. The species naturally occupies a wide variety of tree enclosed habitats (Spitz 1986). Pigs recently introduced into North America and Australia have rapidly colonised non-tree enclosed habitats (Barrett 1978; Graves 1984). It has been suggested that the success of pigs as a pioneer species is their flexible feeding and foraging behaviour (see Stolba and Wood-Gush 1989) and their wide omnivorous diet (see Barrett 1978; Dardaillon 1989). Juvenile pigs consume the widest range of food types and this early experience of broad diet diversity allows them to adapt feeding strategies to fluctuations in food availability (Dardaillon 1989).

The feeding and foraging behaviour of wild boar and domestic pigs has been shown to involve a wide range of behaviours including: pressing and pushing with the rooting pad; grubbing out, digging, scooping and levering with the snout; raking with the forelimbs; gnawing, licking, grazing and tearing with the mouth; the method employed being dependent upon the nature of the food item being extracted (Stolba and Wood-Gush 1989). Members of the pig family are thus able to cope with a wide range of foraging problems. Once food is located the selection of specific items is thought to be based upon olfaction (Spitz 1986). Studies of free-ranging domestic pigs in the Edinburgh Pig Park showed that they foraged for 75% of their active time budget (Stolba and Wood-Gush 1989); studies of wild boar shows that the amount of time they spend feeding and foraging is related to the trophic quality of their habitat (Barrett 1978; Mauget 1984; Klein 1984). Feeding is generally a social activity with even normally solitary boars joining feeding parties (Spitz 1986). Social factors influence feeding and foraging behaviour through the desire of animals in a group to perform the same behaviour at the same time (social synchrony) and this can cause a temporary increase in the expression of the synchronised behavioural activity (social facilitation). These two processes have a tendency to increase feeding competition (Krosniunas 1979). In populations of feral pigs aggression is only commonly observed when a highly desired food is localised in its distribution (Stolba and Wood-Gush 1989). In commercial pig production aggression is often associated with food presentation (e.g., Carlstead 1986) and mixing of unfamiliar individuals (e.g., Tan, Shackleton and Beams 1991).

Food intake, subsequent growth and reproduction by pigs are dependent on food abundance and the types of food available (Barrett 1978). During periods of high food abundance such as when oak trees are masting (shedding acorns) pigs grow very rapidly and their bodies build up large deposits of fat. Seasonal variation in the body weight of adult pigs can be as much as 30% (Barrett 1978; Klein 1984) implying that free-ranging pigs are naturally food restricted to a higher level than commercially reared domestic pigs. This has been shown to be directly related to food availability with wild boar spending more time foraging in periods of food scarcity (Barrett 1978; Klein 1984). One way in which free-ranging pigs cope with food restriction is by timing reproduction to coincide with periods of high food abundance (Klein 1984; Graves 1984). Commercially reared pigs in such a state of feeding motivation often develop stereotypies, which have not been observed in wild boar or feral pigs (e.g., Terlouw, Lawrence and Illius 1991).

FEEDING MOTIVATION

'Animals need food (1) to provide fuel, in terms of energy, to keep alive and maintain body processes, for muscle contraction, and so on, and (2) as raw materials for building and maintaining cellular and metabolic machinery, and for growth and reproduction.'

Schmidt-Nielsen 1983

This statement illustrates the importance of food for survival and therefore it is not surprising that animals have evolved complex mechanisms to ensure food intake. The physiological mechanisms controlling food intake have been extensively investigated but are not yet fully understood (for a review see Forbes 1986). Ethologists have tried to increase our understanding of the internal mechanisms controlling food intake by observing the way animals behave in response to feeding regime manipulations and from the observations making deductions about the internal mechanisms ('black box' approach; see Dawkins 1986).

Feeding motivation can be assessed from food intake, operant responding (Hogan and Roper 1978; Lawrence and Illius 1989) and from measurement of feeding rate (see Doucet and van Straalen 1980). Food deprivation has been shown to increase food intake (but see Miller 1955), operant responding (Lawrence, Appleby and MacLeod 1988) and feeding rate (see Doucet and van Straalen 1980). The importance of food to animals can be more sensitively assessed by economic analysis of feeding behaviour in experiments where food is obtained operantly (Hogan and Roper 1978). This is done by increasing the level of operant responding an animal has to perform to receive reinforcement. If an animal increases its level of responding to maintain a constant level of reinforcement then this suggests a strong underlying motivation and that the animal regards the reward as a 'necessity'. In contrast if the animal does not increase its responding and therefore receives less reinforcement underlying motivation can be inferred as being less and that the animal values the reward as a 'luxury' (Dawkins 1983). Economic analyses of a range of different reinforcers showed that only those such as food that correct physiological deficits have the inelastic demand properties of necessities (see Hogan and Roper 1978).

FORAGING BEHAVIOUR

If feeding motivation only increased the probability that a hungry animal would consume food when food is presented as a stimuli then it would not ensure survival. Food is often not within an animal immediate environment and therefore must be found by foraging before it can be ingested by actual feeding behaviour. Thus, the expression of feeding and foraging behaviour are certainly the result of internal (physiological) and external (stimuli) factors (Hogan 1980; Toates 1987).

Foraging usually utilises more time, and energy than feeding behaviour, because of the locomotion associated with it; for example, foraging locomotion in pigs accounts for 23% of their active time budget (Stolba and Wood-Gush 1989). Therefore the behavioural mechanisms controlling foraging should be under more evolutionary pressure to be energetically efficient than those related to actual feeding. Thus, it would be reasonable to assume that optimality in foraging behaviour has been more intensively selected for than optimality in feeding (reviewed by Krebs and McCleery

1984).

SPECIES-SPECIFIC BEHAVIOUR

The 'adaptionist' school of evolutionary thought argues that the anatomy, physiology and behaviour of animals are shaped by natural selection to fit their niche (e.g., Dawkins 1976; but see Gould and Lewontin 1979). Therefore, if each animal is adapted to a specific niche within its environment then it will have species-specific behaviours to exploit that niche. However, many studies have demonstrated that behaviour is not only a consequence of an animals genotype. Studies of the development of bird song have shown that behaviour is not completely innate but is based on a species-specific template that can be modified by learning and experience (see Slater 1983).

THE WELFARE OF PIGS IN RELATION TO COMMERCIAL FEEDING REGIMES

The neonatal pig for the first few weeks of life receives all of its nutrients from its mother in the form of milk. In modern husbandry systems the neonate whilst still suckling may also be provided with creep feed (see Appleby, Pajor and Fraser 1991), usually a high protein concentrate diet provided *ad libitum*. Piglets in commercial husbandry systems are usually weaned at between three and six weeks of age, whereas in the wild they would be naturally weaned between 14 and 17 weeks of age (Jensen 1986). Piglets are early weaned in order to reduce the period of lactational anoestrous thereby maximising reproductive output (Whittemore 1987). Early weaning is thought to cause a range of welfare problems such as a reduced immune response (Blecha and Kelley 1981) and a retardment of growth whilst piglets adjust to consuming solid food only (Sherrit, Graves, Gobble and Hazlett 1974). It is also believed to be causal in the development of a number of behavioural vices in later life (see below).

Following weaning, piglets ('weaners') from several litters are usually mixed and group housed with a concentrated diet supplied *ad libitum*. Systems for rearing weaners have been criticised for being barren and the small space allowance per pig does not allow the formation of 'individual space' (e.g., Waran and Broom 1993). Pigs between 30kg and slaughter weight at 70kg-110kg ('fatteners') are also group housed and offered a concentrate diet *ad libitum*. These two weight classes of pigs often show a range of behavioural vices such as belly-nosing (Fraser 1978; see also Hughes and Duncan 1988), and tail-biting (Fraser 1987; Fraser 1987a; Fraser, Bernon and Ball 1991). The origin of such behavioural vices has been suggested to be nutritional (Lawrence, Terlouw and Kyriazakis 1993), for example studies have shown that both mineral and protein deficit diets result in increased tail-biting (Fraser 1987; Fraser 1987a; Fraser, Bernon and Ball 1991).

Pigs used as breeding stock are *ad libitum* fed until an approximate liveweight of 115kg and then both pregnant sows (non-lactating) and boars are restrictively fed to a level that is approximately 1.3 times maintenance requirements (Lawrence, Appleby and MacLeod 1988). This level of food restriction has been shown to result in the development of abnormal stereotypic behaviours (Appleby and Lawrence 1987; Terlouw, Lawrence and Illius 1991) which are thought to be indicators of poor welfare (Mason 1991). Physical restriction in stalls and tethers although not directly responsible for the development of stereotypies (Terlouw, Lawrence and Illius 1991) is thought to exacerbate the conditions that cause them by preventing sows from performing complex and variable foraging behaviour. In time the foraging behaviours that can be express become channelled in to more simple and often repeated forms (Lawrence and Terlouw, in press).

During lactation sows are typically fed a high protein concentrate diet to a level that ensures that they do not lose body condition and are able to produce sufficient milk to feed their piglets (Whittemore 1987). Sows under such conditions suffer from a range of welfare problems created by the behaviourally restrictive farrowing crates (see Vestergaard and Hansen 1984) but none of which are directly linked to feeding behaviour.

GENERAL CRITICISMS OF COMMERCIAL FEEDING REGIMES FOR PIGS

In general commercial pig production systems remove the need to find food (Broom 1987), and physically limit the opportunity to express appetitive foraging behaviour (Lawrence and Terlouw, in press; Waran and Broom 1993).

The importance of the animal's diet in influencing behaviour and welfare has been recently reviewed (see Lawrence, Terlouw and Kyriazakis 1993).

Pigs are offered diets under commercially conditions that differ nutritionally at different liveweights to reflect the changing nutritional requirements of the animal as it develops. Studies of choice feeding pigs suggest that it is unlikely that a single diet could meet an animal's nutritional requirements at all times (Kyriazakis, Emmans and Whittemore 1990). Nutritionally inadequate diets have been shown to significantly alter the behaviour of pigs. Diets low in minerals or protein for fattening pigs result in increased exploratory behaviour (Jensen, Kyriazakis and Lawrence 1993) and tail-biting (Fraser 1987; Fraser, Bernon and Ball 1991). These studies show that specific nutritional needs increase the foraging motivation of growing pigs. This suggests that at some point in time every commercially fed pig will experience increased foraging motivation due to dietary deficiencies.

Lawrence and Terlouw (in press) suggest that stereotypies in sows arise in part from the inability of food motivated animals to express foraging behaviour. However, it is not only food restricted animals that perform abnormal behaviours relating to feeding (see Mason 1991). In zoo environments where food restriction is not usually practised many cases of abnormal behaviour have been reported (Morris 1964) and these behaviours have often been eliminated by the use of environmental enrichment that promotes the expression of appetitive foraging behaviour (for a review see Chamove 1989). This suggests that food restriction *per se* is not alone responsible for the performance of stereotypies and that the behavioural need to perform appetitive behaviour may also have an influence (see Hughes and Duncan 1988).

GENERAL THESIS AIMS

In this thesis the welfare of pigs is only considered in relation to their psychological well-being (Duncan and Petherick 1992). Although, research on stereotypic behaviour is often cited in this thesis, the aim was not to assess welfare by measuring the performance of abnormal behaviour. Thus, this thesis does not focus on such acute welfare problems, but rather on the motivation of animals to perform species-specific appetitive foraging behaviour, the thwarting of which may be causal in the development of abnormal behaviour (Hughes and Duncan 1988).

CHAPTER BY CHAPTER SUMMARY

The aim of the first experiment (Chapter 2) was to assess the use of computerised food intake recording (CFIR), which is presently being used by pig breeding companies for boar testing (Webb 1989). This Chapter considers the behavioural effects of providing groups of 10 pigs with one feeding space. Particular emphasis was placed on the patterns of feeding behaviour expressed by pigs in groups and the means by which pigs adapted to the competition for feeder access that resulted from social synchrony and facilitation (see Young and Lawrence, in press).

Chapter 3 investigates whether *ad libitum* fed sows have a behavioural need to perform foraging behaviour. This investigation used a contrafreeloading experimental paradigm where animals are offered the choice of acquiring food *ad libitum* either from a trough (free food) or making operant responses to obtain identical food (response contingent food; see Osborne 1977). Three hypotheses were tested regarding the origins of contrafreeloading; namely that it is a response to i) variability of information associated with food delivery ii) the magnitude of the food reinforcer and iii) the sensory quality of the food reinforcement.

Chapter 4 evolved out of the previous experimental chapter, where the design of the operant was thought to have affected the experimental results. This chapter therefore investigated the responses and choices of fattening pigs fed *ad libitum* in a barren environment offered first operant devices that apparently differed in how much species-typical foraging behaviour was required to operate them. The pigs were first offered these devices singly and subsequently as a choice. One of the operant devices was arbitrary in design (see Roper 1983), whilst the other was designed so that pig could operate it by a mixture of species-specific rooting and chewing responses.

The results of Chapter 4 suggested that designing operant devices around species-typical behaviour allowed for a more accurate assessment of feeding motivation. However, although in Chapter 4 it had proved possible to design an operant that allowed more species-typical foraging (i.e., rooting and chewing), one major component of normal foraging behaviour locomotion was omitted. Therefore a foraging device was designed (The 'Edinburgh Foodball'; see Young, Carruthers and Lawrence, in press) that allowed pigs to perform species typical foraging behaviour including locomotion. Furthermore the device was designed to deliver food in a manner that mimicked the distribution of food that free-ranging pigs might be expected to encounter (i.e., randomly in time, space and magnitude). The experimental investigation in Chapter 5 considered the Foodball's potential as an operant for measuring feeding motivation, its effect on the time budget of restrictively fed sows and its potential for environmental enrichment.

Chapter 6 closely examined the effect of The Edinburgh Foodball on the time budget of sows in relation to the rate at which the device delivered food to restrictively fed sows. The second objective of this experiment was to establish whether or not it was possible to restrict the food intake of pigs using the Foodball through the manipulation of reinforcement rate. The final objective was to quantify the foraging responses of pigs to a change in reinforcement rate and how this interacted with the expression of other behaviours; this last aspect was analysed in terms of behavioural resilience (see Houston and McFarland 1981).

Chapter 2

Feeding Behaviour of Pigs in Groups Monitored by a Computerised Feeding System

INTRODUCTION

The study of feeding behaviour has relevance to a number of scientific disciplines and an array of techniques have been developed for its measurement, for example total food intake can be measured by weighing the amount of food refused or spilt over a given time period (e.g., Kyriazakis, Emmans and Whittemore 1990). In addition to total food intake, information on individual meal size, meal duration, feeding rate and diurnal patterning of feeding can be obtained by computerised monitoring of operant feeding where a device such as a panel is pressed to obtain food (e.g., Bigelow and Houpt 1988). However, it has been shown that operant feeding can affect the feeding behaviour of animals, by reducing the number of meals consumed per day (Kissileff 1970). The use of infrared beams to measure the presence of the animal at the food trough, can yield data on diurnal patterning of feeding without modifying feeding behaviour (Hsia and Wood-Gush 1984). Although giving more natural measures of feeding behaviour, this technique cannot, accurately estimate meal sizes or feeding rate. One solution has been to use a continuously weighed food bin to give both diurnal patterning and information on discrete meals (Montgomery, Flux and Carr 1978). A further development has been to incorporate an electronic identification system into an off-centre weigh cell connected to a food bin (Nienaber, McDonald, Hahn and Chen 1991). This allows measurement of the individual feeding behaviour of animals in a group housed situation. However, such systems do not provide continuous recording but instead rely on a short scanning interval (30 secs in Nienaber et al 1991) and are therefore not entirely accurate at distinguishing individuals. Most of the above methods are not applicable to the study of the feeding behaviour of animals in groups and the one technique mentioned that is, has a lower accuracy than those techniques that can be applied to singularly housed animals. Consequently accurate information on feeding behaviour relates to individually housed animals.

Pigs fed under ad libitum conditions consume several discrete meals per day (Auffray and Marcilloux 1980). The amount of food consumed at a meal has been found to be positively correlated with the time to the start of the next meal (post-prandially correlated), but not for all individuals (Auffray and Marcilloux 1983). Meal frequency is 10.2 meals per day at 30-40kg and 8.1 meals per day at 60-70kg (Bigelow and Houpt 1988; see Schouten 1986 for a review of literature). Feeding rate is affected by housing condition; lowest in individually housed pigs (Bigelow and Houpt 1988), highest in competitively fed pigs (Tindsley and Lean 1984) and intermediate in group housed pigs (Feddes, Young and DeShazer 1989).

Pigs older than 6 weeks show strong diurnal patterning of food intake, with two peaks of feeding behaviour one at the beginning and one at the end of the light period (Feddes, Young and DeShazer 1989; Montgomery, Flux and Carr; Schouten 1986). The light period has a greater influence on the diurnal patterning of the feeding behaviour of pigs, than a diurnal change in temperature (Feddes, Young and DeShazer 1989). It has also been shown in both group and singularly housed pigs (Nienaber et al 1991; Nienaber, McDonald, Hahn and Chen 1990), that a server cold stress reduced feeding rate and meal duration, increased meal frequency and in group housed animals did not affect meal size.

The generality of this data on feeding behaviour of pigs must, however, be questioned, given the strong indications that social factors can influence feeding behaviour (see Chapter 1). For example group housed pigs often show synchronised feeding behaviour as a result of social facilitation (Hsia 1981). This can lead to feeder access competition in group housed animals provided with less feeding spaces than animals (Hansen, Hagelso and Madsen 1982; Hsia and Wood-Gush 1983).

Until recently there have been few techniques available with which to measure feeding behaviour of individuals in groups. The advent of computerised feeders using transponder technology for individual recognition originally developed for sow feeding systems (e.g., Edwards and Riley 1986), allows accurate recording of individual feeding behaviour, in group housing conditions, at a low cost per measurement (Webb, Brampton, Smith and Close 1990). Such computerised food intake recording systems, generally provide a single feeding space for small groups of 10 to 14 individuals, allowing one individual to feed at a time when a measurement of food intake can be made.

Computerised food intake recording systems for pigs have been developed to improve the accuracy of genetic selection. There is evidence that genetic correlations achieved on commercial farms are lower than expected from test station results (Merks 1988 cited in Webb 1989). The testing of selection lines is usually carried out on individually housed pigs, in contrast to conditions on commercial farms where pigs are group housed. Previous work on the effect of individual penning found that individually housed pigs gained weight significantly faster than group penned pigs (Patterson 1985). These differences, may be due to social behaviour, such as competitive behaviour at the food trough, not being expressed in the testing environment (Webb 1989).

Pigs that live in stable social groups show a definite hierarchy (Ewbank 1976) and low levels of aggressive behaviour (Ewbank, Meese and Cox 1974). Hierarchy formation appears to start almost immediately after birth when piglets can be seen to aggressively defend a teat on their mother (Ewbank 1976). Heirarchies in pigs may be linear, complex linear or triangular (Ewbank 1976; Hsia 1981). Aggression appears to be regulated by subordinate pigs spatially avoiding dominant ones (Jensen 1982). Aggression in stable groups is normally only associated with the presence of localised and limited resources such as food or a mate (Schnebel and Griswold 1983; Stolba and Wood-Gush 1989). Some studies of dominance in the domestic pig have reported that the heaviest member of the group and males are most dominant (Beilharz and Cox 1967; Tindsley and Lean 1984), however, Meese and Ewbank 1973 found no such relationships. It has been found that the presence of a 50% larger animal in a group of pigs suppresses aggression (Szekely et al. 1983; Rushen 1987). Heirarchies in pigs are not maintained by sight alone and pheromone production may be involved (Ewbank et al. 1974).

In a farm situation fighting most frequently occurs during the mixing of unfamiliar pigs and normally lasts up to 24 hours, after which the social hierarchy stabilises (Ewbank 1976). Periods of aggressive behaviour result in an increased in feeding rate (Tindsley and Lean 1984) and are followed by decreases in production traits such as growth rate, food conversion efficiency and food intake (Ewbank 1976; Tan et al. 1991). Fighting between pigs normally involves bites, and butts with the head to the head and face of the other pig (McGlone 1985; Rushen and Pajor 1987). A fight may be ended by a pig performing submissive behaviour (turning its body away from the attacking pig; McGlone 1985) or by a pig giving up from fatigue (Rushen and Pajor 1987). Fights last longer when the body weight of two pigs are similar and when a losing pig continues to retaliate (Rushen 1987). Large variation in body weight has been found to reduce aggression when mixing unfamiliar pigs (Rushen 1987). Tranquillisers reduce aggression when unfamiliar pigs are first mixed but when their effect wears off fighting occurs (Csermely and Wood-Gush 1990; Tan et al. 1991), the use of sedatives has been more successful in reducing fighting (Bjork et al 1988). Although, aggression in farm housed pigs is normally associated with the mixing of unfamiliar individuals, the current trend to use feeding systems that provide less feeding places than pigs also increase fighting (Nienaber et al. 1991; present study).

In addition to their relevance to animal breeding, computerised food intake recording systems also provide the important opportunity to measure the effect of social factors on feeding behaviour. This chapter presents results of feeding behaviour of pigs maintained in groups, and obtaining food from a computerised food intake recording system. Evidence is presented to suggest that social factors have a considerable impact on feeding behaviour of pigs in this system.

MATERIALS AND METHODS

Animals, allocation to group and housing

The animals were 30 male and 30 female sexually immature juvenile Large White X Landrace pigs (Cotswold Pig Development Co. Ltd, Lincoln, UK). They originated from several litters, which had been mixed at random.

At 15 weeks of age the pigs were weighed and divided up into six groups of ten, balanced for sex and initial body weight (mean 32.1kg), within a pen, but not between pens. Whilst being weighed each pig also had a transponder ear tag inserted to enable individual identification by the computerised food intake recording system.

The experimental house was an open fronted building and therefore the pigs were exposed to natural light and temperature levels (experiment carried out between November and December). The pens containing the computerised food intake recording systems equipment each had an open area measuring 4.6m x 2.8m where the feeding stall and a bowl drinker were located, and an insulated kennel area measuring 2.4m x 2.1m and 1.2m high (Figure 2.1).

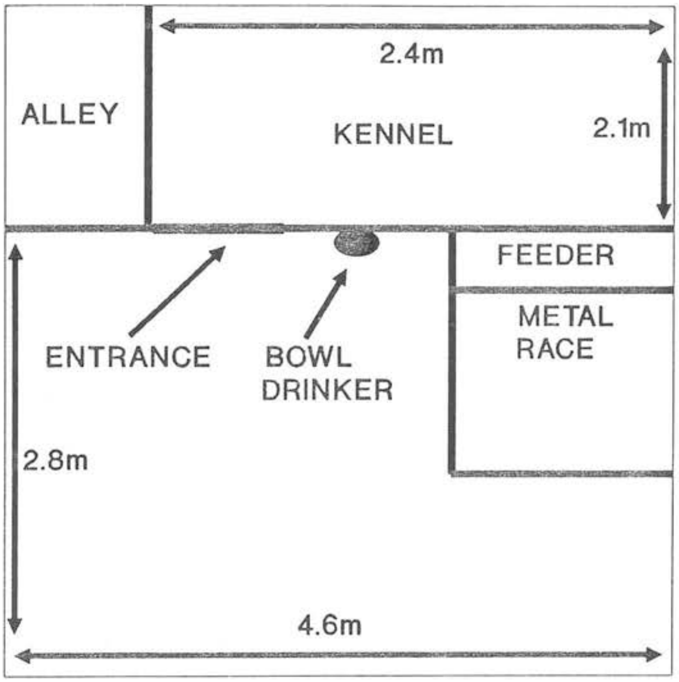
Acclimatisation

Prior to the start of the trial, pigs were maintained within the experimental house and offered food from multi-space feeding troughs. After weighing they were moved to pens containing the computerised food intake recording systems equipment. The pigs were allowed 2 weeks in which to become accustomed to the computerised food intake recording system (Feed Intake Record Equipment, F.I.R.E. system developed by Hunday Electronic Ltd, Newcastle Upon Tyne, UK) before any feeding behaviour was recorded. The object was to remove any differential effects that learning the system might have on recorded feeding behaviour.

Management and food composition

Before the trial began, the weighing system of each feeding stall was calibrated, by the manufacturers recommended method to an error of less than 2 percent on each delivery of food (FIRE 2.22D software manual, Hunday Electronics Ltd, Newcastle Upon Tyne). The food in the feeder was replenished every day at 0900h.

Figure 2.1: Experimental pen layout



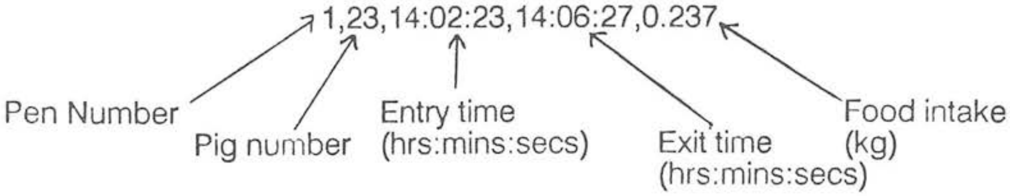
Each pen was cleaned every other day and fresh straw was provided daily. The pigs were weighed once a week. During the experiment two transponders failed and the data for these two animals were lost.

The pigs were offered a standard pelleted growers food, each kilogram containing 14MJ of digestible energy, 203g of crude protein, 44g of crude fibre, 40g of oil, 67g of ash and 870g of dry matter.

Data recording

Each feeding stall allowed access to only one pig at a time. When a pig visited the stall it was identified by its transponder tag, and its entry and exit times and the amount of food consumed (see below) were logged by a control box, and subsequently transferred to a personal computer. Records of this type were generated continuously by individual pigs, on the feeding system, for an average of 38 days per pig.

