Chapter 2

External Influences on the Feeding of Carnivores

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INTRODUCTION

As subjects for experimental studies of feeding behavior, most carnivores present the obvious problems of being expensive to feed and house; they breed rather slowly and can be dangerous to handle. It is fortunate, therefore, that at least two domesticated representatives of the order Carnivora are readily available for study—the dog *Canis familiaris* and the cat *Felis catus*. In this chapter I present data on the feeding behavior of these species, and discuss the potential implications of these data for the behavioral ecology of other carnivores. Since large individual differences in the feeding behaviors of cats and dogs are commonly observed, and since the extrapolation of findings from highly domesticated forms to wild relatives can be quite risky, verification of some of my hypotheses in wild carnivores is ultimately required.

The emphasis of this chapter is on environmental (e.g., social context of a meal), experiential (e.g., prior diet), and sensory factors (e.g., role of food odors) which affect ingestive behavior. Since the significance of these can only be properly understood in the context of the homeostatic systems for food intake which act via internal metabolic signals for hunger and satiety, a brief review of these influences follows in the next section.

CHARACTERISTICS OF INGESTIVE BEHAVIOR

Experimentally supported models of ingestive behavior generally emphasize energy relationships between the animal and its food, as when caloric intake is adjusted by modification to consumption rate, meal size, duration, and frequency of feeding (e.g., Hatton, 1975; Toates and Booth, 1974). Most of these consumption data have been related to theoretical mechanisms which might regulate food intake via gastric (Sudakov and Rogacheva, 1963), glucostatic (Mayer and Thomas, 1967; Nagamachi, 1972), lipostatic, and oral signals. Many of the data have been obtained by exclusive reference to the rat and man, but a small body of comparative evidence suggests that different mechanisms have evolved in response to the particular circumstances facing free-living carnivores.

The neuroanatomical structures that mediate eating have been explored in some detail in the rat and cat, and a similar involvement of the lower brainstem and hypothalamus has been confirmed for both species by lesioning and direct electrical stimulation techniques (Bernston and Hughes, 1974; Skultety, 1969). However, the same brain areas do not necessarily respond to identical blood-borne chemical factors characteristic of the satiated versus hungry animal. Thus, whereas injection of 2-deoxy-D-glucose initiates eating in both rats and monkeys by inhibiting intracellular glucose utilization (Smith and Epstein, 1969), it depresses food intake in the cat (Jalowiec *et al.*, 1973). Whereas rats are able to maintain a relatively constant caloric intake from diets diluted to give a wide range of caloric densities (Booth, 1972; Jacobs and Sharma, 1969), the dog and cat are probably more influenced by the bulking qualities of food within the stomach (for data on the dog and cat, respectively, see Janowitz and Grossman, 1949; Kanarek, 1975). Such interspecies differences in ingestive behavior are to be expected among animals adapted to such different nutritional media as are available to an omnivore and a predaceous carnivore, and whose availability makes such different demands upon their ability to procure food.

The position facing most predators can be summarized as alternating periods of famine and feast, under conditions that favor individuals capable of rapidly consuming and digesting their kills. For instance, the wolf has developed a remarkable gorging ability; in a single meal, 7-day fasted wolves were reported by Young (1944) to consume up to 17% of their own body weight in meat.

Among domestic dogs, some individuals will also take relatively enormous meals. We have measured free access meal sizes of dogs normally fed only to their theoretical caloric requirements once per day. A male Labrador was remarkable for having once eaten 10% of its own body

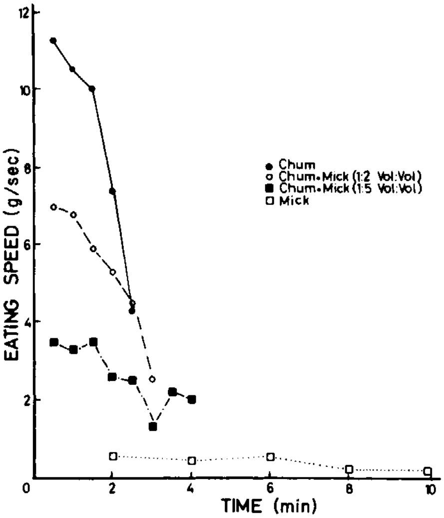

Fig. 1. Mean consumption rate of dog foods during free access meals by Beagles.

weight of a complete canned food, which it subsequently regurgitated! Eating speeds and meal sizes among a group of 16 Beagles were characteristic of both the diet and of the individual dog. Figure 1 shows consumption rate of Pedigree Chum* (which is a highly palatable canned food providing about 82 kcal/100 g), Mick (a dry biscuit dog food providing about 360 kcal/100 g), and various admixtures of the two. The more palatable and calorically dilute Pedigree Chum was consumed significantly more rapidly ($p < 0.001$) than the 1 : 2 mixture of Pedigree Chum and Mick, which itself occupies an intermediate position between Pedigree Chum and Mick when presented alone. Interestingly, this meal dynamic of Pedigree Chum is very like that reported by Le Magnen and Devos (Le Magnen, 1971, Fig. 7) for consumption of a dry diet by the rat.

