Feeding behaviour in the cat—recent advances

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ABSTRACT

The domestic cat, *Felis catus*, provides one of the few representatives of the order Carnivora whose behaviour may be studied within the laboratory environment. In recent studies of cat feeding behaviour, there has been a fundamental shift in emphasis away from internal factors of control, the homeostatic model, towards investigation of the controlling influence of external environmental factors on food choice and feeding patterns. Food choice is discussed in relation to prior dietary experience and the motivational level of the animal. Feeding patterns are shown to be strongly associated with food availability and energy economy rather than the momentary physiological state of the animal.

INTRODUCTION

The development of a strong social relationship between animal and owner is one of the most important aspects of pet ownership. As food must be recognized as one of the most powerful reinforcers of behaviour, an understanding of feeding behaviour and food intake regulation is essential for the commercial pet food manufacturer whose diets have to maintain healthy pets over many years.

The domestic cat, *Felis catus*, also provides a readily available representative of the carnivores which is relatively easy to house, feed and handle. Although in many ways the cat has resisted pressures of domestication and retains a behavioural repertoire which makes it very successful in the feral state, the extrapolation of findings from the domestic forms to their wild relatives can be quite risky.

In the short-term, feeding behaviour is usually assumed to be a function of the quality and quantity of the food items offered, the physiological and psychological state of the animals at that time and prior dietary experience. Total intake is then regulated by the integration of these momentary responses, the homeostatic control mechanism which acts via internal metabolic signals for hunger and satiety. Hence feeding studies have been dominated by a search for those physiological factors which relate directly to the initiation and termination of food intake.

Most of the data have been related to theoretical mechanisms which might regulate food intake via gastric, glucostatic, lipostatic and oral cues, especially in relation to the rat and man. However there is a growing body of comparative evidence suggesting that different mechanisms have evolved in response to natural feeding habits. Omnivores utilize a wide variety of abundant but energy dilute food items and eat frequent meals of long duration and low intensity (McClymount, 1967). In contrast carnivores have little direct control over the timing and size of meals because their prey has to be located, stalked and hunted and is unlikely to be easily captured. Thus, in the wild, predacious carnivores tend to take infrequent large meals whenever the opportunity arises (Schaller, 1966, 1970).

In the laboratory an *ad libitum* or free-access feeding regime has been adopted to maintain a wide variety of species and is generally used for the study of feeding behaviour. By definition a free-feeding situation provides no external constraints on food availability and allows the animal to have direct control over the timing and size of meals. For carnivores this is a situation somewhat removed from the natural environment and as such only provides information on the physiological and psychological factors affecting feeding behaviour. Analysis of free-feeding indicates that the basic parameters are meal frequency, meal duration, rate of feeding, choice among the food items offered and the interval between meals. There is considerable controversy as to the importance of the latter parameter and its relationship with meal size. Panksepp (1973) suggested that significant correlations between meal size and the following interval before the next meal may be largely a statistical artefact, but de Castro (1975) corroborated the existence of this post-prandial relationship in rats especially when measuring meal size as actual weight eaten rather than the more usual time duration.

In nature, cats, like most carnivores, are opportunistic feeders taking advantage of food items when available. Considerable effort may have to be expended in the hunting and procurement of prey. In recent years there has been a fundamental shift towards the study of the so-called ecological determinants of feeding behaviour (Collier, Hirsch & Hamlin, 1972) and the effect of constraints on food availability on feeding behaviour. The most important factor in food regulation then becoming the overall feeding cycle, rather than ingestive responses, and its effect on the total food economy of the animal.

Feeding behaviour is an enormous subject; this paper will concentrate on three areas which we have been involved with, namely the effect of prior dietary experience on food choice and patterns of feeding under free-access and constrained food availability regimes.

EFFECT OF PRIOR DIETARY EXPERIENCE ON FOOD SELECTION

Animals are continually faced with the demands of procuring and selecting food items which satisfy their nutritional requirements both in terms of quantity and

quality. Inbuilt patterns of behaviour play a large part in discriminating the useful food items, as is indicated when orphaned animals are raised by hand without the benefits of learning from their natural parents. However feeding experience, especially during early development, would be expected to influence selection habits in the adult. The published literature suggests that at least two alternative feeding strategies are developed in early infancy. On the one hand there is the process of 'food imprinting' (Hess, 1964) or 'fixation of food habits' (Kuo, 1967), while on the other hand there is the tendency for laboratory rats (Morrison, 1974) as well as cats and dogs (Mugford, 1977) to prefer foods having a novel flavour or physical character.

These apparently contradictory feeding strategies have even been reported within a single species, the rat. Adult rats have been found to influence the early dietary preferences of their young which will actively seek and preferentially ingest the diet the mother has eaten during the nursing period, and also are strongly attracted to feeding sites by the vicinity of adults (Galef & Henderson, 1972; Galef & Clark, 1972). Toxic edibles constitute one of the most serious challenges to survival of the young and it is suggested that this challenge is met by preference for familiar over novel food (ingestational neophobia) (Damjan, 1973). Neophobia for a novel food item can be readily attenuated by pre-exposure to the item and the information that the food item is nutritionally safe, is maintained by the animal over a considerable period (Best, Damjan & Haskins, 1978).