Example of a pig visit record by the computerised feeding system;



STATISTICAL ANALYSIS

Data were primarily analysed by analysis of variance, using the ANOVA facility of SPSS-X (version 3.0; SPSS-X 1986). The normality of each variable was assessed using the NSCORE facility of Minitab (version 6.1.1;

see Ryan, Joiner and Ryan 1985). The data, with the exception of the frequency of feeder visits, which was transformed to natural logarithm +1, were square root transformed to normality to meet the requirements for parametric statistics.

All the variables considered in the analyses were averages for individual pigs, to avoid repeated measures in the analyses. The six variables used were mean feeder occupation time per feeder visit, mean feeding rate per feeder visit, mean food intake per feeder visit, mean frequency of feeder visits per day, total feeder occupation time for 38 days and total food intake for 38 days. The covariate used was initial body weight of the pigs immediately prior to the start of the acclimatisation period. The factors used were pen, sex and time of day.

Three non-feeding variables were also used in the analysis, the total number of non-feeding visits, the mean amount of time the feeder was occupied during a non-feeding visit and the total duration of all non-feeding visits. The total number of non-feeding visits (log transformed) was also analysed by analysis of variance using time of day as a factor.

For each pig pre-prandial (the time between a feeder visit and the following meal size) and post-prandial (present meal size with the time to the next meal) correlations were calculated (for a discussion of prandial correlations see Le Magnen 1985). Each pig was classified depending on which significant positive ($p<0.05$) correlation it showed. This classification was then used as a factor in an analysis of variance on the variables used previously. Again initial body weight was used as the covariate.

A number of authors (e.g., Machlis 1977) have pointed to the importance of distinguishing intra-meal feeding from inter-meal feeding in order to be able to define a meal. Thus, the time between feeder entries were analysed by log survivorship (see de Haer and Merks 1992) and by log frequency analysis (see Sibly, Nott and Fletcher 1990).

The feeder entries within each pen with the exception of pen 4 where two transponder tags failed, were analysed to determine whether the entries of individual pigs were random events (see Stricklin and Gonyou 1981). This was done by lagging (moving all cases in a column of data down by a given number of rows) the sequence of feeder entries by one and performing a Chi-square test against the original data. Thus producing a Chi-squared table of standardised residuals for the next pig to visit the feeder in relation to the pig that had previously visited the feeder.

The data for all the feeding and non-feeding variables, initial body weight, gain in body weight and non-feeding visits variables were analysed by Pearson's linear correlation and multiple linear regression analysis, using Minitab (version 6.1.1; see Ryan, Joiner and Ryan 1985). All constants and predictors given in linear regression results are significant ($p<0.05$). It should also be noted that linear regression equations given in the results section, are there for explanatory purposes and not for prediction.

RESULTS

Effect of Pen and Sex

All the variables except total food intake (F= 0.9; d.f. 5,57; p= 0.46) were significantly affected by pen (F-values for mean feeder occupation time, total feeder occupation time, mean feeding rate, mean food intake and mean frequency of feeder visits: 5.1, 3.4, 11.7, 6.2, 2.9; all d.f. 5,57; $p<0.05$). This suggests that although all pens achieved the same total food intake they did so by significantly different methods of feeding behaviour. Sex had no significant effects but strong trends were observed for mean feeder occupation time (F= 3.8; d.f. 1,57; p= 0.059) and mean food intake (F= 4.0; d.f. 1,57; p= 0.052), with males tending to have shorter feeder visits than females and consuming less food.

Effect of Time of Day

To establish the effect of time of day, the six feeding variables were averaged for each hour of the day, each pig having 24 records. The effect of time of day (see Figures 2.2 to 2.5) was significant for all variables (F-values: for mean feeder occupation time, total feeder occupation time, mean feeding rate, mean food intake, total food intake and mean frequency of feeder visits: 6.7, 34.0, 4.0, 4.7, 4.1, 60.7; all d.f. 23,1391; $p<0.001$). T-Tests were used on adjacent time values for the six variables, to determine when the most significant changes were occurring. Between 0600 and 0900h the mean frequency of feeder visits increased significantly each hour (t= -3.6; d.f. 109; $p<0.001$ lowest value observed) whereas mean feeder occupation time decreased between 0800 and 0900h ($t = 2.1$; d.f. 111; $p < 0.05$). Also between 0800 and 0900h mean feeding rate was tending to increase ($t = -1.8$; d.f. 112; $p = 0.08$) and mean food intake to decrease ($t = 1.5$; d.f. 108; $p = 0.15$). All 6 variables were significantly correlated to each other (Table 2.1) and appeared to change in response to each other. After 0800h food intake bouts decreased in size and duration, but occurred at a greater frequency and were consumed at a higher feeding rate. An opposite, but not such a strong effect was seen between 1600 and 1700h when only mean frequency of feeder visits was found to decrease significantly ($t = 3.8$; d.f. 106; $p < 0.001$). At this time of day the other variables only changed significantly if longer time periods than 1 hour were considered, suggesting that the changes in the morning occurred at a faster rate than the changes in evening feeding behaviour.

Effect of Prandial correlations

Sixty percent of all pigs showed no type of prandial regulation, of those with prandial regulation 26% showed post-prandial (mean r value= 0.101; range= 0.06 to 0.157), 10% pre-prandial (mean r value= 0.096; range= 0.058 to 0.153) and 4% both types of correlation (mean r value= 0.165; range= 0.128 to 0.201). A significant relationship was found between type of prandial correlation and total feeder occupation time ($F = 2.9$; d.f. 3,57; $p < 0.05$), mean frequency of feeder visits ($F = 3.4$; d.f. 3,57, $p < 0.05$) and as a trend mean food intake ($F = 2.1$; d.f. 3,57, $p = 0.108$) with pre-prandially correlated pigs occupying the feeder longer, consuming larger meals and making fewer feeder visits than those showing post-prandial, non-prandial or both pre- and post-prandial correlations.

Table 2.1: Correlation matrix of the feeding variables in relation to time of day (n=24)

	MFR	MFO	TFI	MFV	MFI
MFO	-0.753				
TFI	0.815	-0.867			
MFV	0.820	-0.955	0.966		
MFI	-0.568	0.950	-0.746	-0.746	
TFO	0.815	-0.867	1.000	0.966	0.746

All values are significant to p<0.01. (MFR= mean feeding rate; MFO= mean feeder occupation time; TFI= total food intake; MFV= mean frequency of feeder visits; MFI= mean food intake; TFO= total feeder occupation time).

Table 2.2: Frequencies and standardised residuals of selected pigs within pen 1 following or not following each other into the feeding stall

Pig		2	6	10	12	15	16	25	31	33	41
31	O	40	42	28	48	75	43	47	147	43	15
	E	46.2	60.1	38.1	42.1	67.3	55.2	56.0	85.5	46.2	32.1
	R	-0.9	-2.3	-1.6	0.9	0.9	-1.6	-1.1	6.6	-0.5	-3.0
33	O	39	27	16	23	36	22	36	53	13	20
	E	25.0	32.5	20.6	22.8	36.3	29.8	29.7	46.1	25.0	17.3
	R	2.8	-1.0	-1.0	0.1	-0.1	-1.4	1.2	1.0	-2.4	0.6
41	O	20	27	18	15	22	27	23	13	22	11
	E	17.3	22.6	14.3	15.8	25.2	20.7	20.6	32.1	17.3	12.0
	R	0.6	0.9	1.0	-0.2	-0.7	1.4	0.5	3.4	1.1	0.3
Total Obs.		285	371	235	260	415	340	339	528	285	199

A selected data set showing the relationship between the heaviest pig (31) and the lightest (41). Pigs on the horizontal axis are following pigs on the vertical axis into the feeding stall. A positive standardised residual greater than 2 indicates a strong following relationship and a negative residual less than 2 a non-following relationship (Cell layout; O= Observed frequency, E= Expected frequency and R= Standardised residual).

Figure 2.2: The relationship between total number of feeder visits, mean food intake and time of day

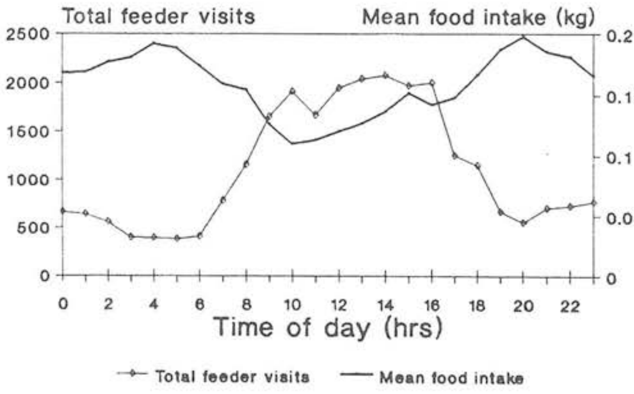


Figure 2.3: The relationship between mean feeding rate, mean feeder occupation time and time of day

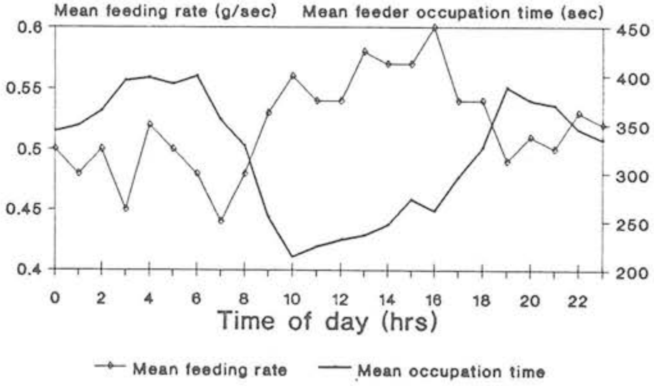


Figure 2.4: The relationship between total food intake and time of day

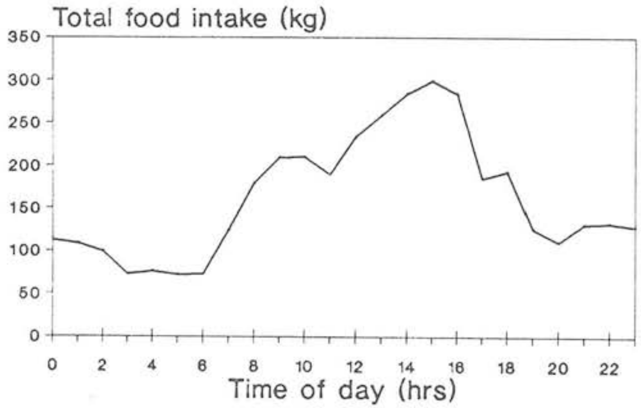
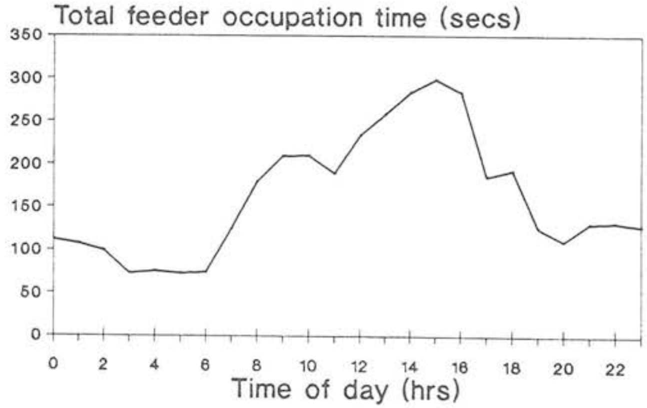


Figure 2.5: The relationship between total feeder occupation time and time of day



However, type of prandial correlation observed had no significant effect on total food intake and was not significantly related to body weight.

Log survivorship analysis and log frequency analysis

These analyses produced a wide spectrum of curves and it proved impossible to objectively classify these into different curve types (see Begon, Harper and Townsend 1986) or to determine the bout criterion interval (see Martin and Bateson 1986). Consequently the analyses were not used to classify meal sizes, meal intervals or meal duration and the mean food intake variable used here should not be regarded as equivalent to a meal.

Frequency of feeder entries

The mean frequency of feeder visits for all pigs was 12, the number of daily feeder entries ranged from 3 to 69 per day. When the total number of non-feeding visits were removed the average became 11 and the daily range of feeder visits 3 to 65. Non-feeding feeder visits accounted for 10.5% of all feeder visits.

The greatest mean frequency of feeder visits appeared to be made by the heaviest pigs and the smallest mean frequency of feeder visits by the lightest pigs (see Table 2.2; pig 31 heaviest and pig 41 lightest). However, initial body weight and mean frequency of feeder visits were not found to be significantly correlated (see Table 2.3). Pigs with the highest mean frequency of feeder visits had the lowest mean feeder occupation time and mean food intake, that is they made a high frequency of short duration feeder visits and consumed only a small amount of food per feeder visit (Table 2.3).

Sequence of feeder entries

The analysis of feeder entries found that entries were non-randomly distributed (Chi-square values 192.3, 2001.4, 340.3, 638.1 and 352.6 for pens 1 to 3 and 5 to 6 respectively, all d.f. 81; $p<0.001$). However, there was no other easily discernible pattern to feeder entries in relation to bodyweight.

Analysis of production parameters

The covariate initial body weight significantly affected total food intake ($F= 4.2$; d.f. 1,57; $p<0.05$), mean food intake ($F= 7.7$; d.f. 1,57; $p<0.01$) and mean feeding rate ($F= 20.8$; d.f. 1,57; $p<0.001$). However, although initial body weight and gain in body weight were significantly positively correlated together, gain in body weight was more highly positively correlated with total food intake and total feeder occupation time than initial body weight (Table 2.3). Linear regression analysis showed that as predictors of total food intake, initial body weight accounted for 9.4% and gain in body weight 59.0% of the variance. The best single predictor of total food intake was total feeder occupation time accounting for 24.6% of the variance.

Table 2.3: Correlation matrix of feeding and non-feeding variables, initial body weight and gain in body weight (n=58)

	MFR	MFO	TFI	MFV	MFI	TFO	TNF	MNF	DNF	IBW
MFO	-0.267^{a}									
TFI	0.211	0.261^{a}								
MFV	0.082	-0.745^{c}	0.069							
MFI	0.140	0.875^{c}	0.401^{b}	-0.782^{c}						
TFO	-0.592^{c}	0.270^{a}	0.509^{c}	0.247	-0.043					
TNF	-0.385^{b}	-0.432^{b}	-0.021	0.637^{c}	-0.552^{c}	0.352^{b}				
MNF	-0.445^{b}	-0.013	-0.149	0.030	-0.193	0.267^{a}	0.365^{b}			
DNF	-0.568^{c}	-0.134	-0.100	0.246	-0.350^{b}	0.410^{b}	0.652^{c}	0.887^{c}		
IBW	0.388^{b}	0.070	0.331^{a}	-0.093	0.315^{a}	-0.213	-0.238	-0.276^{a}	-0.254	
GBW	0.169	0.148	0.773^{c}	0.010	0.273^{a}	0.341^{b}	-0.134	-0.181	-0.185	0.280^{a}

^{a}= $p<0.05$; ^{b}= $p<0.01$; ^{c}= $p<0.001$. (MFR= mean feeding rate; MFO= mean feeder occupation time; TFI= total food intake; MFV= mean frequency of feeder visits; TFO= total feeder occupation time; TNF= total number of non-feeding visits; MNF= mean duration of non-feeding visits; DNF= total duration of non-feeding visits; IBW= initial body weight; GBW= gain in body weight).

Multiple linear regression analysis of the variables in Table 2.3 on total food intake, showed that 88.8% of the variance could be accounted for by the following three variables mean food intake, mean feeder occupation time and total feeder occupation time (regression equation: total food intake = 9697 + 339(mean food intake)-173(mean feeder occupation time) + 0.429(total feeder occupation time)).

The average daily growth rate for pigs in this experiment was 922g/day. gain in body weight was only significantly predicted by its reciprocal relationship with total food intake, which accounted for 59% of the variance in gain in body weight (regression equation: gain in body weight = 9.22 + 0.000384(total food intake)).

The average food conversion efficiency was 0.53 (±0.0079). Food conversion efficiency was significantly negatively correlated with total food intake ($r = -0.343$; $n = 58$; $p < 0.01$) and positively correlated with gain in body weight ($r = 0.323$; $n = 58$; $p < 0.05$). Thus, pigs that consumed the most food apparently utilised it least efficiently and pigs that gained the most body weight the most efficiently. None of the feeding variables were useful in predicting food conversion efficiency.

Feeding rate and non-feeding visits

Feeding rate was positively correlated with initial body weight, but linear regression analysis showed that initial body weight only accounted for 13.6% of the variance in feeding rate and was not a significant predictor. Therefore feeding rate could not be explained by a simple body weight relationship.

All non-feeding variables were significantly negatively correlated with mean feeding rate and positively correlated with total feeder occupation time (Table 2.3), suggesting that those pigs which consumed food at the fastest rate made the fewest non-feeding visits.

Total number of non-feeding visits showed a significant time of day effect ($F= 3.96$; d.f. 23,1391; $p<0.001$). However, total number of non-feeding visits was significantly positively correlated with mean frequency of feeder visits in relation to time of day ($r= 0.951$; $n= 24$; $p<0.001$) and significantly correlated overall (see Table 2.3). Linear regression analysis showed that mean frequency of feeder visits accounted for 90.0% of the variance in total number of non-feeding visits (regression equation: total number of non-feeding visits= -38.8+0.1763(mean frequency of feeder visits)). Thus, the diurnal pattern of total number of non-feeding visits was a consequence of its correlation with mean frequency of feeder visits.

The comparable feeding and non-feeding variables were compared by paired t-tests. It was found that total number of non-feeding visits was significantly smaller than the total number of feeder visits ($t= -16.04$; d.f. 65; $p<0.001$). Mean duration of non-feeding visits was significantly smaller than mean frequency of feeder visits ($t= -13.68$; d.f. 92; $p<0.001$) and that total duration of non-feeding visits was significantly smaller than total feeder occupation time ($t= -31.85$; d.f. 62; $p<0.001$). Thus non-feeding visits occurred at a lower frequency, at a shorter average and a shorter total duration than feeding visits.

DISCUSSION

Previous data on pig's feeding behaviour is largely from individually housed animals. The present results differ in some important respects. First, only a single peak in feeding behaviour was observed, in the middle of the light period whereas previous work has reported peaks at the start and the end of the light period (Montgomery, Flux and Carr 1978; Schouten 1986). The frequency of feeder entries was considerably more variable than those reported in any previous study (see Schouten 1986). In this study pigs were found to show a range of types of meal regulation pre-, post-, non- and both pre- and post-prandial regulation in contrast to previous work which largely found post-prandial correlations in pigs (Auffray and Marcilloux 1983). The sequence of feeder entries was found to be highly structured. There are a number of potential factors, that may explain these results. Evidence points towards the importance of social facilitation and competition effects on feeding.

There are several possible explanations for the single peak in feeding behaviour reported here. First, it could be an entrained response to the fluctuations in light and ambient temperature. However, the lighting and thermal conditions in this experiment did not differ greatly from those in experiments where two peaks have been reported (e.g., Montgomery, Flux and Carr 1978; Bigelow and Houpt 1988). Second auditory cues can also be important stimuli for feeding where they are associated with the presentation of food (Carlstead 1986). However the peak in feeding activity occurred some 3 to 4 hours after the commencement of farm activity (0800h) and replenishment of the hoppers (0900h). Last, the peak in feeding activity could be due to social synchronization and facilitation. Social animals tend to show synchrony of behaviour and a number of studies have suggested that other group members can temporarily facilitate feeding behaviour and increase food intake (e.g., Hsia 1981).

The diurnal changes observed in feeding behaviour are not however, explainable solely in terms of social synchrony and facilitation. During the single peak in feeding activity pigs increased their number of feeder visits and decreased their average time in the feeder. They also tended to increase feeding rate and decrease food intake per visit. Feeding rate has previously been shown to increase with competition (Gonyou and Stricklin 1981), and the observed feeding rate in this study was equivalent to that measured under competitive (aggressive) conditions (Tindsley and Lean 1984). Other studies have shown that competition for feeder access can occur with only four (Nienaber, McDonald, Hahn and Chen 1991) or five (Hansen, Hagelso and Madsen 1982) pigs per feeding place. In the present study with 10 pigs per feeding place it seems likely that the tendency for pigs to synchronise their feeding behaviour and the restrictions on feeder access increased social competition with consequent changes in feeding behaviour. The slower changes in evening feeding behaviour are most likely to result from a relaxation in social competition. Evening feeding may have been performed by pigs that were unsuccessful at competing for feeder access during the light period.

When the increases and decreases in feeding variables in relation to time of day are combined they tend to cancel one another out. This is illustrated by the fact that although pens differed in methods of feeding behaviour, they achieved the same total food intake. This implies that the average pig was able to behaviourally compensate for the environmental, social and physically restrictions it encountered. The compensation may have been through varying the temporal patterning of feeding or by altering regulation of meal size and frequency (see below).

Further evidence for social competition is found in the analysis of prandial correlations. It has been suggested that animals with a significant positive pre-prandial correlation are regulating food intake by a satiety mechanism, whilst those with significant positive post-prandial correlations with by a hunger mechanism (Savory 1981). In a previous study pigs showed post-prandial regulation (Auffray and Marcilloux 1983), which is typical of nearly all species (for a review see Le Magnen 1985) except humans (DeCastro 1988) and weanling rats (DeCastro and Balagura 1976) who show pre-prandial regulation. Adults rats that normally show post-prandial regulation (Balagura and Coscina 1968) can show pre-prandial regulation by scheduling a smaller number of meals per day than a rat would consume when free feeding (DeCastro 1988). Thus pre-prandial regulation can be a result of large infrequent meals resulting from external scheduling constraints.

It is inferred that pigs with post-prandial regulation, those showing the type of correlation previously reported for singularly housed pigs (Auffray and Marcilloux 1983), were less affected by the prevailing experimental conditions than those with the pre-prandial correlations. Pigs with pre-prandial correlations may have been unable to feed freely during peak feeding activity and therefore forced into feeding at other times when they consumed large amounts of food. Pigs with no prandial correlations or both were most likely to be a result of pigs feeding in a random manner. Thus, although all animals were exposed to the same physical environment, individuals experienced different social constraints in that environment. Type of prandial correlation may then be a measure of the behavioural control a pig has over its feeding behaviour where social competition interferes with feeder access.

Other evidence for the influence of social competition on feeder related behaviour was the high frequency of non-feeding visits. These might have resulted from attempts to defend the feeder but this seems unlikely given their short duration. It seems more probable that these short non-feeding visits resulted from pigs being physically displaced from the feeder before they could consume any food. Social competition may also have been responsible for our inability to define meals using log survivorship and log frequency, through the substantial number of arbitrary meal terminations arising from disputes over feeder access. One study of group housed pigs using a computerised food intake recording system has reported being able to define a meal criterion (de Haer and Merks 1992) using log survivorship analysis. However, the difficulty in using a meal criterion approach on feeding data from group housed animals is illustrated by de Haer and Merks (1992) using a common meal criterion of 5 minutes for all animals, when a number of studies (e.g., Slater 1974; the present work) have reported large individual differences in meal patterns.

The only consistent result from the analysis of feeder entries was that the largest pig in each pen followed itself into the feeder significantly more than by chance. However, body weight was not related overall to the sequence of feeder entries, although it has been found to be related to social dominance (Beilharz and Cox 1967; Tindsley and Lean 1984). At present we can only speculate on the highly structured sequence of feeder entries. Possible explanations of this phenomenon are an avoidance order base on a social hierarchy (Jensen 1982), kin recognition (see Hepper 1991) or other types of affiliative bonds (e.g., Stricklin and Gonyou 1981).

In general terms successful adaptation to the system appears to be measured by total feeder occupation time, as pigs which spent longest in the feeder consumed most food. Growth rate was strongly related to total food intake. There were however, a number of means by which pigs could achieve a high total feeder occupation time, for example by having a few visits of long duration or the reverse. The present study does not allow us to separate these different possibilities. The behavioural processes that result in longer occupation times requires further attention.

The results of this study suggest that social synchrony and facilitation of feeding behaviour in combination with the use of a single feeding place results in competition for feeder access. The consequences of this were apparently changes in the temporal patterning of feeding behaviour and alteration of feeding variables. The result suggest that type of meal regulation might also be altered by social conditions and care needs to be exercised therefore in the use of meal criterion. Social competition appeared to affect physical performance in the system most strongly through its influence on total feeder occupation time and food intake.

Chapter 3

Investigations of contrafreeloading in pigs

GENERAL INTODUCTION

At present there is considerable public concern about the effects of intensive housing systems on the behaviour and welfare of domestic livestock. In particular there is concern about animals being unable to express natural patterns of behaviour under commercial conditions (e.g., Hughes and Duncan 1988). Livestock housed under intensive conditions, are provided with many of their functional needs (i.e., they have no major physiological deficits), thereby often reducing the need to perform appetitive behaviours. Broom (1987) for example notes that the need to find food for many farm animals under intensive conditions has been removed. However, animals under these conditions are often observed performing appetitive behaviours. For example, starlings show a preference for food that requires searching rather than eating the same food free (Inglis and Ferguson 1986) and rats prefer to handle than wait for food (Shettleworth and Jordan 1986). Also it has been shown that domestic fowl (Hughes, Duncan, Brown 1989) and pigs (Arey, Petchely and Fowler 1992) prefer to construct a new nest rather than use an artificial nest or even a nest that they have previously constructed. This implies that the performance of certain behaviours may in themselves be reinforcing (Hughes and Duncan 1988; also see Chapter 4).