When the same group of dogs was monitored for meal size and eating speed with other types of dog food (Fig. 2), it was found that both data were largely determined by the diet's moisture content (and thus, indirectly, its caloric density). Meal size and eating speed were found to be highly correlated ($r = 0.85$).

Domestic cats are also influenced by the moisture content of the diet, which determines meal size and eating speed in the manner described for dogs. The data in Fig. 3 are means from a group of nine cats accustomed

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* Diets named in the text were manufactured by Pedigree Petfoods, England, and Kal Kan Foods, Inc., California.

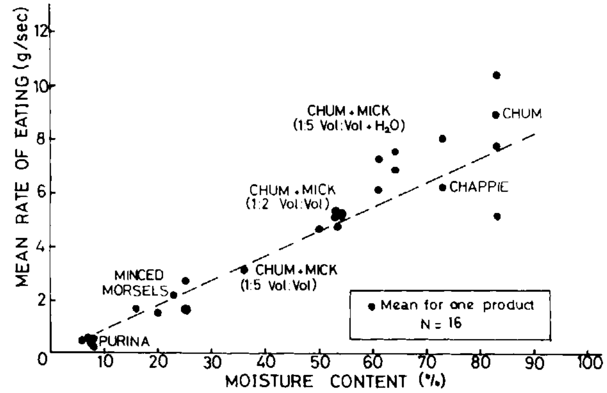

Fig. 2. Average consumption rates for dog foods of varying moisture contents.

to once-daily feeding. Whiskas is a canned cat food comprising meat chunks similar to Pedigree Chum, while Munchies is a dry food which (like Mick) is consumed at a slow and constant rate.

Whether the wolf or other predaceous carnivore can sustain a level of food intake much in excess of its metabolic requirements has probably not been investigated under rigorous experimental conditions. Our studies

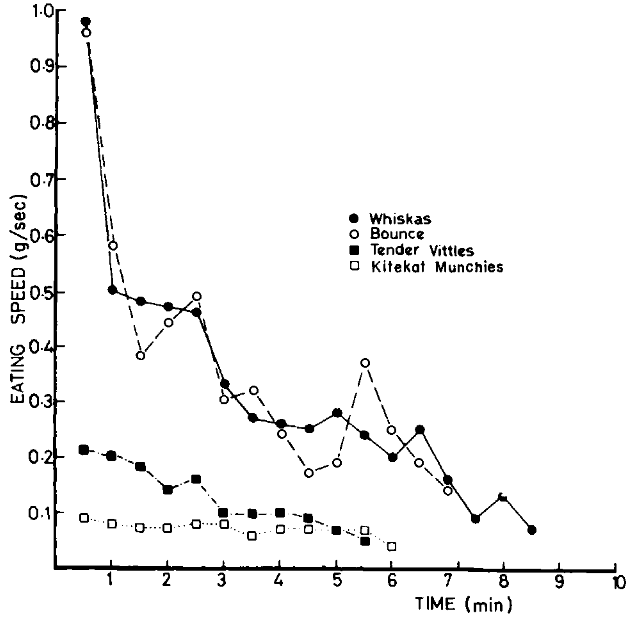

Fig. 3. Mean consumption rate of cat foods during free access meals.

with the domestic dog would lead one to anticipate that related wild canids might also tend to become obese when food is plentiful, though cats form a better balance between intake and expenditure.

We have observed enormous variation in the efficiency with which dogs regulate their food intake, both between breeds and individuals within the same breed. A group of 16 Terriers (eight Cairn and eight West Highland White, equal numbers of males and females) were fed twice daily free access meals of commercial dog foods. The diets, which were subject to large variations in both caloric density and palatability, were varied for each meal. The dogs were, therefore, denied the opportunity of adapting to the calorie repleting effect of individual diets, a situation that provokes overeating in both the rat (Le Magnen, 1956) and man (Siegel, 1957). The Terriers' body weights all remained remarkably constant over a 2-year period, individuals varying by < ±10% and the group mean by < ±4%. None of the dogs would be regarded as obese, being well within the range specified by the breed standards (Jones and Hamilton, 1971).