Our studies in which kittens have been maintained on a single diet from weaning are consistently at variance with a 'fixation of food habits' in that the adult cats never developed an enhanced preference for the rearing diet, but preferred to eat the novel alternative (Mugford, 1977). Using commercial pet foods there was an initial preference for the novel diet irrespective of its palatability, as measured by naive animals, relative to the familiar diet. The response is generally transient and within several days the diets assume their expected palatability position. However with puppies the preference has still been measurable after a period of months, suggesting a relationship between the duration of the response and the relative palatability of the diets, the larger the difference between the foods, the shorter-lived the response.

The preference for novel foods in laboratory-housed cats is not restricted to young animals as a measurable effect is produced after feeding adult cats on a single fixed diet for as little as six days. The longer the single diet maintenance period the greater the initial preference for the novel diet.

The apparent dichotomy in the feeding strategies of rats and cats may be a function of their very different ecological niches. The neophobic response to new food items is probably far more important for omnivores utilizing a wide variety of food items than for carnivores whose food items are relatively restricted and nutritionally balanced. Thus the carnivore which preys upon other living animals will rarely be faced with the problem of toxic food items and the neophobic response may be unnecessary.

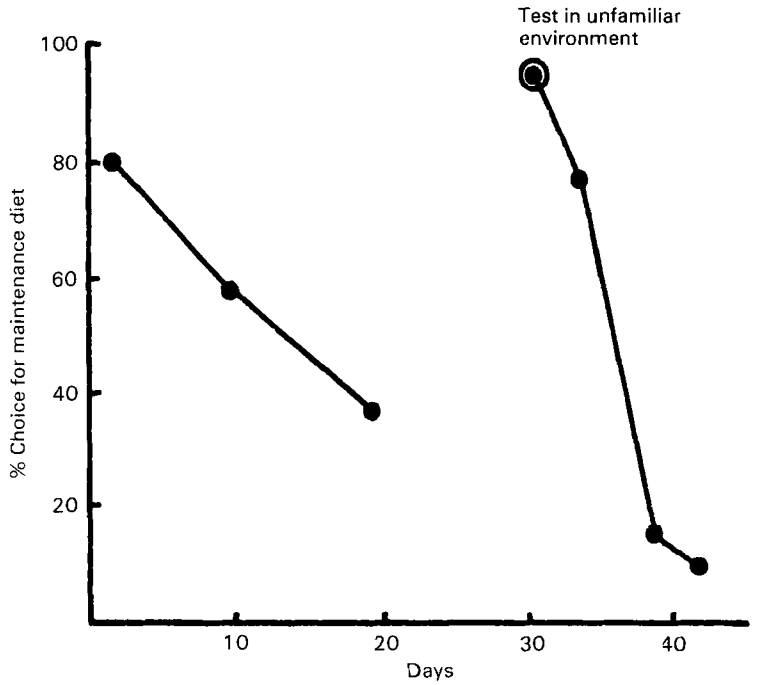

FIG. 1. Decline in preference of a maintenance diet relative to a novel diet with time and the almost total rejection of the novel diet in favour of the familiar diet when tested in an unfamiliar environment.

Our studies have also indicated that the selection of food items may relate to the motivational level of the animal. If stressed there is a tendency for adult cats to select familiar food items. Six cats were offered a single fixed diet for 40 days and choice tests were carried out between this diet and a novel alternative on days 1, 10 and 19 of the trial. As expected across time the preference for the familiar diet declined steadily in favour of the novel alternative (Fig. 1). On day 30 the cats were retested but in an unfamiliar environment, and totally rejected the novel alternative in favour of the familiar food. On returning to their accustomed housing the preference for the novel diet quickly returned.

The selection of food items is a complex behaviour and the final response is directed by both internal and external factors. The parameters are largely predetermined but will differ from species to species in accordance with the particular niche in which the animal is operating.

FEEDING PATTERNS IN A FREE-ACCESS SITUATION

In the laboratory an *ad libitum* or free-access feeding regime has been adopted as the standard procedure for maintaining a wide variety of species and is used extensively for the study of feeding behaviour and food intake regulation. The

majority of these studies have utilized the laboratory rat which, when free-feeding eats discrete meals separated by periods of non-eating, the intermeal intervals. When free-feeding the rat has total control over the size and timing of its eating bouts and the important parameters of the feeding pattern are meal size, meal duration and the intermeal intervals. The relationship between meal size and the intermeal interval has been examined in many studies with rats, but there is still contention as to the reality of these correlations. A significant correlation between meal size and the following post-prandial interval has been regularly reported, but several studies have failed to replicate this finding for rats.

Literature relating to the cat is limited but our studies of a free-feeding situation with adult cats have shown the feeding pattern to be remarkably similar to that of the rat (Mugford & Thorne, 1980). In all cases irrespective of diet type the cats ate several distinct meals throughout the 24-hour period. Kanarek (1975) found that two cats free-feeding on a dry diet took 8–12 meals/day in a predominantly nocturnal pattern. In our analysis of feeding patterns, three cats took between 7 and 16 meals/day but perhaps the most important finding is the large variability between individual cats. In both this and Kanarek's study no significant relationships could be found between meal size and pre- or post-meal intervals, and we have concluded that the size and timing of cats' meals is largely random.