Currently, scientists are divided about whether not being able to express natural behaviour patterns reduces animal welfare. Baxter (1983) for example, suggests that if the end-point of a behaviour is adequately provided for, then the animal will have no motivation to perform that behaviour and therefore there will be no reduction in welfare if the behaviour is prevented. This argument may be untestable if only the individual animal can decide when the end-point of a behaviour is adequately provided for. Given that lines of identically selected livestock show considerable individual differences in their preferences (e.g., Petherick, Waddington and Duncan 1990), this theory even if correct cannot be practically used to forward animal welfare. Many animal welfare researchers believe that the performance of behaviour is important to maintain a good level of welfare (e.g., Hughes and Duncan 1988) and there is evidence to support this viewpoint based on the misbehavior of animals (e.g., Breland and Breland 1961; Timberlake 1984), contrafreeloading studies (see Osborne 1977) and from the general psychological literature (for a review see Gardner and Gardner 1988).

'Contrafreeloading' is a direct test of the hypothesis that the performance of behaviour is rewarding to animals and has therefore been used in this series of experiments. When offered the choice between performing an operant response to obtain food, in the presence of identical continuously available free food, animals often choose and may prefer to make an operant response (contrafreeload; Tarte 1981). This choice can be interpreted as evidence that the performance of the operant behaviour is in itself reinforcing (Hughes and Duncan 1988; Hughes, Duncan and Brown 1989).

The phenomenon of contrafreeloading contradicts the least effort hypothesis of animal learning and behaviour (see Osborne 1977), because animals are apparently not exploiting the most profitable source of reinforcement. The results of studies where animals show low levels of contrafreeloading could be explained by sampling behaviour (see Krebs and McCleery 1984; Dow and Lea 1987; this phenomenon maybe related to information-primacy discussed below) or partial preferences (the most energetically profitable food source is sometimes accepted and sometimes rejected possible explanations of this phenomenon are discussed by McNamara and Houston 1987). However, the levels of contrafreeloading in most studies are too high to be explained by these phenomena (see Osborne 1977). Contrafreeloading was originally ascribed to the intrinsic appeal of performing the operant (Jensen 1963). More recently the phenomenon has been considered in relation to reinforcement theory (Osborne 1977). An evolutionary explanation of the phenomenon is that the genetic ancestors of domestic livestock evolved in environments where the performance of appetitive behaviour was essential to survival and that the effects of artificial selection has not altered this genetic programming (see Barrett 1978; Stolba 1988). The phenomenon of contrafreeloading has also attracted the interest of applied ethologists as a method of assessing the requirements of animals to perform appetitive behaviour (Duncan and Hughes 1972).

A review of contrafreeloading experiments by Osborne (1977) suggested that contrafreeloading could be explained as the result of experimental artifacts. For example, in many of the studies animals were only trained to feed from the operant food source, even when neophobic subjects such as rats were used (see Mitchell, Scott and Williams 1973; Mitchell, Williams and Sutter 1974). The present study has therefore been designed around the criticisms of Osborne (1977) in an attempt to eliminate the effect of such confounding factors.

The hypothesis of the present experiment was that performance of appetitive foraging is reinforcing in the pig. To test this hypothesis pigs were offered the choice between performing a simple appetitive behaviour, pressing a panel with their snout to obtain food, or eating identical food available *ad libitum* from a trough. Three alternative explanations for the causation of contrafreeloading based on previous work were tested: (a) contrafreeloading is based on a requirement to obtain information on the environment; (b) contrafreeloading is a response to the positive feedback effects of the food reward; (c) contrafreeloading occurs because of secondary reinforcement from the stimulus change associated with the behaviour. The following experiments have implications for the provision of opportunities to express appetitive behaviours for animals kept with no major physiological deficits, such as those in zoos, laboratories and certain farm animals.

GENERAL MATERIALS AND METHODS

Animals

The same six Large White X Landrace (Cotswolds Pig Development Company Ltd, Lincoln, U.K.) nulliparous gilts (sexually mature young adults) were used in all experiments. They had an initial mean body weight of approximately 150 ± 5kg.

Food and Management

In all experiments pigs were offered a standard pelleted sow food each kilogram containing 13.2MJ/DE, 170g of crude protein, 53g of crude fibre, 40g of oil, 63g of ash and 870g of dry matter.

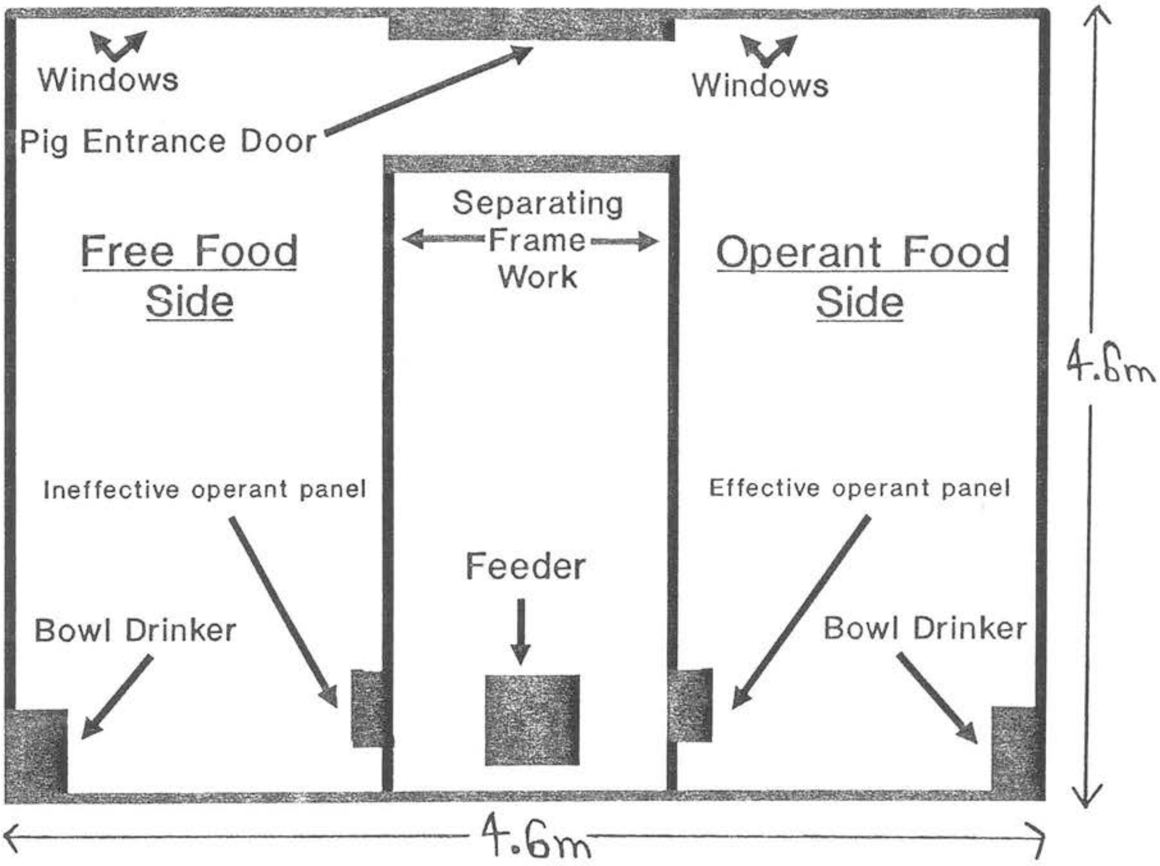
Whilst in the holding pens the animals were cleaned out every day between 0900h and 0925h, and offered an *ad libitum* supply of fresh food at 0930h. Experimental rooms were cleaned out in periods between training and testing. They were also cleaned if an animal had urinated or defecated near, on or into the experimental apparatus.

Experimental housing, temperature and lighting

At 90kg of body weight the animals used in this experiment were moved to the experimental unit (detailed in Hsia 1981) containing 3 experimental, and 2 holding rooms. Three animals were placed in each holding room, each of which contained four individual pens. The pens measured 1.8m x 2.3m and had a concrete floor to the front with slats to the rear. Drinking bowls were placed to the rear over the slatted area. The experimental rooms measured 4.6m x 4.6m with a central area (3.6m x 1m) penned off from the pigs, where the operant feeder was housed (Figure 3.1). Drinking bowls were located in all four corners and water was available *ad libitum*.

All rooms were maintained on a 12:12hr light-dark cycle (lights on at 0800h) and maintained at $20 \pm 2^{o}C$. In the holding rooms the animals were floor fed *ad libitum*.

Figure 3.1: Experimental room layout for Experiments 3.1 to 3.3



The animals were maintained in these rooms for 60 days prior to experimentation.

Experimental apparatus

The operant device the animals were conditioned to use in this experiment, was a single sprung metal panel, measuring 0.3m^2 similar to that described in Lawrence et al 1988. Operation of the panel required an animal to push the panel towards a metal frame a distance of 0.015m against two internal metal springs, requiring a force of 356N/m. The amount of force required to operate the panel gave the panel a positive action and made operation by accidental touches unlikely. The panel was mounted 0.72m above the floor and set at an angle of 45^o from the vertical, inclining towards the animal. The operant panel was situated immediately above the food trough (see Figure 3.1).

Food was delivered into the food trough, by a feeder (Orby Engineering Ltd, Co. Armagh, Northern Ireland; modified by the Scottish Centre for Agricultural Engineering, Edinburgh). The operant device and the feeder were interfaced and controlled by a micro-computer (BBC model B, Acorn Electronics, out of production).

The free food trough was identical to the operant food trough. Above this trough was placed an ineffective operant panel, which was identical to the effective operant panel, except that it was non-functional and acted as a control for the effective panel. Thus both food sites appeared visually identical. The feeder was situated half way between the effective operant panel and free food trough, enclosed within a metal frame.

As an attempt to eliminate auditory stimulus change associated with operation of the feeder and external sources of sound white noise was played in the experimental rooms at a level of 60 to 65 decibels. Each of the three experimental rooms had identical experimental arrangements as described above.

Operant training

Food was removed from the animals at 1700h on the day prior to training. At 0930h the following day before feeding the test animals were moved to one of the experimental rooms. The animals were locked into the side of the room containing the effective operant panel and allowed to shape for 4hrs on a fixed ratio (FR) of two or a variable ratio (VR) of two for a 30g food reinforcer. The ratio was then reversed and the pig left for a subsequent 4hrs, this training procedure was balanced across pigs.

Experimental Training

The animals spent the 24hrs after operant training in their home pen. During the next 48hrs, the animals were familiarised equally with the experimental arrangements. Three pigs were locked for 24hrs in the side of the room where food could only be obtained operantly on a VR5 yielding 30g of food each reinforcer or on the free food side for 24hrs with food available *ad libitum* from a trough. For the subsequent 24hrs the animals were then switched between sides, such that an animal, that had been on the operant side was moved to the free food side and vice-versa. After the familiarisation period, the pigs were returned to their home pens and floor fed *ad libitum* for 24hrs.

Data recording

The occurrence and timing of all panel presses (both effective and ineffective), and food reinforcer deliveries were all recorded by the micro-computer. Food remaining in the free-food trough was weighed once every 24hrs at 1000h, any food remaining in the operant trough was also weighed at this time. The food for both feeding sites was identical in composition and was always from the same batch. Care was taken that the food in the feeder's hopper was not more than 24hrs old.

EXPERIMENT 3.1

The effect of operant ratio variability on contrafreeloading.

INTRODUCTION

Information is important to animals foraging in stochastic environments (see Krebs and McCleery 1984). It has been demonstrated that animals are sensitive to variance in food supply (which may be equated to information) and are able to make adaptive foraging decisions based on this information (e.g., risk sensitivity; see Real and Caraco 1986). It has been shown that great tits perform sampling behaviour to obtain information that allows them to maximise food intake by moving to food patches in the order of highest food density (Smith and Sweatman 1974). This implies that sampling food patches has an adaptive function; in pigeons it reduces the short-term optimality through decreased rate of energy intake but increases long-term optimality through increased energy intake (Dow and Lea 1987).

One possible explanation of apparently non-optimal behaviour such as contrafreeloading is that animals under certain conditions are more motivated to obtain information about the environment (information-primacy) as opposed to simply satisfying their physiological state (need-primacy; Woodworth 1958; Inglis and Ferguson 1986). For example, in many contrafreeloading studies free-food is consumed at the beginning of the experiment and operant food later (see Osborne 1977). This suggests that once a certain level of nutrient intake has been achieved, food acquisition shifts from being dependant on physiological need to being more governed by requirements for information (Inglis 1983). The level of contrafreeloading expressed in some studies is in excess of the level of sampling behaviour expressed by animals in foraging experiments and therefore contrafreeloading cannot in these studies be explained as sampling behaviour.

Sensory information in contrafreeloading studies about the two food sources is generally asymmetrical, the free food usually available in a bowl provides constant information, whereas the operant food provides little information, except through the expression of appetitive behaviour. It could be this lack of sensory information about the operant food which motivates animals to express higher levels of contrafreeloading than are shown in sampling studies which are usually symmetrical in the level of information provided. Thus, contrafreeloading could be a response to gain information about a food source with artificially low levels of sensory cues.

Animals prefer and respond at a higher rate to variable response reinforcer contingencies than fixed ones, also suggesting that they may be motivated by requirements for information (Herrnstein 1964; Fantino and Abarca 1985; Inglis and Ferguson 1986). In these situations the variability of the operant schedule maybe equated to information. Furthermore, piglets have been shown to actively seek out novelty driven by inquisitive exploration (Wood-Gush and Vestergaard 1991) demonstrating that information acquisiton is not only motivated by primary reinforcers such as food and water. The aim of this experiment was to investigate whether pigs fed *ad libitum* (i.e., able to satisfy their functional requirement for food) would contrafreeload and also if the level of contrafreeloading could be affected by the variability of the operant ratio as a means of manipulating the level information attached to food rewards. The prediction was that if information was important to pigs they would show higher levels of response on a variable than a fixed ratio.

MATERIALS AND METHODS

At the start of the experiment the pigs were moved to an experimental room at 0930h before feeding, where the pigs were allowed continuous access to both food sites. This was the first of three 120hr continuous choice tests, separated by 24hrs in the home pen where the animals were *ad libitum* floor fed. The operant was set at either a FR5 or a VR5, delivering 30g of food per reinforcement and identical food was available *ad libitum* from the free food trough. During the choice periods three animals were exposed to the operant ratios as follows, FR5 to VR5 to FR5; the other three animals to; VR5 to FR5 to VR5. Thus all pigs were exposed to a total choice time of 360hrs.

STATISTICAL ANALYSIS

The data were primarily analysed by paired t-test (Genstat 5, version 2.2; Lawes Agricultural Trust 1987). All data values used in the analysis were mean values per pig each day. The treatments analysed in this experiment were the variability of operant ratio type (FR5 vs VR5). The variables considered were number of reinforcers obtained, number of operant responses, number of responses on the ineffective operant device, the proportion of operant food consumed and the total amount of food consumed (operant and free food). The following variables were square-root transformed to meet the requirements for parametric statistics: proportion of operant food consumed, number of reinforcers obtained, number of operant responses and the number of responses on the ineffective operant device. The other variable, the total amount of food consumed, did not require transformation for analysis by parametric statistics.

RESULTS

The data for the treatment effects for the above mentioned variables are summarised in Figures 3.2 to 3.6. The number of operant responses made on the operant panel was not affected by ratio type (Paired t-test; $t= 0.94$; d.f. 5; $p= 0.39$).

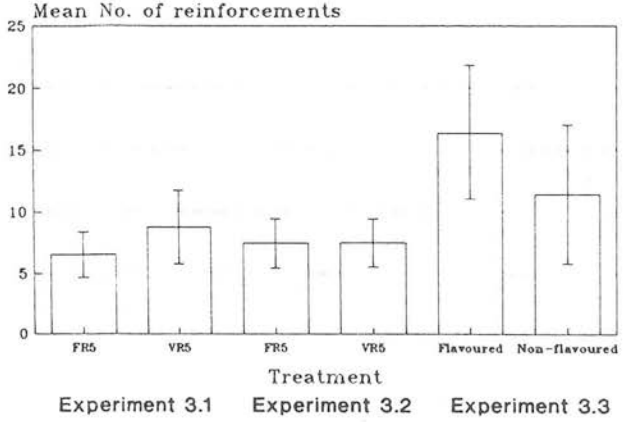


Figure 3.2: Summary of the number of reinforcements earned in Experiments 3.1 to 3.3

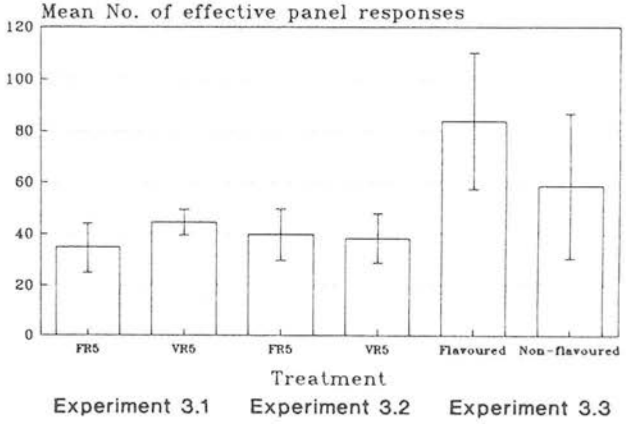


Figure 3.3: Summary of the number of effective operant responses in Experiments 3.1 to 3.3

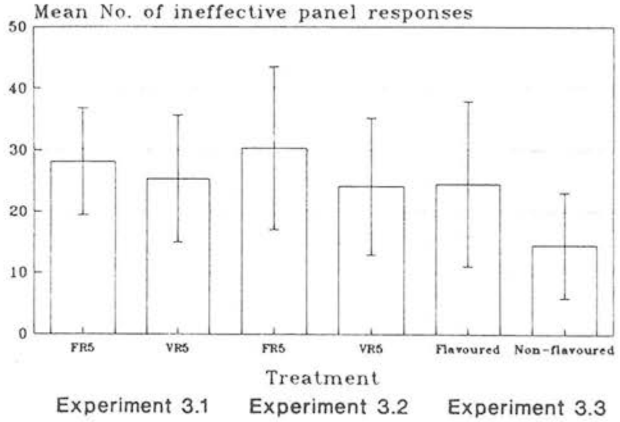


Figure 3.4: Summary of the number of ineffective operant responses in Experiments 3.1 to 3.3

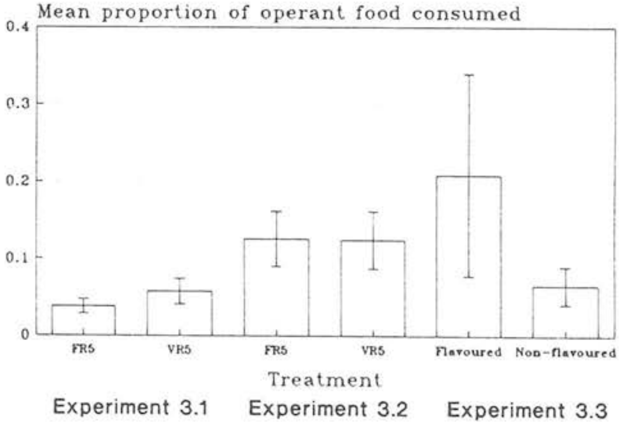


Figure 3.5: Summary of the proportion of operant food consumed in Experiments 3.1 to 3.3

Figure 3.6: Summary of total food intake in Experiments 3.1 to 3.3

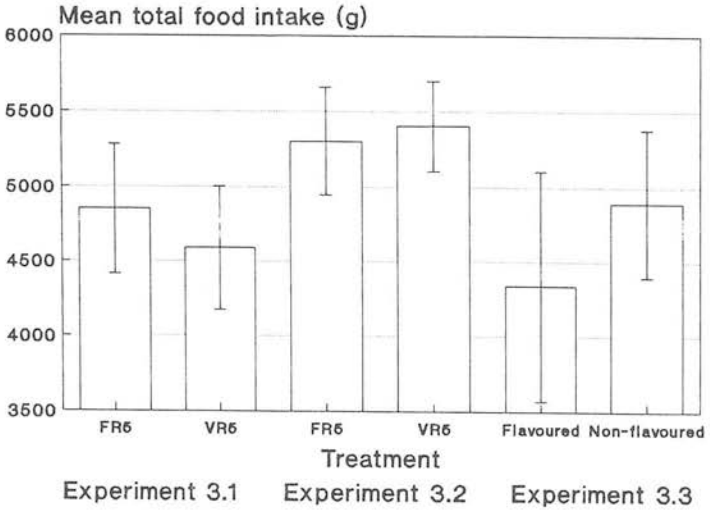
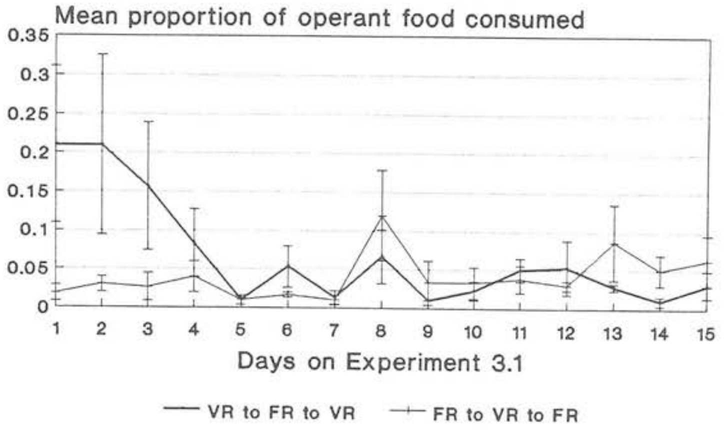


Figure 3.7: The effect of initial operant ratio type on the proportion of operant food consumed



Consequently the proportion of operant food consumed compared to the amount of free food consumed also showed that pigs had a strong preference for free food, irrespective of ratio type (Fixed ratio: Paired t-test : $t = 49.13$; d.f. 5; $p < 0.001$; Variable ratio: $t = 26.37$; d.f. 5; $p < 0.001$) and comparison of the proportion of operant food consumed on each ratio, showed that ratio type had no significant effect (Paired t-test: $t = 1.71$; d.f. 5; $p = 0.15$). A mean daily proportion of 0.05 (±0.01) of operant food was consumed during the experiment.

Figure 3.7 shows that the pigs that were tested VR to FR to VR, showed in their first test period of VR the highest level of contrafreeloading (mean proportion of operant food consumed= 0.13±0.06). This effect was not however, observed when the group tested FR to VR to FR was either exposed to FR or VR for the first time (Figure 3.7). The mean number of ineffective panel responses (26.7±9.1/day) was also not affected by operant ratio type (Paired t-test: $t = 0.51$; d.f. 5; $p = 0.63$).

DISCUSSION

Previous studies on a number of species (see Osborne 1977) have suggested that animals will often choose to contrafreeload in the presence of free food. The present study contradicts those reports as it was found that pigs under the experimental conditions would only show a low level of contrafreeloading. There have been suggestions that contrafreeloading in many studies is the result of experimental artifact (Osborne 1977). As the present experiment controlled for a number of confounding factors (e.g., length of training exposure to operant and free food) it seems that the lack of contrafreeloading found here supports the view that previous studies have not controlled for confounding factors properly.

Contrafreeloading appears to contradict optimality models of behaviour, and it has been suggested that a function of contrafreeloading may be to obtain information about the environment (e.g., availability, variance or quality of alternative food sources; Inglis and Ferguson 1986). This is supported by the observation that contrafreeloading occurs after the free food is consumed (Mitchell, Scott and Williams 1973; Robertson and Anderson 1975) and that operant responding is increased by more variable response reward ratios (Herrnstein 1964; Fantino and Abarca 1985). Again the low level of contrafreeloading and the failure of a variable ratio to increase contrafreeloading in the present experiment would indicate that in this experiment there was no such requirement for information (or exploratory motivation). However, a variable ratio might be expected to only temporarily increase responding until the animal has learned the appropriate contingencies; such a temporary response to VR was shown by the pigs tested VR to FR to VR.

In contrast to previous studies (e.g., Duncan and Hughes 1972) pigs did not increase contrafreeloading with further exposure to the contrafreeloading paradigm, although they never completely stopped consuming operant food. One explanation of the low level of contrafreeloading is that the pigs were 'sampling' the two food sources (Krebs and McCleery 1984) to ensure there was no benefit from switching between food sources. Thus, the pigs in the present work, although not behaving according to an information-primacy system of motivational control may have continued to express low levels of exploratory motivation (or requirement for information) throughout this experiment.

Further support for this came from the observation that the pigs continued to make responses on the ineffective panel. It has been previously reported that non-food deprived pigs will make responses on the ineffective panel and that these responses decrease with time (Lawrence, Appleby, Illius and MacLeod 1989). The results of this experiment are not in agreement with this previous study, although direct comparisons are complicated by experimental differences. Again the responses made on the ineffective panel in this experiment could perhaps reflect exploratory motivation (Inglis 1983). Alternatively such behaviour could be due to non-reinforcement contingent responses such as autoshaping (for reviews of autoshaping see Morgan 1974; Gardner and Gardner 1988).

EXPERIMENT 3.2

The effect of reinforcer magnitude on contrafreeloading

INTRODUCTION

Preference for contrafreeloading has been shown to be dependent upon reinforcer-motivational variables such as magnitude of the reinforcer (Osborne 1977). The effectiveness of small reinforcers in maintaining substantial levels of contrafreeloading is low, whereas for large reinforcers it is high (Robertson and Anderson 1975) which may reflect positive feedback effects of feeding. Positive feedback from the performance of behaviour has been suggested as a mechanism for 'boosting' underlying motivation of the current activity and preventing 'dithering' between alternative activities (e.g., Houston and Sumida 1985). There is some empirical evidence that motivation increases during feeding (Wiepkema 1971). Thus, a large reinforcer might be expected to have greater positive feedback effects than a smaller one (i.e., it may increase feeding motivation more quickly at the start of a meal) thereby increasing operant responding, and contrafreeloading.

Experiment 3.1 found little evidence for contrafreeloading in pigs and this may be a reflection of the small reinforcer size. Therefore in this experiment an increase in reinforcer size was used, as this had previously been shown to increase contrafreeloading in rats (Robertson and Anderson 1975). The possibility of an interaction between reward size and ratio type was also examined by comparing the response to larger reward on both variable and fixed ratios.

MATERIALS AND METHODS

The experimental procedure of Experiment 3.1 was repeated using the same animals but with a 90g food reinforcer and the additional modification that pigs which were previously tested FR5 to VR5 to FR5 were now tested VR5 to FR5 to VR5, to increase the balance of the experimental procedures.

STATISTICAL ANALYSIS

The same statistical tests used for Experiment 3.1 were repeated here.

RESULTS

The treatment effects of the data are summarised in Figures 3.2 to 3.6. The level of operant responses were again not affected by ratio type (Paired t-test: $t = 0.13$; d.f. 5; $p = 0.90$), and these data were therefore averaged for use in subsequent analyses. When the proportion of operant food consumed was compared with the amount of free food consumed pigs were found to have a strong preference for free food, irrespective of ratio type (Fixed ratio: Paired t-test: $t = 10.36$; d.f. 5; $p < 0.001$; Variable ratio: $t = 10.04$; d.f. 5; $p < 0.001$). The proportion of operant food consumed was also not affected by ratio type (Paired t-test: $t = 0.05$; d.f. 5; $p = 0.96$). When the proportions of operant food consumed on both ratios were summed and averaged, pigs consumed a mean proportion of 0.13 (±0.03) of operant food.

A comparison of the mean proportions of operant food consumed for both types of ratio between Experiments 3.1 and 3.2 showed that pigs tended to consume more operant food in this experiment (Paired t-test: $t = 2.04$; d.f. 5; $p = 0.097$). However, when the number of operant responses (for both types of ratio) between the two experiments were compared there was no significant difference (Paired t-test: $t = 0.03$; d.f. 5; $p = 0.98$). The mean number of ineffective panel responses per day (27.2 ±12.0) were not found to be affected by ratio type (Paired t-test: $t = 1.41$; d.f. 5; $p = 0.22$).

DISCUSSION

The increased reinforcer size increased the level of contrafreeloading by the pigs in comparison with Experiment 3.1, but the level of increase was small and non-significant. From the results of previous studies, it would have been reasonable to have predicted a larger increase in the level of contrafreeloading (see Osborne 1977) and therefore the present results again contradict previous studies.

Although the level of contrafreeloading increased with reinforcer size, the number of operant responses (appetitive behaviour) did not increase confirming that when the pigs had performed a response to obtain food, that the food was then consumed even in the presence of free food. This observation is consistent with the observation that there was no food remaining in the operant troughs during the experimental periods, and only a small amount during the operant training periods. This might suggest that once a pig has expended energy obtaining food by making a operant response, it is then more energetically efficient to consume that food than to walk to the free food. Alternatively, the pigs could have been behaving in accordance with the 'Concord Fallacy' (Dawkins 1989), basing their behavioural responses on energy invested and not on potential net energy gain.

This experiment replicated the findings of Experiment 3.1, showing that although the type of operant ratio had no effect on the level of contrafreeloading that a low level of contrafreeloading was maintained throughout the experiment. In addition, pigs continued to make responses on the ineffective panel, contrary to a previous study (Lawrence, Appleby, Illius and MacLeod 1989) and perhaps providing some evidence for explorative tendencies in these pigs although not sufficient to support an information-primacy model of behaviour.

EXPERIMENT 3.3

The effect of different food flavours on contrafreeloading

INTRODUCTION

Stimulus change has been shown to be important in the performance of contrafreeloading (see Osborne 1977). In previous studies it has been shown that animals contrafreeloading using an operant system that provides an auditory or visual stimulus upon the delivery of reinforcement, cease to contrafreeload when the stimulus change is eliminated (Osborne and Shelby 1975).

Both response-dependent reinforcers and free reinforcers act as primary sources of reinforcement. It has been proposed that animals contrafreeload because of the secondary reinforcement effects created by the stimulus change, associated with the operantly obtained food resulting in a greater level of reinforcement (Osborne 1977). Whether the stimulus change results from the effects of conditioned reinforcement or sensory reinforcement is unclear. The conditioned reinforcement explanation of the effects of stimulus change on contrafreeloading would only be applicable when the experimental subjects have experienced repeated stimulus-reinforcer pairings. In all other cases a sensory reinforcement explanation is more probable since previous research has shown that the effects of sensory reinforcement increase with reinforcer complexity (Barnes and Baron 1961).

In this experiment the effect of a stimulus change on contrafreeloading was examined, by altering the flavour of the operant and free food. This approach was adopted because previous studies have only considered sound and sight and because it is known that rats respond to variety in food flavours by temporarily increasing their food intake (Treit, Spetch and Deutsch 1983). Also this experiment provides asymmetrical sensory information about the two food sources (see Experiment 3.1 Introduction). It was predicted that the pigs would respond to the alteration in food flavours by increasing their level of contrafreeloading.

MATERIALS AND METHODS

This experiment was carried out using a 'double blind' procedure. In the 6 days previous to this experiment the animals were offered the same food as in Experiment 3.1 with or without added flavour (International Additives, Liverpool, U.K.) on alternate days in their home pens, to familiarise them with the new food (see Kyriazakis 1989) and to remove any novelty effect.

The animals were tested in a similar manner to that outlined in Experiment 3.1 with the exception that only FR5 and a reinforcer size of 30g was used, because Experiments 3.1 and 3.2 had shown that type of operant ratio and reinforcer size had little effect on contrafreeloading.

Each animal was tested for its preference for flavoured food over two 120hr periods during which the positioning of the two foods was alternated in a balanced manner (i.e., three animals were exposed to the flavoured operant food versus non-flavoured free-food for 120hrs and three animals the reverse of these conditions; the positions of the foods was then reversed for the second 120hr period).

STATISTICAL ANALYSIS

The same statistical approaches used for Experiment 3.1, were repeated here.

RESULTS

The data for the treatment effects are summarised in Figures 3.2 to 3.6. The proportions of the two types of food when offered operantly were compared and not found to differ significantly (Paired t-test: t= -1.33; d.f. 5; N.S.). There was considerable individual variation in the proportion of flavoured food consumed (range= 0.01 to 0.85). The mean proportion 0.22 (±0.13) of operant food consumed was greater than that found in Experiments 3.1 and 3.2 but this effect was not statistically significant. In this experiment pigs showed a strong preference for the free food irrespective of either type of food being offered operantly or free (Flavoured offered operantly: Paired t-test; $t = 6.08$; d.f. 5; $p < 0.001$; Non-flavoured $t = 35.23$; d.f. 5; $p < 0.001$). The pigs continued to make responses on the ineffective operant panel in this experiment, with an overall mean of 19.5 per day (± 10.9).

DISCUSSION

Food flavour appeared to influence the proportion of operant food consumed increasing the levels from those in Experiments 3.1 and 3.2. Since the pigs were pre-exposed to the feeds this effect cannot be explained by novelty. These results are therefore, in qualitative agreement with previous studies of rats where variety of flavour has been shown to stimulate food intake (Treit, Spetch and Deutsch 1983) and suggest that stimulus change may contribute to contrafreeloading. However, the levels of operant responding were still not sufficient to demonstrate a preference for contrafreeloading although again contrafreeloading and ineffective panel pressing were maintained across the experiment.

GENERAL DISCUSSION

The results presented here demonstrate that pigs under the present experimental conditions would only show low levels of contrafreeloading and that this low level of contrafreeloading was little affected by ratio type or reinforcer flavour (stimulus change). Increased reinforcer size did increase the proportion of operantly obtained food consumed but not the number of operant responses. Changing the flavour of the operantly obtained food increased the level of contrafreeloading but not to a level where the pigs expressed a preference for operant food. These results therefore contradict most previous studies into contrafreeloading (see Osborne 1977 for a review). The low level of contrafreeloading by pigs in these experiments would appear to be the expression of a low level of exploratory motivation. In general the results support the view that contrafreeloading is largely an experimental artifact (see Osborne 1977). Also that pressing a panel or any other simple form of enrichment such as the use of a single type of novel object has only short term effects on the behaviour of pigs.

In general the present results suggest that the major difference between the present study and previous reports of contrafreeloading is the degree to which confounding factors were controlled. Of particular relevance here perhaps was the equivalent levels of training on free and operant food thereby excluding the possibility that the operant responding was a reflection of stronger conditioning. Furthermore the results of Experiment 3.3, suggest that stimulus change (in the form of alteration to the reinforcer flavour) can increase contrafreeloading. This suggests that the efforts to minimise stimulus change associated with contrafreeloading in Experiments 3.1 and 3.2 may have further reduced contrafreeloading.

Given the apparent reduction in contrafreeloading in response to control over the confounding factors (training and stimulus change) the present results do not provide strong evidence for an information-primacy system of motivational control. There was evidence however for low levels of exploratory behaviour in that low levels of contrafreeloading were maintained throughout all three experiments and for the continued use of the ineffective panel. It might be argued that those responses reflected the general lack of stimulation in the environment or boredom (Wemelsfelder 1990). However, the consumption of the operant-dependent food rewards is not consistent with this view.

An additional principal criticism with this and previous experiments into contrafreeloading is with the operant technology used (see Sato and Sakagami 1985; Wilkie 1985). The operant devices used are often chosen arbitrarily (Roper 1983) and do not necessarily take into account species-specific food acquiring behaviour (see Bolles 1988). For example, the relevance of pressing a panel for a pig to obtain food may be low, as this behaviour had little resemblance to appetitive foraging behaviour displayed by free-ranging pigs, which normally involves sensory input, locomotor activity, rooting and digging with the snout (Graves 1984; Spitz 1986). It is possible that the free food trough was a more species-specific operant than the operant panel and trough, as (it provided sensory cues) pigs could dig in it with their snout and then ingest food, which is arguably a more natural behavioural sequence than that required to obtain food by pressing a panel.

In terms of animal welfare this series of experiments does not support the idea that the performance of appetitive behaviour is important to pigs. Even if this assumption from the present experiments is correct it does not mean that allowing animals to perform appetitive behaviour does not improve welfare. For example, much of the research into behavioural enrichment has shown that allowing animals to perform appetitive behaviour has a number of advantages such as reduction in aggression and abnormal stereotypic behaviour patterns (e.g., Kastelein and Wiepkema 1989; Chamove 1989). The limitations of the present experiment (see above) do suggests how investigations into the reinforcing properties of behavioural performance could be improved. The main areas identified being the effects of stimulus change and the provision of species-specific operants.

Chapter 4

The effect of operant design on choice and level of responding by pigs

INTRODUCTION

The term operant behaviour was originally used by Skinner (1938) to describe behaviour that was guided by its consequences. Such operant behaviour was characterised by its goal-directedness and that it had some effect on the environment. More recently, the term operant behaviour has been extended to behaviour outside of the operant chamber (e.g., foraging) and outside of learning situations (Staddon 1983).

In 1932 Skinner developed a method for studying reward and punishment where rats were trained to perform an arbitrary response (lever pressing) to obtain a motivationally significant goal such as food (the reinforcer). This methodology gave rise to the'Skinner box' which since its inception has played a dominant role in the research of psychologists interested in developing theories and rules that govern the learning processes of all animal species (Roper 1983). Part of the reason for the success of this experimental approach is because it provides easily quantifiable measures of animal behaviour and automated data capture (Gardner and Gardner 1988). Later this methodology was used by psychologists interested in studying the motivational systems that control the expression of behaviour by animals (e.g., Toates 1987)

The measurement of motivation is central to the study of animal welfare and operant experimental paradigms are widely used to study animal motivation in relation to welfare (for a review see Kilgour, Foster, Temple, Matthews and Bremner 1991). The analysis of motivational demands of animals inform us of what is important to animals, since motivational requirements are often directly linked to fitness (Dawkins 1990). It has been argued that if an animal cannot learn to make an operant response to receive a particular reinforcer then the animal may have low motivation to obtain that reinforcer (Beilharz and Zeeb 1981).

Experiments by Thorndike (1911) and Skinner (1938) showed that animals could learn to make unnatural responses to obtain a reinforcer. This experimental evidence was used to suggest that all pairs of events can be associated with equal ease, in any species (the theory of equipotentiality; see Roper 1983 for a review). In attempting to develop a general theory of learning it was therefore important to psychologists that the design of operant devices were arbitrary, that artificial environments were used to eliminate species-specific behaviour and any species of animal could be used (Gardner and Gardner 1988). Generally, the only consideration of the device chosen was its' size in relation to the animal. In fact it has been suggested that the Skinner box used with rats and pigeons has evolved over 30 years to fit the subjects prefeeding behaviour and this is the reason for its success as a piece of experimental equipment (Staddon 1980; Bolles 1988). Thus, the bar pressing of rats and the key pecking of pigeons in a Skinner box are not arbitrary behaviours, a fact which is perhaps not always appreciated by psychologists.

Natural selection provides animals with learning capabilities that are appropriate to the environment in which they evolve (Rozin and Kalat 1972). Animals are more successful at, and will attempt to solve problems, that closely match those found in their environment, a capability termed biological preparedness (Chance 1988). This has been experimentally confirmed in a comparison of Blue and Great tits, which when offered simultaneously foraging problems appropriate to both their natural habitats, expressed a preference for, and were more successful at those problems relevant to their natural habitat (Partridge 1976). This suggests that animals have evolutionarily determined constraints on their learning capabilities. This is supported by the observation that many animals perform an inappropriate operant response to obtain a reinforcer when the response required is very different from the species-typical response-reinforcer pairing. Fish can learn to bite a wire to gain access to an aggressive encounter, but when the same fish has to bite a wire to gain access to a mate it will often show species-typical courtship behaviour to the wire as opposed to biting it (Sevenster 1973).

Video analysis of pigeons pecking a disc for food or water has shown that although the response they are conditioned to perform is arbitrary the response they develop is either a species-specific feeding or drinking peck depending on whether the reinforcer is food or water (Moore 1973). This suggests that the pigeon may mistake the operant device for the reinforcer and is directing species-specific pre-feeding behaviour at the device. Thus, operant conditioning is usually more successful if the operant device contains a classically conditioned component (Roper 1983), because the animals may show species-specific response towards the device. If the required operant response is different from the species-specific response for that reinforcer, operant conditioning may be difficult or impossible (see Dawkins and Beardsley 1986; Bolles 1970) and result in 'misbehaviour' (see Breland and Breland 1961). The theory of equipotentiality accounts for animals failing to respond as expected in experimental situations, due to the limitations on different species motor and sensory capacities, and not due to constraints on learning (see Hinde and Stevenson-Hinde 1973; Roper 1983).

Many psychological studies using operant techniques to investigate animal behaviour are criticised by ethologists for being artificial (Houston 1980). Psychologists defend their position by attacking ethologists for lack of control in their experiments (Wynne 1986). A theoretical synthesis between psychological and ethological approaches to the study of animal behaviour has recently been attempted (e.g., Wynne 1986; Toates and Jensen 1991), but a methodological approach remains elusive.

In this experiment pigs were conditioned to perform an operant response to obtain a food reinforcer. The pigs were offered two types of operant device, that differed in apparently how easily species-specific prefeeding behaviour could be directed at the devices. One device, was a commonly used design of 'panel' that required a pig to press it with its' snout to obtain food. The other device was a 'paddle' designed around the food acquiring behaviour of pigs (Graves 1984; Spitz 1986), where a reinforcer could be obtained by rooting or chewing on the device. In the first part of the experiment pigs were offered each device singly, to test whether the type of operant device affected the absolute level of responding. During the second part of the experiment the two devices were offered simultaneously as a choice, to determine if pigs would express a preference for either operant device. This study has implications for the methodology used to measure motivation, especially in relation to animal welfare.

MATERIALS AND METHODS

Animals

The animals were 16 female Large White X Landrace sexually immature juvenile pigs (Cotswold Pig Development Company, Lincoln, U.K.), originating from several litters' that had a mean initial weight of approximately 45±3kg. The pigs were divided randomly into two groups of eight, one as an experimental group and the other as a companion group. All experimental pigs had a specific companion animal and had been previously housed together and were therefore familiar. All animals were allowed 14 days in which to acclimatise to the building, before any training or testing began.

Housing, Temperature and Lighting

The animals were housed in a controlled environment building that was divided into five rooms. The first two rooms in the house were used for holding the animals. The three remaining rooms were used for experimentation. Each room was divided into 4 partially slatted pens measuring 1.8m x 2.3m (detailed in Hsia 1981) with a 1.0m wide corridor in the centre. Each pen had one bowl drinker located over the slatted area and water was supplied *ad libitum*.

All rooms were maintained at a temperature of 20±2^{O}C. The lighting was set on a 12:12 light dark cycle (lights on at 1000h).

Management and Food

Whilst in the holding pens the animals were fed *ad libitum* from troughs. The pens were cleaned every day at 0945h. Experimental rooms were cleaned during periods between training and testing. They were also cleaned if an experimental animal had urinated or defecated near, on or into the experimental apparatus.

The animals were offered a commercial 'growers' pelleted diet (320 Ultragrade, Dalgety Agriculture Ltd, Bristol, U.K.) throughout the experiment. Each kilogram of the diet contained 13.8MJ/DE, 195g of crude protein, 40g of crude fibre, 55g of oil, 60g of ash and 870g of dry matter.

Experimental room layout

In each of the experimental rooms an experimental animal and a companion were placed in diagonally opposite pens. The companion animals' pen had a wooden screen positioned so that the experimental animal was unable to see the companion eating. The purpose of the companion animal was to reduce social isolation and thus reduce the activation of escape behaviour in the animals, known to affect the responses of isolated experimental animals (e.g., van Roojen 1990). Furthermore social isolation is known to depress food intake in animals previously housed in a group (Clayton 1978) an effect undesirable in the present experiment.

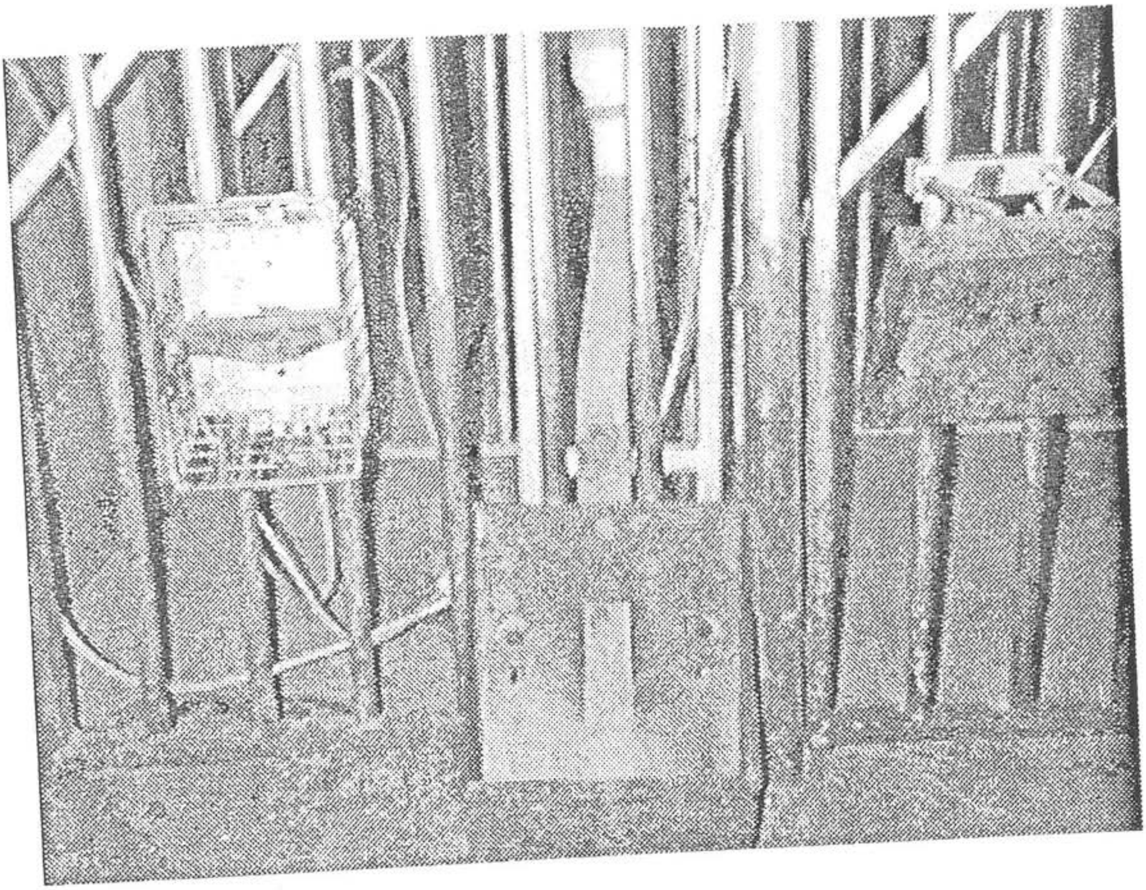
Pilot Study of Operant Designs

The criterion for the design of the two operant devices used in this study were as follows. One device should allow species-specific food acquiring behaviour (i.e., rooting and chewing; see Graves 1984; Spitz 1986) to be easily performed with it. The other device should have an arbitrary design. Therefore, a device (paddle) was designed that could be operated by a pig either rooting or chewing it. The second device chosen was a panel used previously with pigs (e.g., Lawrence, Appleby and MacLeod 1988).

Apparatus

Each experimental pen had a food trough attached at the centre of one pen wall (see Figure 4.1) and one of the two operant devices (see Figures 4.2 and 4.3; both constructed by the Scottish Centre for Agricultural Engineering, Bush Estate, Penicuik, U.K.) mounted 0.4m above the floor and either 0.25m left or right of the food trough. The two operants were calibrated using a spring balance (Slater, London, U.K.), so that an equal force (100±0.5N/m) was required to operate them. Food was delivered into the food trough via a feeder (Orby out-of-parlour calf feeder modified by the Scottish Centre for Agricultural Engineering). The operants and feeder were interfaced and controlled by a micro-computer (BBC model B, Acorn Electronics, U.K.).

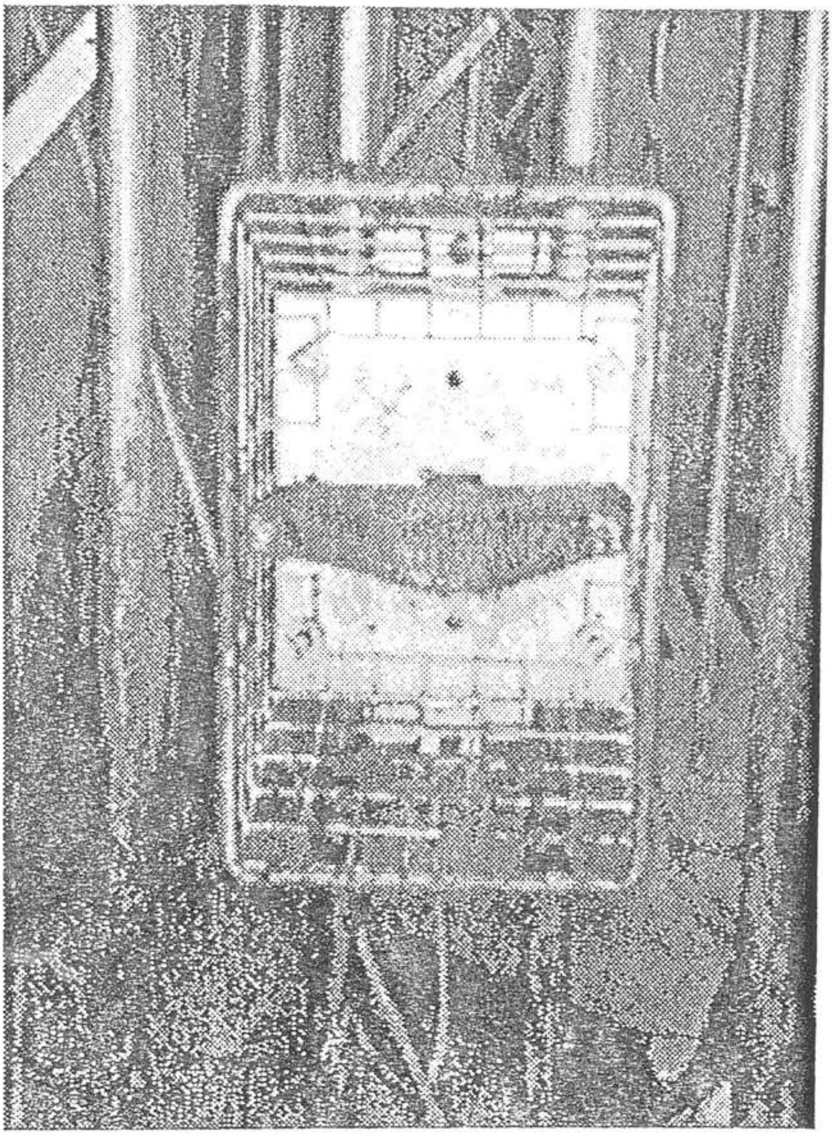
Figure 4.1: Experimental set-up



Paddle Food trough and feeder Panel

Figure 4.2: Panel

Figure 4.3: Paddle



Experimental training

The day before training began, the food was removed from the test animal's pen at 1800h. On the days of training or testing the companion animals were moved to their pen in one of the three experimental rooms at 0945h and offered food. At 0950h the experimental animals were moved to their pen in the experimental rooms; the order of operant device presentation being balanced across pigs. At 1000h the operant device was activated. Initially the pigs were trained to a fixed ratio of one response (FR1) for 30g of food and this was gradually increased over the next 48hrs to FR5. Following this, experimental animals were returned to their holding pens for 24hrs. The pigs were subsequently trained to the other type of operant device in an identical manner, before being returned to their holding pens for 24hrs.