In summary on a free-feeding regime cats will adopt a nibbling food intake strategy with several small meals taken at random throughout day and night. Although total daily intake was roughly in proportion to the cats' differing bodyweights, individual cats are highly variable, and no relationship could be found between meal size and meal intervals. Kaufman (1980) also suggests that the interval between meals, at least in freely feeding cats does little to determine the size of the meals or *vice versa*.

In the wild, the diet of the carnivore is nutritionally balanced and of high caloric value but food items are seldom readily available. Hence carnivores have developed relatively simple digestive systems capable of dealing with large amounts of food in a short period (Schaller, 1972). When faced with a reduction in the caloric concentration of their diets, cats maintained bulk rather than caloric intake under *ad libitum* conditions (Kanarek, 1975). Also Skultety (1969) has reported that cats do not decrease food intake when the caloric content of the diet is increased, but continue to consume the same weight of food. However our studies using commercial cat foods of good palatability with a range of caloric densities (80–350 kcals/100 g) have shown the cats to be able to adjust their intake reasonably well, even in the short-term. Table 1 shows weight and energy intakes for a group of cats fed twelve diets on an *ad libitum* feeding regime where each diet was presented over consecutive 24 hour periods. Apart from diets I (an exceptionally palatable diet) and K (a low palatability diet) the cats' mean energy intake at each meal remained remarkably constant even though weight intakes per meal varied by a factor of 8.

The control of intake in the cat is not merely due to the bulking effect of the diet, there is certainly a reasonably accurate control of energy intake at least over 24

TABLE 1. Mean meal size for a group of five cats in a free-feeding regime with diets changing every 24 hours

Diet		Energy content kcals/100 g	Mean weight eaten per cat per meal (g)	Mean energy intake per cat per meal (kcals)
Dry foods				
A	Commercial dry cat foods	360	8·1	29·2
B			6·3	22·7
C			6·9	24·8
D			8·5	30·6
E			8·7	31·3
F			7·7	27·7
Wet foods				
G	Fresh food	136	26·1	35·5
H	Meat and jelly canned products	80	37·8	30·2
I		90	49·8	44·8
J	Meat and cereal canned products	115	28·3	32·5
K		115	17·2	19·8
Semi-moist foods				
L		320	9·4	30·1

hour periods. When the cat is presented with diets differing markedly in energy density, moisture content and texture, the pattern of feeding under an *ad libitum* regime remains constant with small discrete meals taken at random. This is rather surprising in that the high water content foods dry out considerably over a 24-hour period and it would be expected that a fresh diet would be preferred and the cats would take fewer large meals when the diet was first presented. The pattern of small meals is not due to any physical limitations on gut content volume as the cat is able to satisfy its requirements on all the above diets when restricted to one meal per day.

FEEDING PATTERNS WHEN FOOD ACCESS IS LIMITED

Availability of food for carnivores is generally restricted. Wild carnivores expend considerable energy in procuring their prey but the domestic cat is dependent upon its owner as to the timing and size of its meals. The relationships between meal procurement cost and the feeding patterns of caged domestic cats have been studied using increasing fixed ratio schedules of bar presses to obtain a meal. In these studies cats are able to adjust their feeding pattern in relation to the amount of work required to obtain food. As the energy cost of a meal is increased the cat takes fewer meals per day and increases the average meal size and duration relative to the free-feeding pattern (Kanarek, 1975). Similar modifications of feeding patterns are

displayed by rats and guinea pigs in the same situation (Collier, Hirsch & Hamlin, 1972; Hirsch & Collier, 1974).

An identical change in meal patterns has also been reported for an uncaged cat (Kaufman *et al.*, 1980) suggesting that the alteration in feeding pattern is not merely a result of increased access to alternative activities as demonstrated by Richter (1927), but is a relationship between availability of food and the energy expended in obtaining that food.

DISCUSSION

The classic depletion-repletion theory of feeding has related food choice and feeding patterns to the physiological state of the animal and a large proportion of studies have been directed towards a search for the controlling metabolites. Recent work has shown the importance of external factors on feeding behaviour. Food choice is affected by prior dietary experience both in early life and just prior to the meal, but changes in the environment can override these controlling influences. Similarly the momentary physiological state of an animal appears irrelevant in feeding pattern studies as the cat will adjust its feeding pattern with respect to food availability. It is possible that the cat has a behavioural repertoire containing different patterns of feeding, each being used when appropriate. When food is continuously available the cat will exhibit the feeding pattern of many small meals which will be changed to infrequent large meals when food availability is limited, thus maintaining an overall energy economy.

The adaptability of the cat's behaviour is ideally suited to its life style as an opportunistic feeder, enabling the animal to use food availability to the best advantage in terms of energy balance. Many of these factors may be ascribed to genetic influences, but there are idiosyncracies of feeding behaviour whose origins remain unknown and complex and require further study.

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