Experiment 4.1

Post-training the animals were twice offered each device singly for two 48hr (continuous) periods. This was done in a balanced manner across pigs. Each test period was separated from the previous one by 24hrs in the home pen.

Experiment 4.2

The experimental animals were given three separate periods of testing lasting 72hrs (continuous), when both types of operant devices were presented simultaneously. The animals were allowed to freely choose which device they operated to obtain food; both were set to deliver food on a FR5. The controlling computer software was written such that an animal only received a reinforcer if it made five consecutive presses on either of the two devices. In the last period of testing the position of the devices was switched around.

Data recording

The number of responses, food deliveries and their times were recorded by the micro-computer for subsequent analysis. Also any refusals of food were weighed at the end of each 24 hrs during training and testing.

STATISTICAL ANALYSIS

The results of the pilot experiment were analysed by a Chi-squared test (Minitab version 7.2; Ryan, Joiner and Ryan 1985) to determine the probabilities of a root or chew response following each other during the intra-reinforcer response sequence.

After the experimental training period no food refusals were found in the food troughs and therefore food intake was solely assessed from the record of operant responses. The data were analysed by paired t-tests using Genstat (Version 5 Release 2.2; Lawes Agricultural Trust 1987). All variables used were averaged for individual pigs and all met the requirements for parametric statistics without transformation. In Experiment

4.1 the variables considered were total number of operant responses made on each type of operant device and the amount of food consumed. The total number of operant responses on each device when offered singly was calculated by averaging the data by day. Thus, the amount of food consumed was calculated by dividing the number of responses by 5 and multiplying the obtained figure by 30. Also a Pearson's correlation (Minitab version 7.2; Ryan, Joiner and Ryan 1985) was used to assess comparative levels on responding on both operant devices. In Experiment 4.2 the mean number of operant responses on both devices for all three test sessions (a total of 216 hours) were calculated. The proportion of responses made on each operant device were analysed by paired t-test.

RESULTS

Pilot Study

Previous observations indicated that pigs operated the panel by pushing it with their snout (Lawrence, Appleby and MacLeod 1988). Observations of individual pigs using the paddle showed that pigs operated it with a mixture of rooting and chewing responses. The sequence of responses of one pig was analysed by close-up video played back in slow motion. This showed that for a FR5 for 30g of food reinforcement, the mean probability transition sequence per reinforcement was root (1.0), root (0.71), chew (0.57), root (0.79) and root (0.64). From these results it was decided that this device fulfilled the criterion that it should allow the pig to perform rooting and chewing pre-feeding responses.

Experiment 4.1

All pigs were found to consume more food from the paddle than from the panel (Paired t-test: $t= 6.29$; d.f. 7; $p<0.001$). The mean amount of food consumed from the paddle was 1933g (±181) and from the panel was 1246g (±157). Individuals showed differing levels of food consumption (Table 4.1) and also there was a significant positive correlation between the amount of food consumed from each type of operant device ($r= 0.800$; $n= 8$; $p<0.05$).

Experiment 4.2

A comparison of the pigs preference for the two devices was made by paired t-tests and pigs were found to strongly prefer the paddle ($t= 6.40$; d.f. 7; $p<0.001$). The pigs made on average 0.78 (±0.0415) of their responses on the paddle. All pigs preferred the paddle but some individual differences were observed (see Table 4.2).

Table 4.1: The mean amount of food obtained by individuals using both operant devices singularly.

Pig No.	Mean Food Obtained (g) Panel	S.E.M.	Mean Food Obtained (g) Paddle	S.E.M.
1	1050	372	1545	186
2	1380	232	2505	72
3	690	59	1537	277
4	1470	352	1950	255
5	1380	90	1733	169
6	1815	390	2288	580
7	540	91	1620	371
8	1628	184	2670	271

Table 4.2: Paddle vs Panel data summary

Pig No.	Total Paddle Responses	Total Panel Responses	Proportion Paddle Use
1	2539	967	0.72
2	2759	782	0.78
3	1832	412	0.82
4	3235	269	0.92
5	3332	229	0.94
6	3606	540	0.87
7	2487	1164	0.68
8	1167	1057	0.52
Mean	2620	677	0.78

(Total responses given are for all four test sessions of three days duration)

DISCUSSION

The results of this experiment clearly demonstrate that the design of operant device can affect the level of operant responding (Experiment 4.1). They also suggest that pigs prefer an operant device that apparently allows them to perform more species typical behaviour. Thus, the present results provide further evidence to dispute the theory of equipotentiality (see Roper 1983) in that the pigs did not make the association between each type of device and the same reinforcer, with equal ease.

The results of operant studies can be influence by many confounding factors such as the effort of operant response, position of the operant device and individual differences. It has been previously shown that increasing the effort of an operant response reduces the frequency of responding and the inter-response interval (Armus 1986), and optimal foraging theory would predict that animals would choose the response requiring least effort (Krebs and McCleery 1984). In the present experiment an equal force was required to operate both designs of operant discounting this explanation of the results. The position of the operant from the point of reinforcement affects the level of operant responding by mice (Roper 1973). Position effects can be discounted in the present experiment, since the positions of the operant devices were the balanced, alternated and the same distance from the food trough. All the pigs used in this experiment were reared within the same husbandry system and therefore the effect of previous environmental experience should have been broadly similar. The differing levels of reinforcement obtained by individual pigs on either device probably reflected intrinsic levels of feeding motivation. Individual differences were also observed in operant design preference, although all pigs preferred the paddle. These differences may have reflected differences in foraging ability, which have been shown to reflect how profitability (in terms of net energy intake) an animal can utilise a food resource (Partridge 1976).

It has been shown that species-specific behaviours often resemble fixed action patterns and the behavioural responses of animals to classical conditioning (see Introduction and Roper 1983) in that they are relatively inflexible sequences of behaviour. Therefore the lower responding and use of the panel may reflect a partial incompatibility between response and reinforcer (Sevenster 1973; Dawkins 1990). However, since pigs in this experiment did learn to use both operant devices to obtain reinforcement, the differences in the amount of reinforcement obtained from the two designs of operants cannot totally be explained as a learning constraint. Also the fact that pigs expressed a preference for the paddle design, suggests others factors were involved. Maze learning behaviour in rats is more rapid when the reinforcer is ingested through the mouth rather than being intragastrically injected (Miller and Kessen 1952) this is thought to be due to additional reinforcement from oral sensory feedback. Pigs may therefore have responded more and expressed a preference for the paddle possibly because it allowed expression of more rewarding appetitive behaviour through sensory feedback from tactile stimulation of the snout and oral stimulation of the mouth. This suggestion is supported by the observations during the pilot study where pigs using the panel only pressed it with the flatten end of their snout, whereas those with the paddle showed a sequence of rooting and chewing responses. Hughes and

Duncan (1988) review studies into contrafreeloading, specific nutritional deficiencies, vacuum activities, stereotypies and 'misbehavior', and suggest that the performance of appetitive behaviour is reinforcing (see also Breland and Breland 1961; Morgan 1974; Osborne 1977).

The control of the variables used in this experiment and the ethological aspects of the experimental apparatus suggest that a successful methodological synthesis between psychological and ethological approaches to animal behaviour is possible, allowing for more accurate assessment of animal behaviour. This is particularly important in animal welfare studies where the results of operant investigations into motivation are being used as evidence to bring about changes in the way captive animals are treated, for example the behavioural needs of laying hens to have a dustbath (Dawkins and Beardsley 1986).

Furthermore the operant technology used by applied ethologists has had little time to evolve around the behaviour of their subjects. The present results for example show that the use of an arbitrary operant device (panel) results in an under-estimation of feeding motivation in pigs. Beilharz and Zeeb (1981) would interpretate Experiment 4.1 results relating to the panel as pigs having a low motivational demand for food (see Introduction), however the results of Experiment 4.1 relating to the paddle would strongly dispute this interpretation. These results also provide some evidence that the performance of a behaviour may in itself be reinforcing and represent an important motivational demand (see Chapter 3). The consideration of the animal's ethology in environmental design and the reinforcing properties of the performance of appetitive behaviour will be developed further in the next experimental Chapter (5).

- Chapter 5 -

The effects of food level and a foraging device on the behaviour of pigs

INTRODUCTION

Economic and production reasons dictate that the breeding stock of domestic pigs and broiler hens are normally fed a food ration less than their free feeding intake (Whittemore 1987; Savory 1992), and commercial levels of food restriction have been shown to result in sustained feeding motivation (Lawrence, Appleby and MacLeod 1988; Savory 1992). The effect of food restriction on feeding motivation may be exacerbated by selection for fast growing progeny with large appetites (Savory 1992). Studies of feeding motivation are usually conducted using operant conditioning procedures which have been accused of imposing artificial conditions (see Gardner and Gardner 1988) on the animal. The validity of such studies undertaken in artificial conditions has been challenged because of problems with operant conditioning procedures such as 'misbehaviour' (see Timberlake 1984), mismatch between response and reinforcer (see Kilgour et al 1991), and resistance to satiation (see Morgan 1974).

The practice of food restriction with dry sows and broiler breeders has been directly linked to the performance of stereotypic behaviour (Appleby and Lawrence 1987; Terlouw, Lawrence and Illius 1991; Kostal, Savory and Hughes 1992; Savory, Seawright and Watson 1992) which maybe interpreted as an indicator of poor welfare (Mason 1991). Stereotypies in sows have often been associated with physically restrictive housing such as stalls and tethers. However, restrictive housing is now known not to be directly responsible for the development of stereotypies in pigs as these behaviours can also develop in loose housed sows if they are also food restricted (Terlouw, Lawrence and Illius 1991). The performance of stereotypies may then reflect underlying feeding motivation and the subsequent potentiation foraging behaviour (Hughes and Duncan 1988). Stereotypies may arise where restrictive housing in some way interferes with the expression of that foraging behaviour perhaps by modifying or channelling complex and variable foraging behaviour into more simple and often repeated forms (Lawrence and Terlouw, in press).

Behavioural enrichment can be used to reduce the performance of abnormal behaviours such as stereotypies by allowing captive animals to express a time budget similar to that expressed by free-ranging conspecifics (Chamove 1989; Bayne, Dexter, Mainzer, McCully, Campbell and Yamada 1992). This can be done by promoting the expression of a range of species typical appetitive behaviours through the use of operant type devices, and thereby avoid the channelling of behaviour into stereotypic forms. Successful behavioural enrichment reduces both the absolute and proportion of time spent in performing abnormal behaviours when the effects of behavioural enrichment on the time budget are controlled (see Terlouw, Lawrence and Illius 1991). Thus, successful behavioural enrichment should not only alter an animals time budget allocation but actually replace the performance of abnormal behaviour.

Animals have a limited time budget in which to perform their behaviour repertoire. The robustness of a behaviour in maintaining its time allocation in a reduced time budget (e.g., when an environmental manipulation allows the expression of more behaviours) is referred to as its behavioural resilience (Houston and McFarland 1981). The measurement of behavioural resilience requires the manipulation of the animals whole time budget which is methodologically difficult to achieve (see McFarland 1985). To avoid this problem an analogous procedure called consumer demand theory has been used in conjunction with operant conditioning (Kagel, Battalio, Green and Rachlin 1981). Although methodologically more simple to apply consumer demand theory only allows the assessment of behaviours singularly.

The aims of this experiment were to: (a) assess the use of a foraging device as an operant for measuring feeding motivation, (b) test the hypothesis that food restricted pigs are food motivated and if given the opportunity will express their feeding motivation as foraging behaviour, (c) assess the effects of increased foraging time on the time budget of pigs and (d) examine the device's potential for behavioural enrichment.

MATERIALS AND METHODS

Animals

The animals used in this experiment were six Large White X Landrace primiparous gilts (sexually mature young adults; Cotswold Pig Development Co. Ltd, Lincoln, UK) that had an initial average weight of 150 ± 5kg.

Housing

The animals were housed in one of two adjacent strawed pens (one holding and one experimental pen) within the same open fronted building (detailed in Kerr, Wood-Gush, Moser and Whittemore 1988). The pens both measured 9m X 3m.

Management and food composition

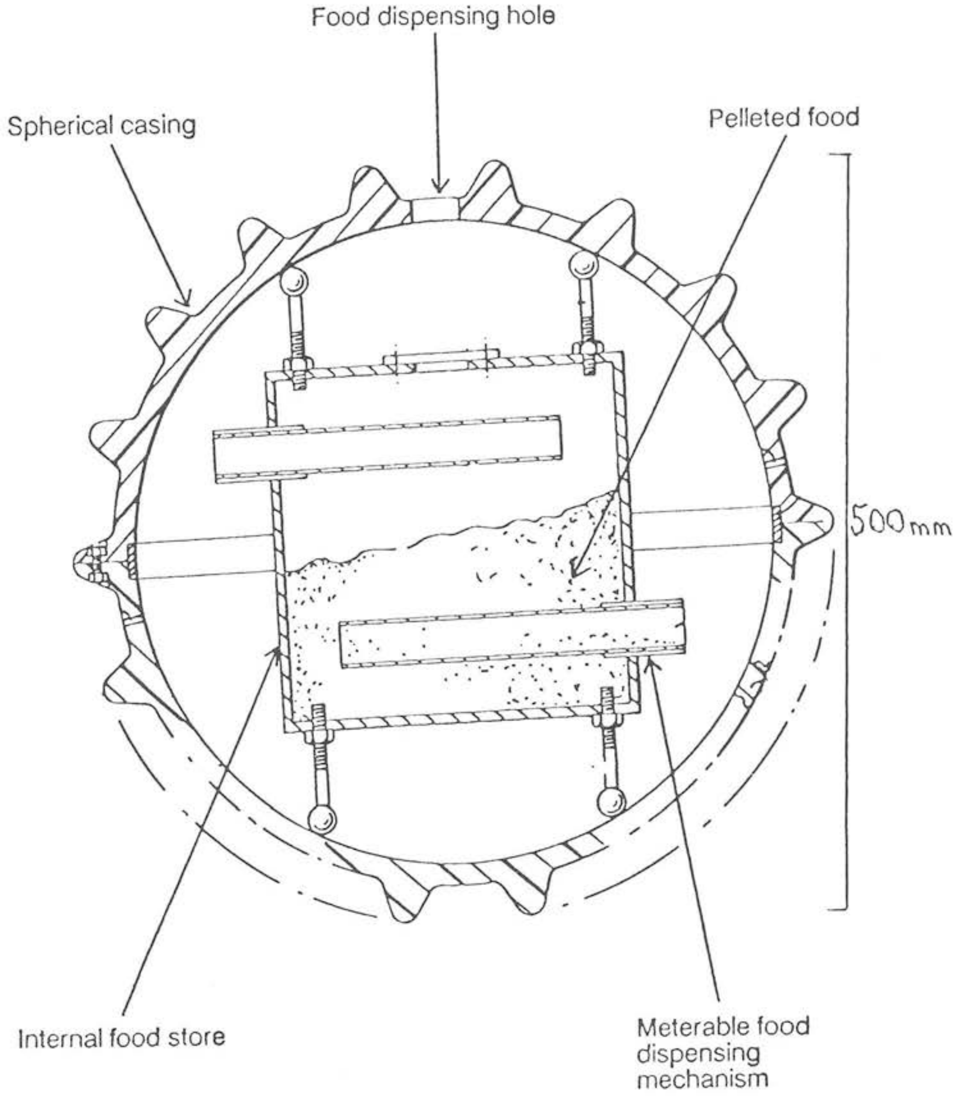
Both pens were covered by a deep layer of straw and fresh straw was added daily (two bails per week); the pens were cleaned out twice a week.

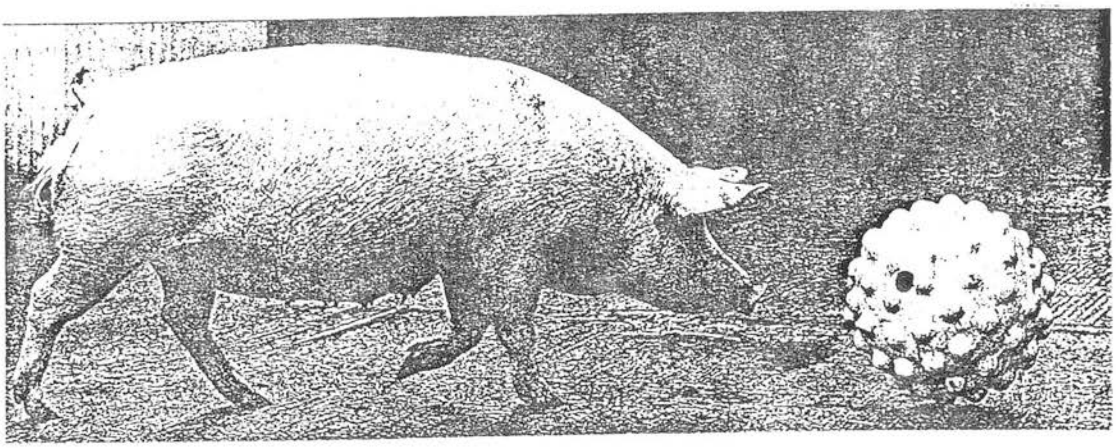
Pigs in the holding pen were group fed from two troughs with sufficient feeding space for all animals to feed simultaneously. Food was evenly distributed in both troughs, to ensure that all individuals received approximately the same quantity of food. The pigs were offered a standard pelleted sow diet, each kilogram contained 13.2MJ/DE, 170g of crude protein, 53g of crude fibre, 40g of oil, 63g of ash and 870g of dry matter. The pigs in the experimental pen were offered approximately 2kg per individual of this diet at 0830h.

'The Edinburgh Foodball'

The foraging device used in this experiment was the 'Edinburgh Foodball' (designed by R.J. Young and J. Carruthers; British patent no. 9200499.3 held by the British Technology Group Ltd., London). An outline of the feeder's design is given in Figure 5.1.

Figure 5.1: The 'Edinburgh Foodball'





The device was designed using the following criterion; (a) that the dispensing of food was dependent upon sows directing species-specific foraging behaviour towards the device (walking and rooting); (b) that the device delivered food in a manner similar to the distribution of food under more natural conditions with the food being distributed randomly in time (i.e., variable interval schedule of reinforcement), space and quantity.

The Foodball was comprised of a spherical casing (500mm in diameter) containing a food dispensing hole and an internal food store which was fitted with a meterable food dispensing mechanism (total weight when not containing food 18kg). Food was initially dispensed from the food store to the inside of the Foodball casing when the Foodball was rolled over the plane of the dispensing mechanism. The food was subsequently delivered from the inside of the Foodball casing to the animal when the food dispensing hole made contact with the ground. The spherical shape of the Foodball meant that it could be moved by the animal around its environment. The number of food deliveries from the food store to the inside casing and subsequent delivery of food to the animal was dependent upon how the animal rolled the Foodball.

Experimental protocol

The pigs were exposed to four consecutive test periods (outlined below) and were all tested individually.

BASELINE (days 1 to 4); The experimental pig was moved to the experimental pen at 0825h and offered 2kg of food in the centre of the experimental pen at 0830h. The animal was returned to the holding pen at 1700h.

At 1700h on day 4, the experimenter entered the pen and placed a Foodball containing 5kg of food and set to deliver 11g/revolution from the food store to the inside casing of the Foodball; in the centre of the pen. The experimenter then placed Foodball in front of the animal and rolled the Foodball around the pen. This was continued until the animal began to root the Foodball. The animal had to root the Foodball for a minimum of 45mins before it was considered to have learnt how to use the device. All animals fulfilled the learning criterion within 1hr and were returned to the home pen at 1800h.

FOODBALL (Days 5 to 7); The animal was introduced into the experimental pen as in days 1 to 3 and the Foodball (set to deliver food at 11g/revolution) was placed in the centre of the pen at 0900h and remained in the pen until 1700h, giving the pig the opportunity to obtain an extra 5kg of food from the Foodball on these days. The extra amount of food consumed on Foodball days, was estimated by weighing the food remaining in the Foodball.

EXTINCTION (Days 8 to 9); These days were identical to days 5 to 7, except a Foodball was placed in the pen that contained no food. This Foodball instead contained 2.5kg of gravel, the dispensing mechanism was closed so that this was not dispensed. The objective was to simulate the weight and sound of the Foodball used in days 5 to 7.

FOOD (Days 10 to 12); These days were identical to days 1-3, except that the amount of food offered was increased by the amount of food dispensed from the Foodball on days 5-7, such that the amount of food the animal received on days 10 to 12 was matched to that received on days 5 to 7. At 0830h the pig was offered 2kg of food with the additional food being offered at 0900h.

Data recording

The pigs were time lapsed videoed on all experimental days from 0900 to 1700h (Panasonic time lapse video recorder model AG-6720; Matsushita Electric Industries, Japan). Behavioural data were collected every 30secs on checksheets into the following three categories; posture, behaviour (including locomotion) and substrate's (see Table 5.1).

STATISTICAL ANALYSIS

For the purposes of analysis two behaviours, push and feed were combined into a measure called Foodball activity and three behaviours root, push and feed were combined into a variable called foraging activity, nose was not included as the analyses suggested it had a different function to root (see Results). Three substrates straw, Foodball and food, were combined into a variable called foraging substrate.

Table 5.1: Ethogram

Category	Description of activities
Postures	Standing, lying (on side or stomach) and sitting (whilst performing any activity listed below).
Activities	Root (straw directed only), push (roots directed at Foodball), feed, nose (exploratory investigations of substrates with snout), drink, sleep (lying eyes closed), openeyes (no obvious expression of behaviour with eyes open), comfort (substrate directed) and other (see Results). Walking, slow walking (low walking gait) and stationary.
Substrates	Straw, Foodball, food, drinker and pen.

All data were converted to proportions of observations per day animals spent in or interacting with the various postures, activities and substrates. The data were then averaged across test periods within pigs. The time periods outlined in the materials and methods were considered as four different treatments. Thus, each pig had a mean value for each category for each time period (i.e. four values for each posture, locomotion, behaviour and substrate listed in Table 5.1). Each of the categories in Table 5.1 were then analysed by analysis of variance using a within pig analysis and one factor (with four treatment levels; Genstat 5, Lawes Agricultural Trust 1987). Post-hoc comparisons of treatment differences were determined by paired t-tests. The behaviours feed and push only occurred in two treatments and were also analysed by paired t-tests. Transformation of variables was done so as to maximise the normality of each data set. The following variables were square-root transformed: stand, sit, slow walk, root, drink, openeyes, nose and straw. The category walk was logt transformed and stationary was arcsine transformed. The following variables required no transformation: push, feed, foodball activity, foraging substrate, lie, sleep, comfort and pen.

To examine the relative effects of Foodball on behaviour push and feed were subtracted from the time budget. To examine the effect of food level on activity sleep was removed from the time budget on the assumption that sleep would increase with food level. The effect of these controls were examined for their effect on root, drink, walk, nose, comfort, openeyes and sleep using the same structure of anova described above. The previously used transformations were applied to the adjusted data sets.

RESULTS

Description of Foodball directed behaviour

The pigs rooted the Foodball with the upper side of their snout in a manner similar to that described by Stolba and Wood-Gush (1989) for feral pigs foraging for food items just below the surface of the ground (called 'pushing' in this thesis to distinguish it from the rooting of straw bedding). That is they inserted the end to the middle of their snout under an exposed edge and then quickly raised their head propelling the foodball forward. Rooting of the Foodball was usually performed whilst walking. If the foodball came to rest in a corner pigs quickly learned to root it out at right angles from the corner. Also unless food was released the pigs usually did not allow the foodball to stop moving and this probably reduced the energetic cost of using the foodball by conserving momentum.

On the upward stroke of the root directed towards the foodball, pigs usually made an audible sniff. This appeared to be the primary means by which pigs detected when food was released from the foodball, since when food was dispensed during a rooting stroke (whilst sniffing) the pigs head moved down on to the food without any apparent use of visual cues. When released the food trickled down between the straw bedding, the pig then stood stationary rooted out and ingested the food. The fact that no food was found in the pen at the end of an experimental session suggests that this was a efficient method of detecting food (also see below).

Naive pigs initially rooted the foodball in apparently random patterns around a pen, but after about two days of continuous exposure more consistent geometric patterns of foodball use emerged. The most common geometric patterns were 'S' shapes, figures of eight and circles, however it should be noted that these patterns of use were broken up by periods of random geometric patterns. The factors causal in the development of these patterns were unknown, although pen size probably had an influence. Also it was observed after a few days that pigs would avoid rooting the foodball through the area where they made a sleeping nest. Implying that the patterns the foodball were rooted in were not only a response to physical characteristics of their environment and that these patterns were probably learned responses.

Immediately after a bout of rooting the foodball all pigs were observed to accurately retrace patterns that they had used to root the foodball and in the same area of the pen. This implies that the foodball was not only stimulating foraging behaviour when it was in use but also provided residual foraging stimulation; as pigs apparently searched for food dispensed from the foodball that had not been consumed when the foodball was in use. Again this behaviour probably accounted for the fact that no food was found in the pen after an experimental session.

Statistical results

During FOODBALL pigs obtained an average of 2608g (± 257) of food from the Foodball. Dividing the average amount of food consumed by the average amount of time spent in Foodball activity (push and feed combined), showed that pigs obtained 21.8g/min (±1.4) of Foodball activity. Separating out the effects of push and feed shows that pigs obtained food at 35.4g/min (±2.7) when pushing (which maybe equated to searching time) and 59.9g/min (±5.1) when feeding (which maybe equated to handling time). Thus, the mean ratio of searching to handling time was 1.0:1.8secs (±0.1). Pigs showed considerable individual variation in the rate in which they obtained food from the Foodball (Table 5.2).

Pushing was found by paired T-test to occur significantly longer during FOODBALL when compared with EXTINCTION (t= 6.1; d.f. 5; p<0.01; Table 5.3). The behaviour feed only occurred during FOODBALL and FOOD, and again it was found by paired T-test to occur longer during FOODBALL (t= 3.0; d.f. 5; p<0.05; Table 5.3). These two behaviours can be combined to indicate the magnitude of the effect of the Foodball on the time budget of pigs. Thus, pigs on FOODBALL were involved in Foodball activity for 0.2350 (±0.0329) of observations (or a mean of 112.8 ± 15.8 minutes per day). When root was added to Foodball activity a total of 0.3483 (±0.0928) observations were spent in foraging activity by pigs on FOODBALL.

An analysis of variance on foraging activity showed significant treatment differences (mean proportions of observations in foraging activity: 0.4000 (±0.1254), 0.3483 (±0.0928), 0.3000 (±0.0802) and 0.1800 (±0.0586): for treatments BASELINE, FOODBALL, EXTINCTION and FOOD respectively: F= 6.20; d.f. 3,15 ; p<0.01). A post-hoc comparison of treatment effects on foraging activity showed only a significant difference between FOODBALL and FOOD (t= 5.28; d.f. 5; p<0.01: Table 5.3). Comparing the behaviour root within BASELINE and foraging activity within FOODBALL by a paired T-test showed no significant difference (t= 0.75; d.f. 5; p= 0.49: means BASELINE 0.4000 (±0.0512) and FOODBALL 0.3483 (±0.0379)). The same comparison for straw against the Foraging substrates within FOODBALL by paired T-test again showed no significant difference (t= 2.08; d.f. 5; p= 0.09: means BASELINE 0.4133 (±0.0539) and FOODBALL 0.3800 (±0.0800)).

Table 5.2: Mean (± s.e.m.) values of individual pigs Foodball directed activities

Pig No.	Foodball Food Intake (g)	Foodball Activity (g/min)	Searching Time (g/min)	Handling Time (g/min)	Ratio (push: feed, secs)
2	1678 ±214	22.3 ±0.5	33.7 ±1.1	65.5 ±0.2	1.9:1.0 ±0.1
3	3278 ±1292	27.7 ±10.4	48.8 ±24.5	69.2 ±10.1	1.8:1.0 ±0.7
7	2867 ±794	17.5 ±6.4	32.1 ±15.5	40.4 ±7.2	1.5:1.0 ±0.5
8	2059 ±403	22.7 ±3.2	32.8 ±4.4	74.7 ±11.5	2.3:1.0 ±0.1
173	3150 ±173	19.3 ±1.2	30.7 ±0.6	53.1 ±7.2	1.7:1.0 ±0.2
175	2615 ±379	21.4 ±2.0	34.7 ±4.5	56.8 ±1.6	1.7:1.0 ±0.2

(Search time= time spent pushing the Foodball divided by the amount of food consumed; Handling time= time spent feeding divided by the amount of food consumed).

Table 5.3: Mean (± s.e.m.) proportions of observations spent in each behavioural category

	Treatment			
Category	BASELINE	FOODBALL	EXTINCTION	FOOD
Postures				
Stand	0.55 ±0.07	0.44 ±0.04	0.41 ±0.04	0.29 ±0.03
Lie	0.42 ±0.06	0.54 ±0.03	0.55 ±0.03	0.68 ±0.03
Sit	0.03 ±0.01	0.02 ±0.01	0.04 ±0.02	0.03 ±0.01
Activities				
Root	0.40 ±0.05	0.13 ±0.04	0.28 ±0.03	0.13 ±0.01
Push	N.A.	0.15 ±0.02	0.02 ±0.00	N.A.
Feed	N.A.	0.09 ±0.01	N.A.	0.05 ±0.01
Nose	0.03 ±0.01	0.02 ±0.00	0.02 ±0.01	0.02 ±0.00
Walk	0.03 ±0.01	0.15 ±0.02	0.02 ±0.01	0.01 ±0.00
Slow Walk	0.13 ±0.06	0.04 ±0.01	0.06 ±0.01	0.03 ±0.01
Stationary	0.85 ±0.06	0.80 ±0.01	0.92 ±0.02	0.96 ±0.01
Openeyes	0.17 ±0.04	0.14 ±0.03	0.20 ±0.03	0.19 ±0.03
Sleep	0.32 ±0.05	0.44 ±0.04	0.42 ±0.04	0.57 ±0.04
Drink	0.03 ±0.01	0.02 ±0.00	0.02 ±0.00	0.02 ±0.00
Comfort	0.01 ±0.01	0.01 ±0.00	0.01 ±0.00	0.01 ±0.00
Other	0.03 ±0.01	0.01 ±0.00	0.03 ±0.01	0.02 ±0.00
Substrates				
Foodball	N.A.	0.16 ±0.02	0.02 ±0.00	N.A.
Food	N.A.	0.09 ±0.01	N.A.	0.05 ±0.01
Straw	0.41 ±0.05	0.13 ±0.04	0.29 ±0.04	0.13 ±0.01
Pen	0.05 ±0.01	0.02 ±0.00	0.03 ±0.01	0.03 ±0.01
Drinker	0.03 ±0.01	0.02 ±0.00	0.02 ±0.00	0.02 ±0.00

(N.A. = not applicable)

The posture of the pigs was found to be significantly affected by treatment (F-values for standing, lying and sitting: F= 6.4, 5.3, and 3.4; all d.f. 3,15; p-values: $p<0.01$, $p<0.05$ and $p<0.05$: Table 5.3). There were no significant effects of pig. Post-hoc comparisons show that the treatment differences in standing are due to pigs on BASELINE and FOODBALL standing the most (Table 5.4), and that treatment differences in lying are due to FOOD pigs lying the most (Table 5.4).

All three categories of locomotion were found to be significantly affected by the treatments (F-values for walking, slow walking and stationary: F= 49.23, 4.17, 7.96; all d.f. 3,15; p-values: $p<0.001$, $p<0.05$ and $p<0.01$). Post-hoc comparisons of walking show that the significant differences are mainly due to FOODBALL pigs walking at a high frequency (Table 5.4). The significant difference in treatments for slow walking was due to pigs on performing more slow walking than when on FOOD (Table 5.4). The post-hoc comparisons of stationary are due to FOOD pigs being stationary the most (Table 5.4). The effects on walking remained even after treatment manipulations were controlled (Table 5.5)

Rooting was significantly effected by treatment (F= 20.3; d.f. 3,15; $p<0.001$), but not by individual pig. Post-hoc comparsions show that the only non-significant comparison was between FOODBALL and FOOD (Table 5.4). When the effects of various behaviours were controlled for in the time budget there were still significant differences between treatments (see Table 5.3 and Table 5.5).

The level of drinking shown by the pigs was significantly affected by treatment (F= 4.11; d.f. 3,15; $p<0.05$). Post-hoc comparisons showed that pigs on FOOD drank less than BASELINE (Table 5.4). Controlling for the effects of the treatment manipulations on the time budget removed the treatment effects on drinking (Table 5.5).

In all four treatments sleeping was found to occupy more than 0.3 of the pigs time budget (Table 5.3) and was found to be significantly different across treatments (F= 5.25; d.f. 3,15; $p<0.05$) but not across individual pigs. Post-hoc comparisons showed that pigs on FOOD tended to sleep the most (Table 5.4). When the effects of push, feed singularly and jointly were controlled for significant treatment effects remained (see Table 5.3 and Table 5.5).

Nosing was not significantly affected by treatment (F= 1.8; d.f. 3,15; N.S.), but was significantly affected by individual pig (F= 4.77; d.f. 5,15; $p<0.01$). This suggests that although nosing appeared similar to rooting they are probably solicited by different motivational systems. When the effects of treatment manipulations were controlled for, no significant treatment differences were observed indicating that the expression of this behaviour was independent of treatment manipulations (Table 5.5).

Openeyes was not significantly affected by treatment (F= 2.39; d.f. 3,15; N.S.) but was significantly different across pigs (F= 11.5; d.f. 5,15; $p<0.01$). Comfort behaviour was found to be significantly affected by both treatment (F= 3.4; d.f. 3,15; $p<0.05$) and individual pig (F= 35.9; d.f. 5,15; $p<0.001$). Post-hoc comparisons showed that the expression comfort behaviour was significantly higher in FOOD than in FOODBALL or EXTINCTION

(Table 5.4).

Table 5.4: Paired t-test results of post-hoc analysis of variance treatment comparisons

Activities	Treatment Comparisons					
	B v Fb	B v E	B v Fd	Fb v E	Fb v Fd	E v Fd
Stand	1.27	2.84^{*}	3.17^{*}	0.71	5.37^{**}	2.31
Ly	1.38	2.07	3.03^{*}	0.19	4.60^{**}	2.61^{*}
Sit	1.72	1.29	0.13	2.91^{*}	1.91	1.70
Walk	6.10^{**}	2.24	2.76^{*}	7.13^{***}	15.96^{***}	2.20
Slow Walk	1.84	1.92	2.29	1.35	1.45	3.00^{*}
Stationary	1.02	2.04	2.28	4.14^{**}	11.00^{***}	2.64^{*}
Root	5.70^{**}	2.85^{*}	5.52^{**}	4.25^{**}	0.39	4.54^{**}
Drink	1.15	2.17	2.95^{*}	0.87	1.13	1.00
Sleep	1.64	1.66	3.42^{*}	0.22	4.17^{**}	2.50
Comfort	1.46	2.24	0.54	0.00	3.16^{*}	3.16^{*}
Straw	5.66^{**}	2.81^{*}	5.63^{**}	4.12^{**}	0.16	4.52^{**}
Pen	5.53^{**}	3.46^{*}	3.80^{*}	0.79	7.00^{***}	2.08

All d.f. 5; $^{*}p<0.05$, $^{**}p<0.01$ and $^{***}p<0.001$

Table 5.5: F-values and significance levels for the behaviour expressed by pigs with controlling factors.

Control Behaviour	Sleep	Push	Feed	Foodball	All
Root	12.16^{***}	11.62^{***}	11.58^{***}	9.94^{***}	5.39^{*}
Drink	0.53	1.42	1.31	1.44	1.52
Nose	0.16	1.01	1.01	2.07	0.47
Openeyes	2.67	0.22	0.38	0.12	1.68
Comfort	0.77	0.25	0.34	0.25	0.56
Sleep	N.A.	6.82^{**}	8.69^{***}	10.39^{***}	N.A.
Walk	37.28^{***}	36.90^{***}	34.26^{***}	37.74^{***}	49.63^{***}

All d.f. 3,15; * $p<0.05$, ** $p<0.01$ and *** $p<0.001$.

When the effects of treatment manipulations were controlled for on openeyes and comfort, there was no significant treatment differences showing that the effects were only absolute and not proportional on the time budget. All other behaviours observed did not occur at a proportion above 0.01 and were therefore grouped together into a category called 'other', this included observe, alert, chew, dig, eliminative, paw and carry. Due to the heterogeneous nature of this category it was excluded from the analyses.

During all four treatment periods only three substrates straw, pen, and drinker were present in each treatment. The substrate drinker was not analysed as the data for drinker were identical to those for drinking. The substrates straw and pen were significantly affected by treatment (F-values for straw and pen: F= 20.2 and 13.3; all d.f. 3,15; p-values: all $p<0.001$). Post-hoc comparisons show that the effect on straw use was the same as root the only non-significant difference being between FOODBALL and FOOD (Table 5.4).

DISCUSSION

Previous studies (Lawrence, Appleby and MacLeod 1988; Lawrence and Illius 1989) suggest that food restricted sows are highly food motivated. However, these studies can be criticised on the grounds that they were conducted under artificial conditions using an arbitrary operant device and testing the animals responses over short time periods in an otherwise barren environment. The present results extend these findings, illustrating that food deprived gilts will express foraging type behaviour over long periods of time in a reasonably complex environment. These results therefore suggest that food restriction in sows gives rise to heightened feeding motivation and that when given the opportunity sows will express this feeding motivation as foraging behaviour. The results also suggest that the Foodball is an useful device for measuring feeding motivation. The very short training period required for the animals to use the Foodball indicate that it represents a species typical foraging response for pigs.

The results from the EXTINCTION period suggests that the use of the Foodball was dependent upon food reinforcement and that without food the Foodball has little reinforcing properties. This finding is in agreement with more classical operant studies where use of operant devices such as levers are similarly dependent on food reinforcement (Mackintosh 1974) and with a behavioural enrichment study where Pacific Walruses would only forage from a behavioural enrichment device when food was available from the device (Kastelein and Wiepkema 1989). This indicates that for a behavioural enrichment device to have a positive long term effect on behaviour it must offer more reinforcement than its initial novelty value.

Pigs showed considerable individual differences in the amount of food they obtained from the Foodball. The rate of food acquisition during pushing can be used as a measure of foraging efficiency (because it compares energy expenditure to energy gain) and the large individual differences between pigs in this measure may have resulted from different levels of intrinsic feeding motivation or differential learning abilities.

The results can also be used to indicate the effects of increased foraging time on pig's time budgets. The effects of the treatments suggest that appropriate foraging behaviour was dependent on feeding motivation and was directed towards the most appropriate substrate. Foodball use was associated with a significant reduction in rooting behaviour. This is likely to be a partial reflection of the extra food as rooting was also depressed during the FOOD treatment. However, the results also suggest that Foodball directed behaviour may have acted to replace the rooting behaviour directed towards straw observed on the other treatments. The continued expression of rooting during the FOODBALL treatment appears largely to have resulted from pigs searching from food dispensed by the Foodball. The results support a previous suggestion that food motivated pigs will direct their foraging behaviour towards the substrates with the highest incentive value in that environment (Lawrence and Terlouw, in press). These results therefore suggest that the increase in activity expressed by food deprived animals is primarily food and not exploration motivated (see Baumeister, Hawkins and Cromwell 1964).

The present and other studies show that high fed pigs are more inactive and sleep longer than low fed animals (Terlouw, Lawrence and Illius 1991). However, the effect of the Foodball showed that this effect is in part dependent on method of food presentation. The effect of food level on sleep results from physiological changes associated with the reinforcement of feeding behaviour (Houpt 1985) and one of its effects may be to modulate the expression of appetitive behaviour in an adaptive manner (see Baumeister, Hawkins and Cromwell 1964). For example, it may reduce the expression of foraging in animals without a major nutrient deficit thereby optimising energy usage and reducing exposure to environmental dangers such as predation (see McFarland 1989). This therefore suggests that the level of sleep animals show, should have a relatively low behavioural resilience to other changes in the time budget which is in agreement with the present results. However, sleep may have net benefits even when animals have a large but non-life threatening physiological deficit such as predator avoidance (see Meddis 1975; McFarland 1989).

The reduction in drinking during FOOD when compared to BASELINE was surprising since drinking would be expected to show behavioural resilience, and water intake normally increases with food intake (Yang, Howard and MacFarlane 1981). It may have been the case that BASELINE pigs consumed excessive amounts of water in response to high feeding motivation as in a previous study (Terlouw, Lawrence and Illius 1991). However, since water intake was not directly measured these results should be treated with caution.

The effects of controlling for treatment manipulations on the following behaviours drink, nose, openeyes, and comfort showed that these behaviours only changed in the absolute time budget and were therefore behaviourally resistant. Whereas the expression of the behaviours root, sleep and walking were changed both absolutely and proportionally in the time budget indicating that these behaviours were less behaviourally resistant. The level of behavioural expression of root, walk and sleep across treatments suggests that this is dependent upon the level of resources in an animals environment such as food.

Pigs with the Foodball expressed a similar foraging and locomotion time budget to that observed in free-ranging conspecifics (see Stolba and Wood-Gush 1989). One criterion of good animal welfare is the expression of a time budget similar to that expressed by free-ranging conspecifics (Bayne, Dexter, Mainzer, McCully, Campbell and Yamada 1992) has therefore been fulfilled. This resulted from the Foodball creating a continuously replenishing foraging environment which stimulated the animals to perform complex and variable species-specific foraging behaviour.

The Foodball therefore appears to be a useful device for increasing foraging opportunities and behaviourally enriching environments for pigs by providing them with a reinforced species-specific behaviour to particularly utilise their time. As an experimental tool the Foodball allows measurement of feeding motivation in a species-specific foraging context. It therefore represents a methodological synthesis between psychological and ethological approaches to the study of animal behaviour. The use of the Foodball in future experiments will enhance our understanding of the relationships between feeding motivation, learning and the expression of foraging behaviour.

- Chapter 6 -

The effects of high and low rates of reinforcement on the foraging behaviour and time budget of pigs

INTRODUCTION

The decision of an animal to perform one behaviour rather than another, and how to express that behaviour is dependent upon the complex interaction of a number of factors including underlying motivational systems (e.g., Toates 1987), environmental constraints (Leger, Owings and Coss 1983) and the time constraint imposed by performing that behaviour (Swennen, Leopold and De Bruijn 1989). These factors interact to produce the time budget expressed by the animal and to modulate the expression of each behaviour.

The ease with which, a behaviour is compressed in time and its proportional change in the time budget is referred to as its behavioural resilience (Houston and McFarland 1981). It is assumed that more important behaviours, such as those correcting physiological deficits will show the greatest resistance to compression and high compensation (Hogan and Roper 1978; Toates 1987).

The evolutionary functions of animal behaviour can be divided into those which are short-term, such as those relating to immediate physiological needs and those which are long-term, such as those relating to genetic survival. Optimality theory predicts that when an animal is in an environment where all functional resources are available an animal should make optimal use of them. If an animal was to use up all its daily time budget correcting its immediate physiological deficits (which may be optimal in the short-term see Dawkins 1986) then it would not have time left to find a mate and reproduce (long-term optimality see Dawkins 1986).

Therefore, such a strategy would ensure individual survival but possibly result in the animals 'genetic death' (Schoener 1971). Furthermore, being an adequate (non-optimal) forager with some time available to perform non-physiologically essential behaviours, such as reproduction, is not an evolutionarily stable strategy (see Parker 1984). Animals entering the environment that utilised their time more efficiently would have more time available to perform other important behaviours such as mate finding and body maintenance (see Lemon and Barth 1992); eventually the genes of the adequate forager would be replaced in the gene pool by the genes of the optimal forager (Dawkins 1976; McFarland 1985).

Optimality theories of animal behaviour are used by ethologists to produce testable models of animal behaviour. Testing of such models from foraging experiments has produced qualitative but often not quantitative support for such models (for a review see Krebs and McCleery 1984; for a criticism see Gould and Lewontin 1979). A problem with testing optimality models is that for methodological reasons the foraging problems that can be posed are often not as complex as those experienced by a forager under natural conditions.

Animals in an environment where a resource such as food is scarcely distributed have many options to gain their desired nutrient intake. They could increase the amount of time they spend performing a behaviour to obtain more of the resource (Dunbar and Dunbar 1988), they could increase the rate or the efficiency of their appetitive behaviour (Collier and Rovee-Collier 1981), they could decrease the expression of energy expending behaviour and wait until food abundance increases (Bekoff and

Wells 1981), they could move to another food patch (Charnov 1976) or use a combination of options.

The present experiment examined the effects of different rates of food supply on the behaviour and time budget of pigs. This was done using a foraging device, 'The Edinburgh Foodball', to supply the food at two different reinforcement rates. In this experiment all aspects of food delivery, time between reinforcers, reinforcer size and position of reinforcer in the pen were dependent upon the animals behaviour. These characteristics of the Foodball meant that an animal using it, could respond to decreased reinforcement rate by a variety of methods (see previous paragraph). It was predicted that the pigs would optimise their foraging behaviour in the following experiment by maximising their food encounter rate (which is equivalent to maximisation of energy intake). This would have the net effect of allowing pigs the maximum amount of time available to perform other behaviours once their physiological requirements for food had been met.

MATERIALS AND METHODS

Animals

The animals were six primiparous Large White X Landrace X Duroc gilts (sexaully mature young adults; Cotswold Pig Development Company, Lincoln, U.K.) that had an initial average weight of 150±4kg.

Housing

The animals were housed in two adjacent strawed pens (one holding and one experimental) within the same open fronted building, both pens measured 9m x 3m.

Management

Both pens were covered by a thick layer of straw. The holding pen was cleaned out twice a week and fresh straw added at this time. Fresh straw was provided daily to the experimental pen (at the rate of approximately 2kg/day) and cleaned out twice per week.

Food

Pigs in the holding pen were floor fed at 0830h and offered 2kg of food per animal. During the experiment animals were offered a standard pelleted sow diet, each kilogram contained 13.2 MJ/DE, 170g of crude protein, 53g of crude fibre, 40g of oil, 63g of ash and 870g of dry matter.

Experimental training

Pigs were trained individually; at 0825h prior to feeding the experimental pig was moved from the holding to the experimental pen. Placed in the centre of this pen was a 'Foodball' (described in Chapter 5; British patent no. 9200499.3 held by British Technology Group Ltd., London; designed by R.J. Young and J. Carruthers, SAC-Edinburgh, Edinburgh) containing

5kg of food and set to dispense 11g/revolution of food from the food store to the inside of the casing. The animal was left to 'shape' to the 'Foodball'. At 1630h the animal was placed back in the holding pen. This procedure was repeated on the next day such that each animal received two days of training.

The Foodball was comprised of a spherical casing containing a food dispensing hole and an internal food store which was fitted with a meterable food dispensing mechanism. Food was initially dispensed from the food store to the inside of the Foodball casing when the Foodball was rolled over the plane of the dispensing mechanism. The food was subsequently delivered from the inside of the Foodball casing to the animal when the food dispensing hole made contact with the ground. The spherical shape of the Foodball meant that it could be moved by the animal around its environment. The number of food deliveries from the food store to the inside casing and subsequent delivery of food to the animal was dependent upon how the animal rolled the Foodball.

Experimental testing

At 0825h the previously trained animal was placed in the experimental pen. The 'Foodball' containing 5kg of food was placed in the centre of the pen. The rate of food delivery was set to either a high (18g/rev) or a low (3g/rev) reinforcement rate. This reinforcement rate was maintained for six consecutive days and then switched to the other reinforcement rate for the next six consecutive days. The experimental design was balanced so that three animals experienced the high reinforcement rate followed by the low one and the other three animals the opposite treatment. Furthermore animals were alternated starting high or low, to randomise any time effects.

Data recording

During the test period animals were time lapsed videoed from 0830h to 1630h (using a Panasonic model AG-6720 Time Lapse Video Recorder, Matsushita Electric Industries, Japan). Behavioural data were collected on days 1, 3 and 6 on both reinforcement rates by time sampling every 30secs onto checksheets. Behaviour was categorised according to the Ethogram in Table 6.1. Also recorded were the frequency of all contacts the animal made with the 'Foodball', that resulted in it moving and the frequency of all reinforcement deliveries. These data were recorded on days 1 to 6 for both treatments and collated on an hourly basis as per the behavioural data. At the end of each day the total amount of food dispensed by the 'Foodball' was calculated by weighing the food remaining in the 'Foodball'.

STATISTICAL ANALYSIS

All data analyses were performed using Genstat (version 5.0, Lawes Agricultural Trust 1987). The food intake data were analysed by a repeated measures analysis of variance (nested structures for treatment period and day) using a within pig analysis with two treatment levels (high and low reinforcement rate).

Table 6.1: Ethogram

Category	Description of activities
Postures	Standing, lying (on side or stomach) and sitting (whilst performing any activity listed below).
Activities	Root (straw directed only), push (roots directed at Foodball), feed, nose (exploratory investigations of substrates with snout), drink, sleep (lying eyes closed), openeyes (no obvious expression of behaviour with eyes open) and comfort (substrate directed). Walking, slow walking (low walking gait) and stationary.

The behavioural data, the frequency of pushing the Foodball and the frequency of feeding data were analysed by a repeated measures analysis of variance (nested structures for treatment period, hour and day) using a within pig analysis with two levels (high and low reinforcement rate). The following variables were square-root transformed to meet the requirements for parametric statistics lying, sitting, slow walking, stationary, rooting, drinking, nosing, openeyes, comfort, sleeping and frequency of bouted drinking. Standing and pushing required arcsine transformation. The following variables frequency of pushing, frequency of feeding, food intake, walking, feeding, latency of pushing and latency of feeding did not require transformation.

The effect of one behavioural variable on the expression of another was examined by linear regression analysis using the least squares method, using a single average value for each pig. Two variables pushing and feeding were added together making a variable Fbactivity to indicate the effect of the reinforcement rate on Foodball use. The effect of Fbactivity on the time budget was then analysed by linear regression analysis. Drinking lasting less than 15 seconds that was preceded and succeeded by pushing or feeding with the Foodball and that was within 1 metre radius of the drinker was called bouted drinking; its frequency was recorded as per the frequency of Foodball directed roots.

RESULTS

The repeated measure analysis of variance on the food intake data showed a significant treatment effect (F= 46.57; d.f. 1,5; $p<0.001$) due to pigs on the high reinforcement rate having a higher daily food intake (mean daily food intake: high= 4184±76.1g and low= 3610±115g). There were nearly significant differences between pigs (F= 4.46; d.f. 5,5; $p<0.1$) and days (F= 2.23; d.f. 5,50; p= 0.066) due to food intake tending to increase across the experiment (see Figure 6.1). There was however, no significant day x treatment interaction (F= 0.23; d.f. 5,50; p= 0.949). The order in which reinforcement rates were presented to the pigs had no significant effect on food intake.

Low reinforcement rate significantly decreased the proportion of time performing the following activities; sit, slow walk and root, whilst increasing walking and pushing (Tables 6.2 and 6.6). The proportions of all behaviours expressed were significantly affected by hour (Table 6.2) with all behaviours except pushing and feeding being expressed at a higher proportion later in the day. This effect was due to Fbactivity decreasing linearly during the day (see Figure 6.2). A significant effect of day on drinking (Table 6.2) was due to the behaviour peaking on day 3. A significant day x treatment interaction was observed for openeyes due to pigs on high reinforcement rate decreasing the proportion of openeyes expressed across the experimental period and those on low increasing openeyes. An hour x treatment interaction was observed for feeding (Table 6.2; Figure 6.3). An hour x treatment interaction was also observed for sleeping (Table 6.2; Figure 6.4).

Figure 6.1: The relationship between food intake and days on treatment

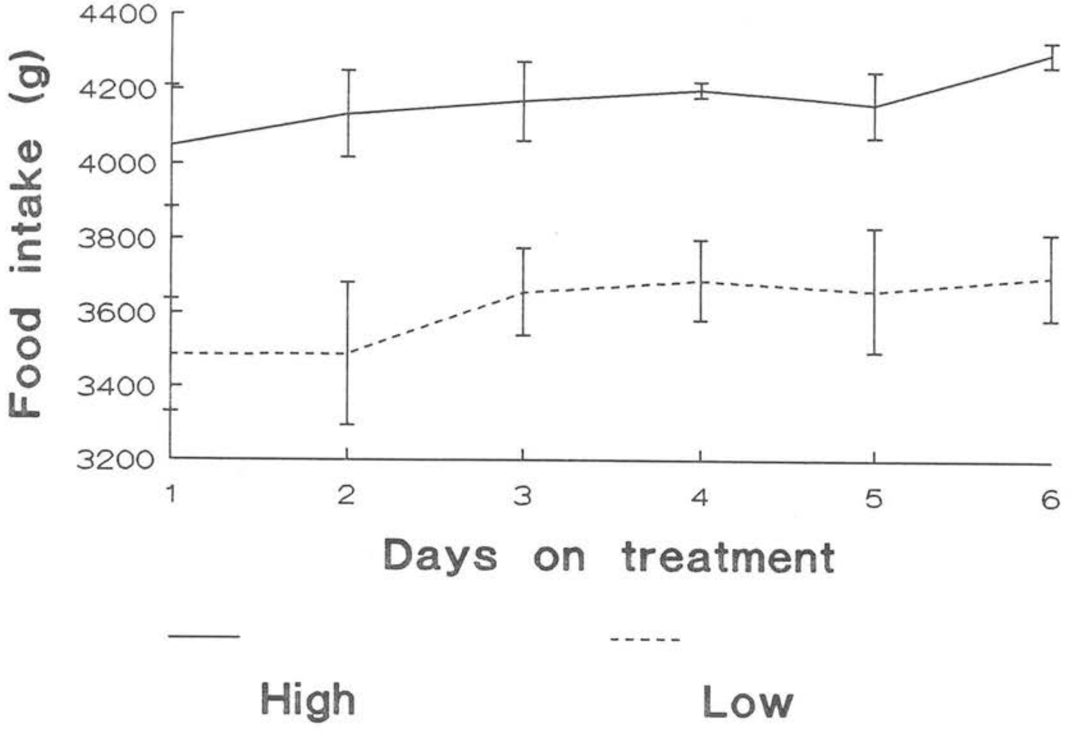


Figure 6.2: The relationship between Foodball activity, all other activities and time of day

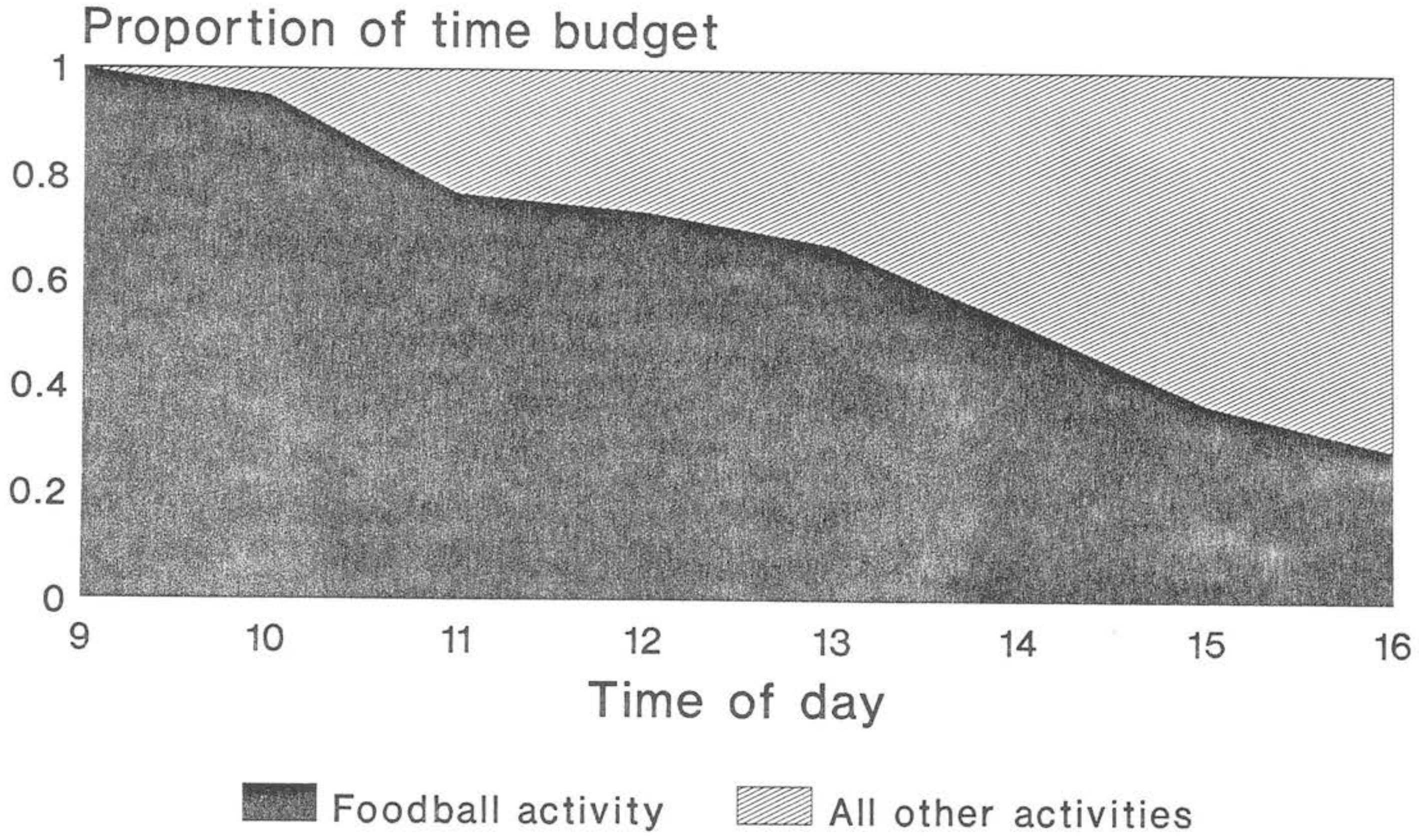


Figure 6.3: The relationship between feeding and time of day

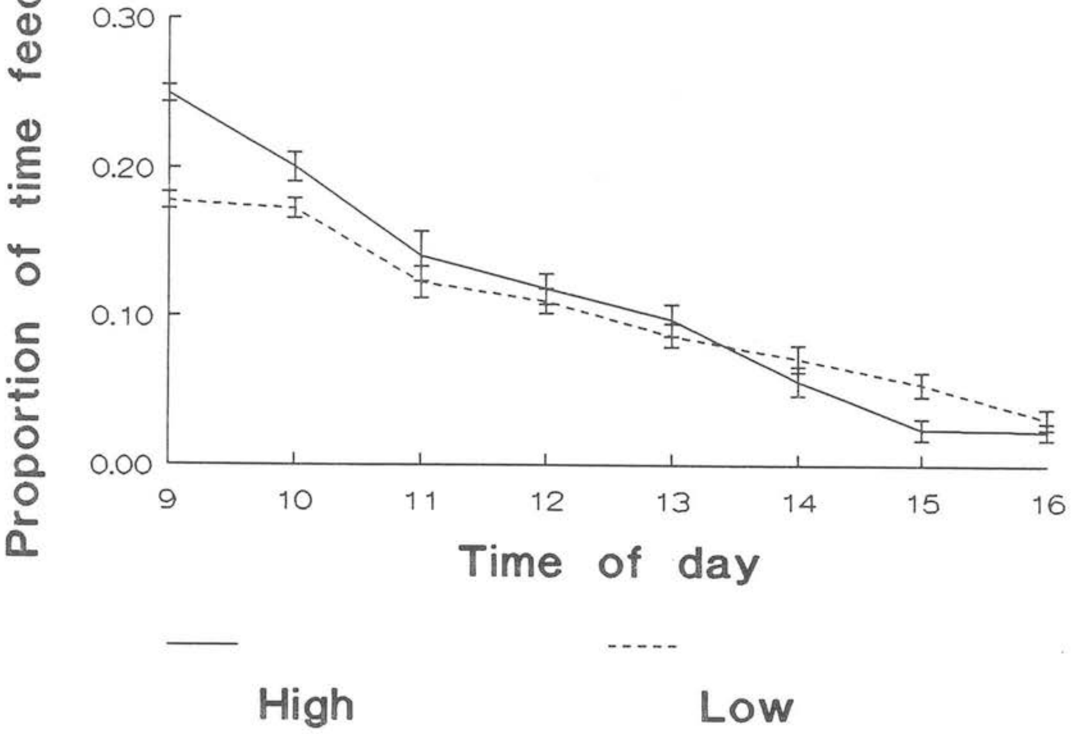


Figure 6.4: The relationship between sleeping and time of day

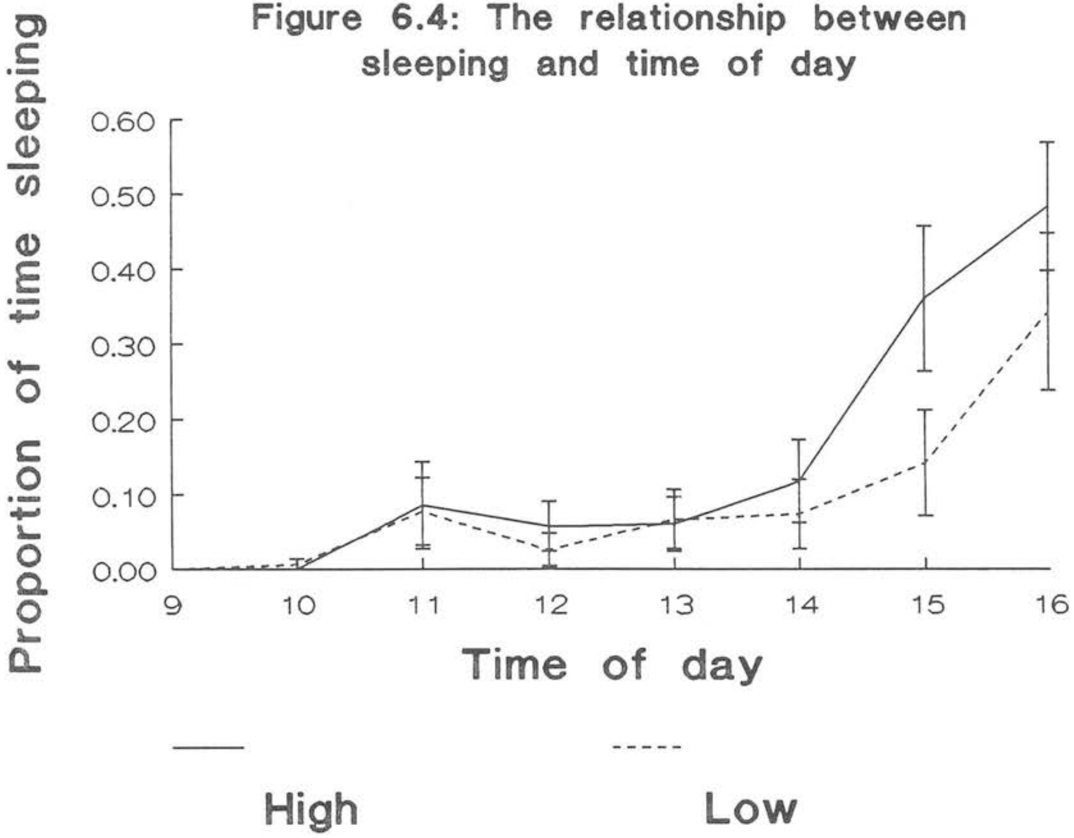


Table 6.2: F-values and significance levels for the analysis of variance on proportion of behavioural activities

Activities	Pig^{a}	Treat^{b}	Day^{c}	Day x Treat^{c}	Hour^{d}	Day x Hour^{e}	Hour x Treat^{d}	Day x Hour x Treat^{e}
Stand	3.42	2.11	0.29	1.23	26.51***	0.48	1.15	1.19
Ly	3.09	1.67	0.45	0.78	24.11***	0.66	0.89	0.77
Sit	11.06**	7.31*	1.16	0.43	2.23*	0.50	0.52	0.99
Walk	2.75	7.65*	0.31	0.11	37.83***	0.64	1.48	0.97
Slow walk	17.76**	86.36***	0.12	1.54	6.81***	0.52	1.89	0.28
Stationary	2.34	6.35	0.55	0.08	33.95***	0.51	0.66	1.03
Root	1.33	7.74*	0.18	1.26	20.87***	0.38	1.08	0.17
Push	2.77	7.03*	0.95	0.09	39.77***	0.66	1.62	0.78
Feed	1.31	1.28	0.63	1.57	141.40***	0.64	7.68***	1.24
Nose	1.09	0.26	0.42	2.62	3.85***	0.50	0.70	0.64
Drink	5.38*	3.48	4.10*	0.00	5.28***	1.22	1.68	0.66
Openeyes	2.18	1.75	0.39	5.67*	12.57***	0.62	0.52	0.47
Sleep	4.57	2.50	0.40	1.58	19.74***	0.91	2.16*	1.11
Comfort	0.80	0.69	0.37	0.41	7.93***	0.91	1.22	0.51

^{a}=d.f. 5,5; ^{b}=d.f. 1,5; ^{c}=d.f. 2,20; ^{d}=d.f. 7,210 ; ^{e}= d.f. 14,210 *p<0.05; **p<0.01 and ***p<0.001.

Table 6.3: F-values and significance levels for the analysis of variance on the frequencies of behavioural activities

Activities	Pig^a	Treat^b	Day^c	Day x Treat^c	Hour^d	Day x Hour^e	Hour x Treat^d	Day x Hour x Treat^e
Push	5.06^*	28.11^{**}	0.54	0.77	129.56^{***}	0.96	3.18^{**}	0.97
Feed	5.43^*	7.52^*	0.90	0.68	303.03^{***}	0.83	2.60^*	0.76

^{a}=d.f. 5,5; ^{b}=d.f. 1,5; ^{c}=d.f. 5,50; ^{d}=d.f. 7,420; ^{e}= d.f. 35,420: $^*p<0.05$; $^{**}p<0.01$ and $^{***}p<0.001$.

Table 6.4: F-values and significance levels for the analysis of variance on the frequency of behavioural activities

Activities	Pig^a	Treat^b	Day^c	Day x Treat^c	Hour^d	Day x Hour^e	Hour x Treat^d	Day x Hour xTreat^e
Bouted Drinking	1.59	4.96	3.59^*	0.64	30.52^{***}	0.35	2.72^*	0.74

^{a}=d.f. 5,5; ^{b}=d.f. 1,5; ^{c}=d.f. 2,20; ^{d}=d.f. 7,210; ^{e}= d.f. 14,210: $^*p<0.05$; $^{**}p<0.01$ and $^{***}p<0.001$.

Table 6.5: F-values and significance levels for the analysis of variance on the latencies of behavioural activities

Activities	Pig[a]	Treat[b]	Day[c]	Day x Treat[c]	Hour[d]	Day x Hour[e]	Hour x Treat[d]	Day x Hour x Treat[e]
Push	3.17	39.45**	0.85	2.66	35.10***	0.76	3.02**	1.27
Feed	2.64	34.18**	0.58	1.72	15.10***	1.08	0.86	0.94

[a] = d.f. 5,5; [b] = d.f. 1,5; [c] = d.f. 2,20; [d] = d.f. 7,210; [e] = d.f. 14,210: * $p < 0.05$; ** $p < 0.01$ and *** $p < 0.001$.

Table 6.6: Mean (± s.e.m.) of proportion of time spent performing behavioural activities

	Treatments	
Activities	Low	High
Stand	0.8652 ±0.0225	0.7874 ±0.0261
Lie	0.1314 ±0.0223	0.1992 ±0.0250
Sit	0.0064 ±0.0034	0.0186 ±0.0010
Walk	0.6334 ±0.0233	0.4900 ±0.0229
Slow walk	0.0151 ±0.0045	0.0315 ±0.0053
Stationary	0.3497 ±0.0220	0.4769 ±0.0220
Root	0.0918 ±0.0134	0.1431 ±0.0146
Push	0.6300 ±0.0231	0.4802 ±0.0240
Feed	0.1034 ±0.0050	0.1137 ±0.0072
Nose	0.0046 ±0.0011	0.0036 ±0.0010
Drink	0.0037 ±0.0007	0.0059 ±0.0007
Openeyes	0.0658 ±0.0089	0.1026 ±0.0137
Sleep	0.0927 ±0.0203	0.1459 ±0.0240
Comfort	0.0041 ±0.0011	0.0052 ±0.0012

Figure 6.5: The relationship between frequency of pushes and time of day

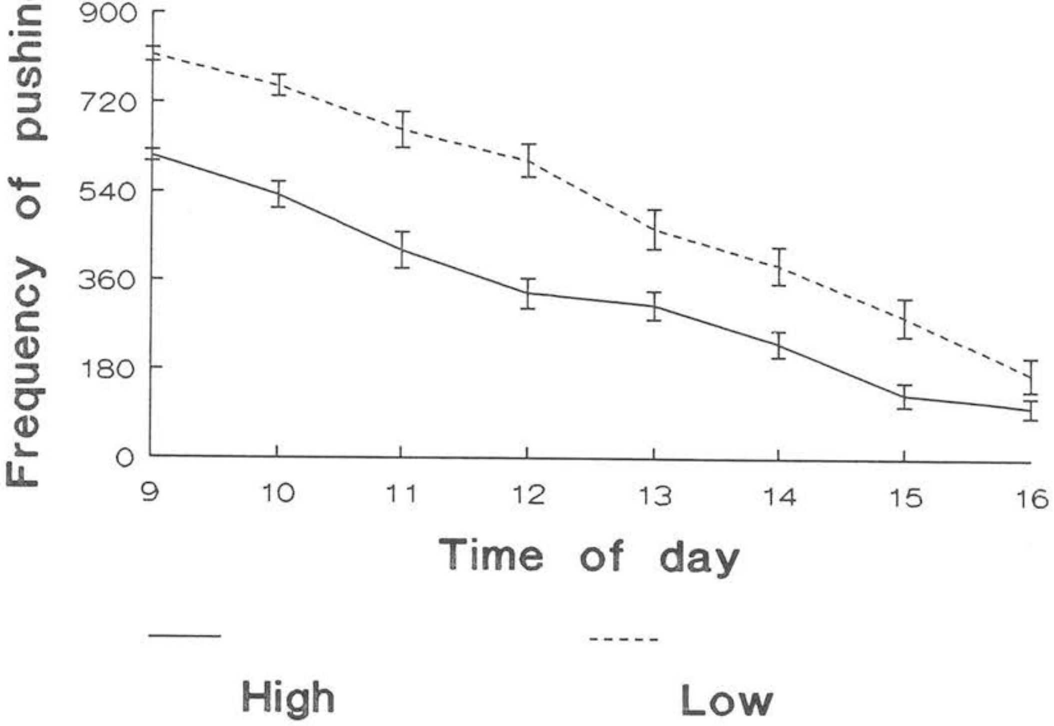


Figure 6.6: The relationship between frequency of feeding and time of day

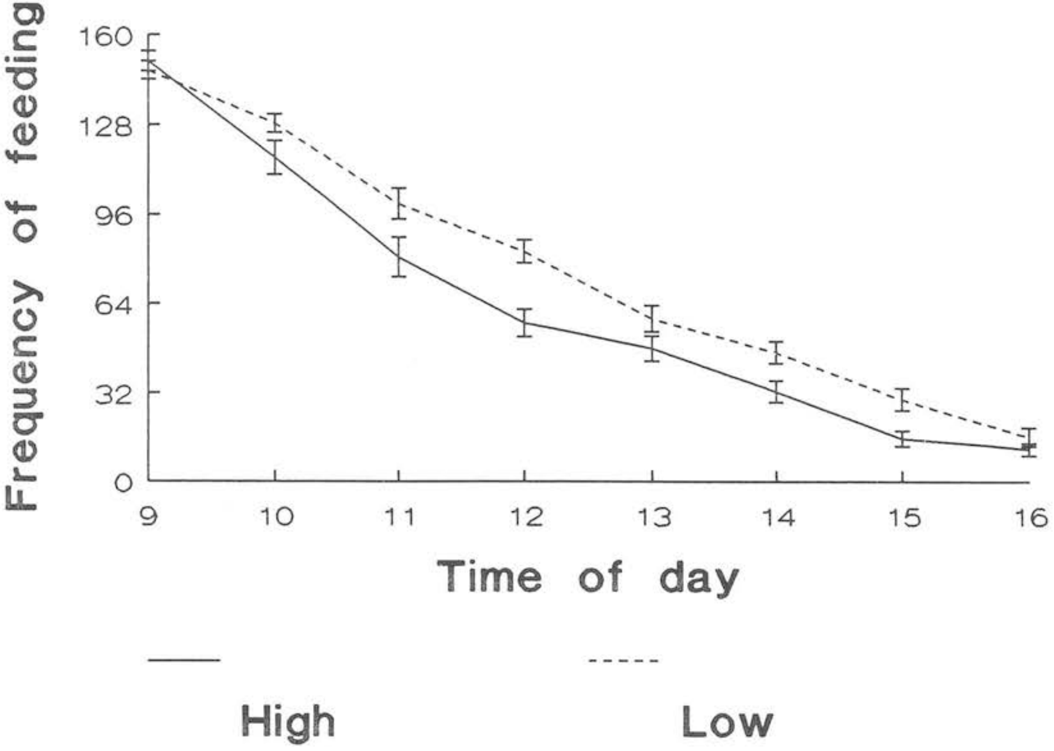


Figure 6.7: The relationship between bouted drinking and time of day

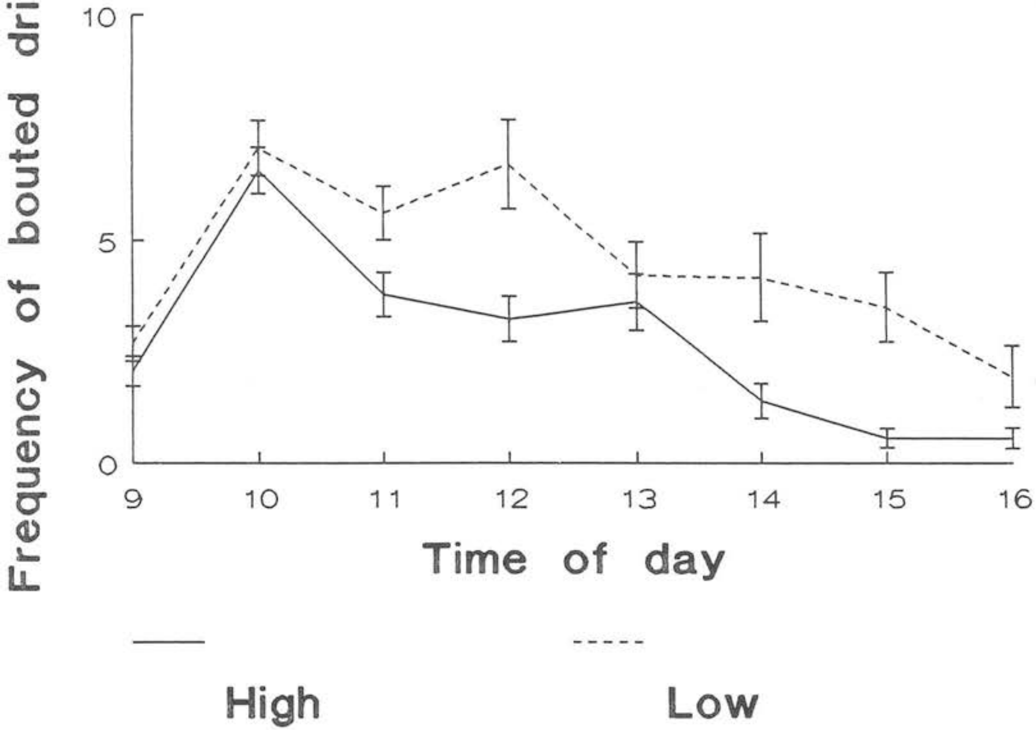


Figure 6.8: The relationship between latency of pushes and time of day

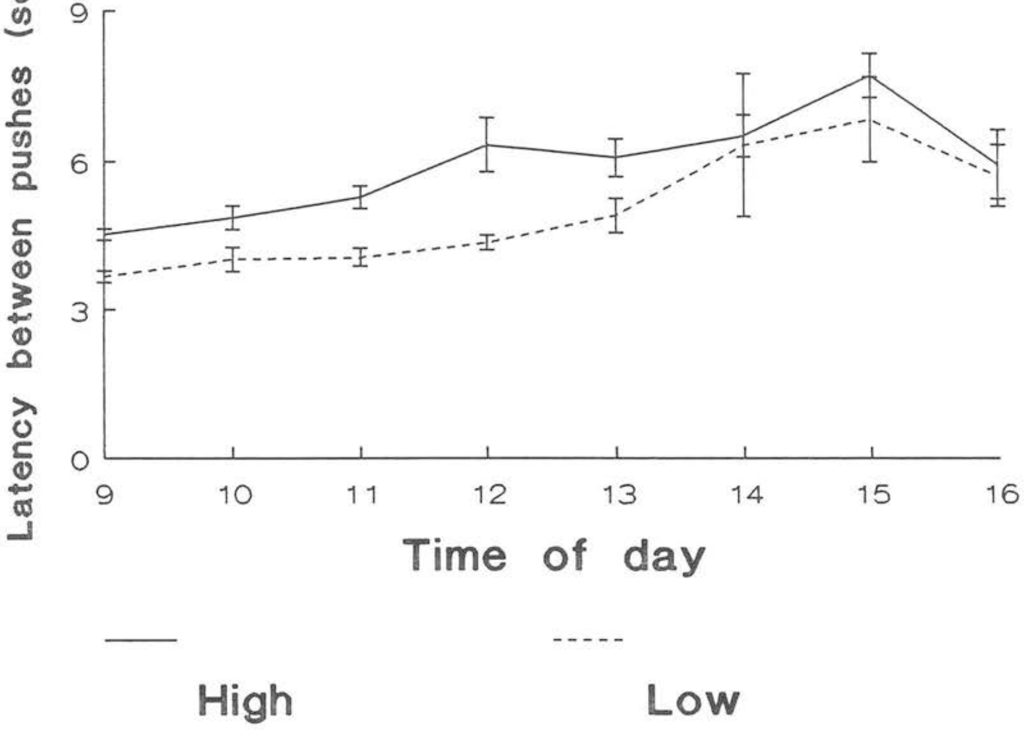
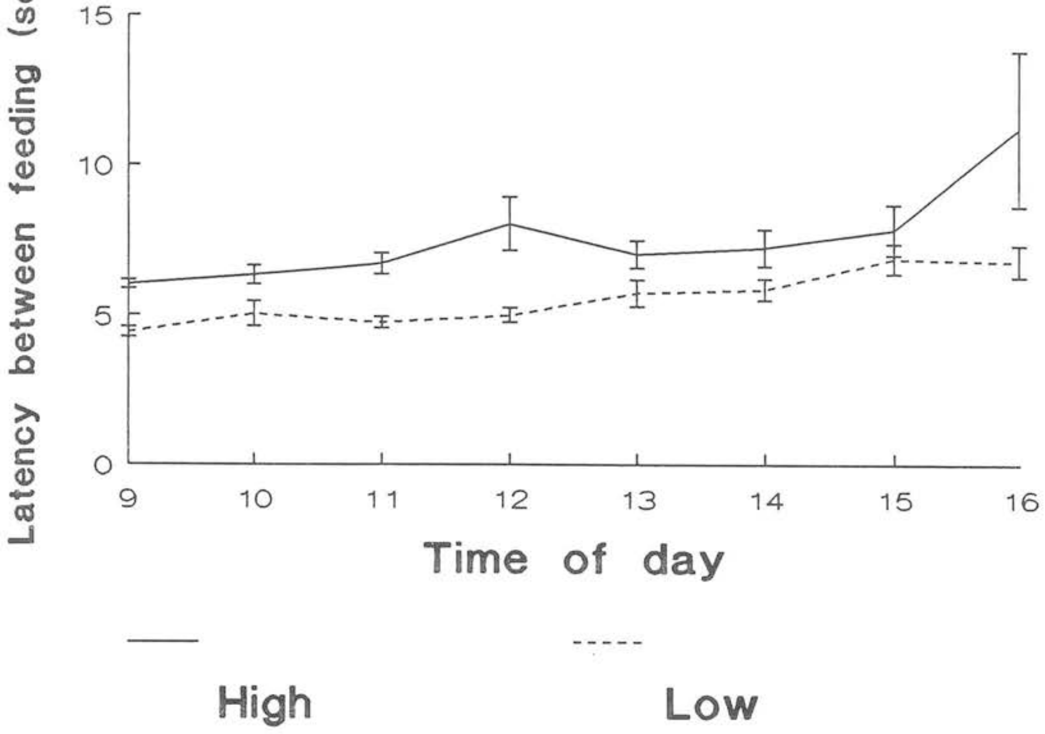


Figure 6.9: The relatiosnhip between latency of feeding and time of day



The frequencies of the behaviours pushing and feeding were significantly affected by treatment and hour and by a significant an hour x treatment interaction (Table 6.3; Figures 6.5 and 6.6) with pigs on the low treatment performed significantly more pushing and feeding. The frequency of pushing and feeding decreased as the day progressed. The day x hour interactions on pushing and feeding were due to the treatments initially diverging and then converging. The frequency of bouted drinking was significantly affected by day and hour and by a significant hour x treatment interaction (Table 6.4) due to treatments diverging between 1100h and 1200h and also between 1400h and 1600h with the low treatment expressing higher levels. Bouted drinking decreased as the day progressed and increased with days on treatment (Figure 6.7).

The latency between pushing and feeding responses were both significantly affected by treatment and hour (Table 6.5). In both cases the low treatment had the shorter latency which increased as the day progressed (Figures 6.8 and 6.9). Pushing also had an significant hour x treatment interaction (Table 6.5) due to the treatments being significantly different between 0900h to 1300h and then converging from 1400h onwards.

The average proportion of time feeding on both treatments was found to significantly predict the mean proportion of time spent pushing on both treatments (linear regression analysis: slope $b = +7.97$; $r^2 = 0.805$; $t_4 = 4.65$; $p < 0.01$). It was found by linear regression analysis that Fbactivity on both reward rates was significantly inversely related to sleeping (High: slope $b = -0.611$; $r^2 = 0.801$; $t_4 = -4.60$; $p < 0.01$ and Low: slope $b = -0.572$;

$r^2 = 0.885$; $t_4 = -6.28$; $p < 0.01$). Also on the low reinforcement rate Fbactivity was also significantly inversely related to openeyes (slope $b = -0.230$; $r^2 = 0.59$; $t_4 = -2.86$; $p < 0.05$).

DISCUSSION

This experiment has demonstrated that the expression of foraging behaviour directly affects the expression of their time budget. Pigs responded to a decrease in the rate of reinforcement by significantly increasing the pushing (searching) time, pushing frequency, feeding frequency and decreasing pushing and feeding latency. Such increases in response rate in the procurement of reinforcement has also been demonstrated in other animals under more artificial conditions (see Collier and Rovee-Collier 1981).

Pigs showed a tendency to increase their food intake on both treatments with increasing days on a treatment. This increase in food intake was not accompanied by an increase in the proportion of time performing Foodball directed behaviours, suggesting that the efficiency of Foodball use increased with experience.

The significant positive linear relationship between feeding and pushing, suggests that foraging pigs may be allocating time to searching behaviour (pushing) based on handling time (feeding) and that pigs stop foraging after a certain proportion of the daily time has been spent feeding. This suggestion was supported by the analysis of variance results that showed significant differences between treatments in the frequency of pushing, the proportion of time spent pushing and the rate of pushing. These results are in contrast to those for feeding where only frequency of feeding differed significantly. The results suggest that pigs do not use total daily food intake when allocating time to food searching behaviour and imply that the pigs in this experiment used a 'rule of thumb' when foraging with the Foodball, spending a constant proportion of time feeding each day by adjusting the proportion of time, frequency and latency of searching behaviour. In a natural situation such a rule of thumb would probably be useful in maintaining a constant level of food (energy) intake.

Time available to perform activities other than those associated with Foodball use (i.e., standing, walking, pushing and feeding) increased in this experiment from 0900h to 1600h. This presumably reflected the decrease in feeding motivation that accompanied the feeding activity, a suggestion supported by the increasing latency between pushing and feeding responses as the day progressed thus. The high proportion of time spent in Fbactivity apparently resulted in pigs utilising sleeping time to perform other behavioural activities. On the low treatment both sleeping and openeyes time was utilised by pigs for Fbactivity. Sleeping time accounted for higher proportion of the variance in Fbactivity than openeyes and had a steeper slope suggesting that sleeping time was utilised more than openeyes. This implies that time to perform Fbactivity was taken from other behaviours in a hierarchical manner. This result is in agreement with economic analyses of behaviour that suggest the least important behaviour will show least behavioural resilience (Houston and McFarland 1981). The present findings are in agreement with the effects of increased feeding time on the time budgets of gelada baboons and oystercatchers, which first decrease the expression of inactive behaviours as foraging time increases (Dunbar and Dunbar 1988; Swennen, Leopold and De Bruijn 1989). The significantly lower expression of rooting on the low treatment suggests that straw directed behaviour had an elastic demand function in the presence of a higher incentive substrate (i.e., the Foodball replaced straw directed behaviour in the time budget).

The pigs in this experiment did not appear to be behaving optimally (i.e., they were not maximising energy intake rate; see also Swennen, Leopold and De Bruijn 1989), as the pigs that had initially experienced a low reinforcement rate, rooted the 'Foodball' at a lower frequency and rate on the subsequent high reinforcement rate. Thus, pigs demonstrated that whilst they could have increased their reinforcement rate (energy intake), they did not leaving them less time available to perform other behaviours. In zebra finches this effect results in increased mortality rate and decreased reproductive success due to decreased time available to perform maintenance activities such as feather preening (Lemon and Barth 1992). This implies that the pigs in this experiment are not adopting an evolutionarily stable strategy (see Parker 1984).

The pigs in this experiment probably started each day food motivated but not water motivated as this was supplied *ad libitum*. Therefore it seems likely that the pigs' motivational priority was too consume food to reduce feeding motivation (see above). However, when feeding the high dry matter content of the diet required pigs needed to drink in order to aid ingestion and digestion (Yang, Howard and MacFarlane 1981). Thus, thirst a lower priority behaviour than feeding still required to be expressed, and the results qualitatively suggest that this may have occurred by time sharing. Time sharing occurs when a behaviour with lower motivational priority is expressed by the disinhibition of a behaviour with higher motivation by both behaviours sharing the behavioural final common path (McFarland 1974). An interesting question that the present study cannot answer is whether the bouted drinking occurred as a response to the sight stimulus of the drinker or whether pigs were goal-directedly pushing the Foodball towards the drinker. Although the mechanism soliciting bouted drinking was unknown, its effect probably reduced the energetic cost of changing behaviour (see Larkin and McFarland 1978).

This experiment has shown that in principle it is possible to restrict pigs' food intake by using the Foodball to decrease reinforcement rate whilst still allowing pigs' to express a large proportion of their daily time budget as foraging behaviour. The pigs' here did not show absolute compensation (i.e., equal food intake on both treatments) between the two rates of nutrient supply, as has been shown in many operant experiments when food is offered as a reinforcer (for a review see Hogan and Roper 1978). By utilising this effect the Foodball could provide a practical solution to some of the welfare concerns raised by food restricting breeding stock of domestic pigs (Lawrence and Terlouw, in press).

The pigs in this experiment did not behave according to a time minimising strategy of behavioural expression and were therefore not behaving according to predictions of optimal behavioural expression. It was also shown that the expression of the time budget was affected by the time required to perform Foodball associated behaviours (foraging behaviours) and that time utilised from other behaviours (inactive behaviours) occurs in a hierarchical manner. In this experiment the searching time (pushing) component of foraging behaviour with the Foodball was based on maintaining a constant total handling time (feeding). Also the Foodball has shown itself to be a practical solution to some of the welfare concerns of the way domestic pigs are fed.

Chapter 7

General Discussion

INTRODUCTION

This thesis has shown that domestic pigs are able to modify their feeding and foraging behaviour to cope with restriction of access to resources by other individuals, and different methods of food presentation. The present chapter will deal with the wider implications of the experiments reported in this thesis. The experimental studies will be discussed both in relation to the study of animal behaviour and animal welfare.

SOCIAL CONSTRAINTS ON FEEDING BEHAVIOUR

The computerised food intake recording (CFIR) equipment used in Chapter 2 is currently being used by pig breeding companies in the U.K. to select boars (e.g., Webb 1989). The results suggest that the use of CFIR equipment result in competition for feeder access could be selecting for pigs on the basis of aggression and not performance. From a welfare perspective such a situation could eventually lead to more aggression associated with food presentation (see Csermely and Wood-Gush 1986) and at mixing (see Csermely and Wood-Gush 1990). The banning of stalls and tethers for sows in 1998, and the return to group housing coupled with the practice of food restricting sows could lead to serious problems in the future if pigs are being selected for aggression. In economic terms fighting has been shown to increase food spillage (Walker 1991), reduce meat quality and increase condemnation of carcasses (Guise and Penny 1989). The possibility that CFIR systems may select for aggressive pigs is continuing to be investigated (Nielsen, Lawrence and Whittemore 1993).

THE EXPRESSION OF APPETITIVE FORAGING BEHAVIOUR

'Rooting is normally part of the appetitive phase of feeding, but in modern husbandry the total nutrient requirements of growing pigs are consumed in a few minutes in a competitive situation and it could be argued that a 'need' to root remains unsatisfied.'

Hughes and Duncan 1988

Hughes and Duncan (1988) suggest that intensively housed farm animals have an 'ethological need' to perform certain behaviours even in the absence of a physiological deficit (but see Baxter 1983). Chapter 3 investigated this question in relation to feeding and foraging behaviour but found little support for the idea that appetitive behaviour will be performed when the animal's physiological requirements have been met. By controlling for the bias apparent in previous experiments the results suggest that previous work which had apparently demonstrated such a need using a contrafreeloading paradigm (as employed in Chapter 3; see Osborne 1977) were the result of experimental artifacts. However, I believe that such an experimental approach does merit further attention because at the time I had not considered the importance of using species-specific operants (see section on EXPERIMENTAL SHORT-COMINGS, below).

THE OPERANT REVISITED

'A pigeon confronts two lighted disks in a small chamber. It pecks one for a few seconds, then the other. A hopper of grain appears and the pigeon eats.'

Shettleworth 1988

This quote illustrates the way in which operant conditioning techniques are being applied to investigate foraging behaviour (Shettleworth 1988). The use of the term operant conditioning has become synonymous with key pecking by pigeons and lever pressing by rats. The reasons for this are largely historical since the term was used by Skinner in 1938 to describe his methodology for training animals to perform arbitrary responses to obtain reinforcement. However, the term has more recently received a wider definition to include all types of goal directed behaviours (e.g., appetitive behaviour, instrumental behaviour and hedonism; Staddon 1980) and has not been limited to describing the behaviour of animals in a Skinner box:

> 'Many of the things animals do can be considered **operant** behaviour: a wild rat (*Rattus*) searching for food; antelope (Bovidae) fleeing from a lion (*Panthera leo*); a cat (*Felis catus*) exploring a novel environment.
>
> Staddon 1987 (my bold)

Although Staddon has tried to free the definition of operant from key pecking and bar pressing, changes in methodology to assess operant behaviour have been slow to follow:

> 'Although some researchers (e.g., Fantino and Abarca 1985) have recognised that principles found in the laboratory must ultimately be tested in successively more natural situations, this has rarely been tried.'
>
> Shettleworth 1988

This fact has also not gone unnoticed by applied ethologists studying welfare problems:

> 'Although the response may be arbitrarily selected it is clear that some combinations of responses, stimuli and consequences are more easily

> trained than others, which finding has been termed "biological preparedness" (e.g. Chance, 1988). Failure to obtain control over behaviour in particular circumstances may, therefore, mean only that an inappropriate combination was selected, not that control by that stimulus or consequence is necessarily impossible.'

Kilgour et al 1991

However, both psychologists and (applied) ethologists have been more concerned with formulating a theoretical synthesis of their approaches to the study of animal behaviour (e.g., Toates and Jensen 1991) rather than considering methodology. In the next sections I will outline a methodological approach to provide a synthesis between psychological and ethological approaches to the study of animal behaviour.

UNIFYING PSYCHOLOGICAL AND ETHOLOGICAL APPROACHES TO ANIMAL BEHAVIOUR THROUGH METHODOLOGY

One of my hopes is that the work in this thesis will improve the accuracy with which motivation is measured, through the design of species-specific operants (see below). I also hope that this approach has shown that a methodological synthesis between psychological and ethological approaches could result in more accurate assessment of animal behaviour. Thus, Houston's (1980) 'Godzilla' (psychologist) and 'the Creature from the Black Lagoon' (ethologist) rather than attacking each other could join together and improve the power of experiments in animal behaviour. Essentially the argument between psychologists and ethologists has centred on methodology. Psychologists criticise ethologists for lack of control in field experiments whilst ethologists criticise the unnatural aspects of psychologists laboratory experiments. Whilst I acknowledge the importance of a theoretical synthesis to provide a common ground (e.g., Toates and Jensen 1991) the argument will only cease when each side is not concerned about the validity of the others methodology.

SPECIES-SPECIFIC OPERANTS

Species-specific behaviour is considered unimportant by operant psychologists and is specifically eliminated in their experiments (Gardner and Gardner 1988). Research into constraints on learning has shown that this approach is fraught with dangers (Hinde and Stevenson-Hinde 1973) that have largely gone unnoticed by operant psychologists, but not by applied ethologists (e.g., Dawkins 1990). The 'paddle' reported in Chapter 4 and the 'Foodball' reported in Chapters 5 and 6 are examples of species-specific operants. I believe that they are a way forward in the measurement of operant responding by animals because they specifically take into species-typical behaviour and constraints on learning. Thus, with this approach it should be possible to condition animals to respond for any type of reinforcer (see Dawkins and Beardsley 1986). Furthermore, they allow animals to make 'natural' responses to obtain reinforcement under controlled laboratory conditions. Thus, by fulfilling the ethologists desire to measure natural behaviour and the psychologists to have control over experimental variables, species-specific operants provide what I believe is a basis for a methodological synthesis between psychology and ethology.

THE MEASUREMENT OF BEHAVIOURAL NEEDS

Economic analyses of animal behaviour which measure the net benefits of behavioural expression are regarded as the optimum approach for determining which behaviours animals are strongly motivated to perform (i.e., behavioural needs; Hughes and Duncan 1988; Dawkins 1990). In most studies behaviour has been analysed in terms of consumer choice behaviour (see Dawkins 1983) which involves the following three concepts: (1) that there are good or services the consumer wishes to buy; (2) the consumer only has a limited amount of income; and (3) the consumer's choice is based on maximizing utility ('satisfaction'). In economic studies of animal behaviour goods or services can be equated to stimuli predictive of appropriate goals; income (money) becomes synonymous with time or energy; and utility can be equated to maximizing fitness. For methodological reasons economic analyses of animal behaviour have used a consumer demand approach (e.g., Dawkins 1983) in conjunction with operant conditioning methodology (for a review see Dawkins 1990). Such experiments have focused on the demand function of different reinforcers singly, only considering whether or not an animal is prepared to pay more to receive the same level of reinforcement (the elasticity of demand). This approach ignores the fact that animals have a limited income and that by spending more time performing one behaviour there is less time and energy available to perform other behaviours (e.g., Leger, Owings and Coss 1983).

An alternative approach to using a consumer demand approach is to measure behavioural resilience of all behaviours in the animals' time budget (Houston and McFarland 1981). This provides information on how animals spend their time and energy in relation to all behaviours (i.e., how behaviours are traded off against one another). The basic methodological approach is to increase the cost and time required to perform one behaviour and record how the time budget changes. The advantage of this approach over a consumer demand approach is that it uses the concept that animals have a limited income and provides information about the importance of many behaviours simultaneously and in a manner in which they can be directly compared (see Chapter 6).

I believe that the use of behavioural resilience would avoid problems associated with using a consumer demand approach to determine behavioural needs. In practice it should be possible using behavioural resilience to conduct only a few experiments per species to determine that species behaviour needs. The methodology I suggest is to increase the range of time required to perform food acquiring behaviour (foraging and feeding) and examine how the time budget of the animal changes. This would provide information on the expression of all behaviours for that species, reducing the number of experiments required and taking into account the concept of limited income.

The two perceived drawbacks with this approach, the laborious nature of collecting sufficient data to construct a time budget and the problem of how to increase the time performing one specific behaviour (McFarland 1985) are I believe no longer valid. First, the advent of video recording technology with time lapse recording facilities means that time budgets can be easily constructed. Second, I have shown in Chapters 4, 5 and 6 that this could be done using a species-specific operant. It also could be done more simply by mixing food with an inert material to increase handling time.

PREDICTABILITY, UNPREDICTABILITY, CONTROL AND INFORMATION

Recently, the effects of predictable versus unpredictable environments on captive animal welfare have been debated (see Rushen 1993; Wood-Gush and Vestergaard 1993). The debate itself is based on the two divergent viewpoints of those who believe unpredictable environments have adverse effects on captive animal welfare (e.g., Wiepkema 1990) and those who believe they have positive effects on captive animal welfare (e.g., Wood-Gush and Vestergaard 1991). Consideration of wild animals shows that in they live in environments that change with time. Most animals have evolved in environments that are in a constant state of change, and animals have evolved learning mechanisms to cope with such change (Provenza and Cincotta, in press). Thus, one can assume that unpredictability *per se* does not adversely affect welfare since animals have evolved mechanisms to cope with such change. For example, animals use sampling behaviour to provide information about aspects of the environment so that in the future when change occurs they can respond adaptively (Dow and Lea 1987; Chapter 3). When animals behaviourally respond to a change in their environment they are increasing the probability that a desired event will occur by manipulating that environment. Thus, the expression of behaviour could be described as asserting control over the environment.

Most experiments that have considered the effects of control have done so in relation to how it is influenced by a chronic stressor such as an electric shock and are really experiments on coping (e.g., Tsuda, Tanaka and Nishikawa 1983). However, application of a stressor is not necessary to reduce welfare in a situation where an animal experiences little control over its' environment. It has been shown that rats which could control their environment showed less emotionality in an open field test than rats with no control (Joffe, Rawson and Mulick 1973). Furthermore, it has been shown that rats are intrinsically motivated and gain 'satisfaction' from the performance of operant tasks that allow them to express control over their environment (Glow 1985). The basis of successful behavioural enrichment is often that animals are able to increase the likelihood of a desired event occurring (e.g., food delivery) through the expression of behaviour (Chamove 1989). That is animals gain a measure of control over an unpredictable situation and use this control to obtain a desired level of positive reinforcement.

I therefore suggest that the welfare problem for farm animals is that they often have little control over their environment. The Foodball reported in Chapters 5 and 6, I believe has potential applications in animal welfare because it creates an unpredictable food supply that a pig may gain some control over, through the expression of foraging behaviour.

EXPERIMENTAL SHORTCOMINGS

The following comments I hope will not read like 'crying over split milk' but hopefully show that I acknowledge my experimental short-comings and can explain why they occurred. A general point that should also be taken into consideration is that of my experimental experience which probably affected the power of my experimental designs and the efficiency with which experiments were carried out.

Chapter 2; Would have benefited from behavioural observations but these were not possible at the time due to the lack of video equipment.

Chapter 3; These experiments would it seems have benefited from the use of the species-specific operant outlined in Chapter 4. Unfortunately I did not have the time to repeat this work within the time constraints of my Ph.D.. I also learned from this experiment the potential dangers of using an experimental procedure that involved prolonged social isolation.

Chapter 4; I believe would have been improved by comparing the learning speeds of the two operants, unfortunately at the time of the experiment I had no formalised way of doing this. However, now I have an operant learning program that allows pigs to learn at their own speed and I hope to use this in the future to compare learning speeds.

Chapter 5; It was a disappointment that I was not able to wholly disentangle the effects of food from Foodball. The treatment that I required to do this was to present naive pigs with a 'Foodball' that did not contain food before presenting them with one that did contain food (i.e., before the Foodball treatment). I did not do this because I was concerned that the pigs may have extinguished to the 'Foodball' and would ignore it in future treatments when it contained food.

Chapter 6; I would have preferred to have conducted the experiment over 24 hours but at the time we did not have an infra-red video camera. Another problem with performing the experiment for 24 hours a day would have been the social isolation involved. Also it would have been better to have used several reinforcement rates rather than just two, but I had insufficient time to achieve this.

CONCLUDING REMARKS

Finally, I hope to have shown that it is possible to allow pigs to express foraging behaviour in commercial environments in a practical manner. I have not been able to provide strong evidence that pigs have a need to forage but I think that with the methodology developed in this thesis it may be possible to address this question more accurately. Also I have shown that pigs are extremely flexible foragers able to rapidly adapt to social constraints and method of food presentation. I realise that this thesis leaves many questions unanswered but I hope that the few answers it does provide will be utilised to improve our understanding of animal behaviour and specifically the welfare requirements of pigs.

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Appendix A: Engineers drawing of the Paddle