However, clinically defined obesity is commonly encountered among the pet dog population of the United Kingdom (Anderson, 1974) and is often attributed to the feeding conditions (indulgent of both quantity and variety) and limited exercise which failed to provoke weight gains among our Terriers (Joshua, 1970). A separate study of food intake by Beagles during daily free access meals was undertaken and confirms the existence of very large individual differences in their predisposition to obesity. Prior to the experiment, the 16 Beagles had been maintained in good condition for 3–5 years on a fixed intake of Chappie (a complete canned food), equivalent to a daily intake of approximately 800 kcal. When allowed free access to the same diet, all of the dogs immediately increased their initial caloric intakes to between two and five times their former levels.

It was expected that this excessive intake would be only transitory (positive overshoot: Hatton, 1975) until set point for body weight was achieved at a slightly higher plane than that obtained by restricted feeding. Indeed, 13 of the 16 dogs did eventually achieve relatively stable food intakes and body weights, but over different periods (1–3 months) and at body weights from 10 to 60% of starting levels. The other three dogs increased in weight so rapidly that consideration of their welfare led us to place them on caloric restriction after 4 months.

Records from two dogs sharing a common history of housing and feeding are shown in Fig. 4. Whereas no. 307 self-regulated at an appropriate 10 kg, no. 334 became clinically obese after a nearly 40% rise in body weight.

Individual differences between the caloric intakes and weight gains of mongrel cats were noted by Skultety (1969). However, obesity is uncom-

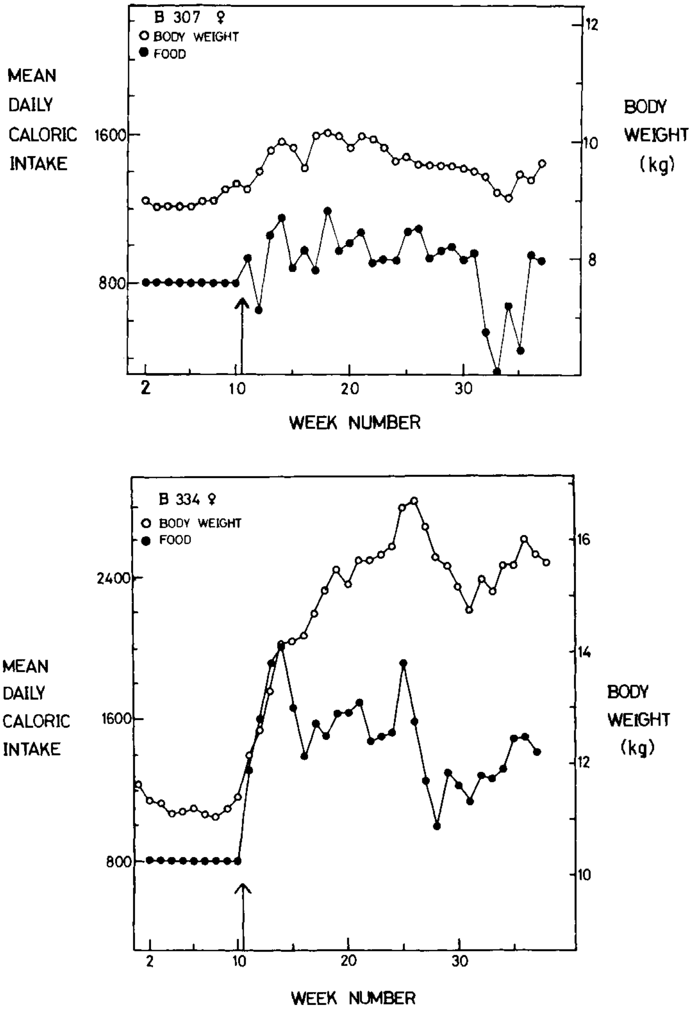

Fig. 4. Weekly means of daily caloric intake and body weight in two Beagles.

mon among domestic cats (Anderson, 1974) and rarely encountered among our (indulgently fed) colony of 400 cats.

The physiological basis for the previously discussed species, breed, and individual differences in regulation of body weight via controls over food intake has not been investigated much, but promises to be a rewarding research area for the future.

SOCIAL FACTORS AFFECTING INGESTIVE BEHAVIOR

With the exception of the lion, the wild felids are mostly solitary hunters relying upon stealth and speed to capture their prey (Ewer, 1973). In contrast, canids such as the wolf and Cape Hunting Dog (Mech, 1975) have adopted highly organized social groupings which enable them to prey upon species both larger and faster than could be killed by a single individual. Social facilitation of feeding *by puppies* (i.e., a greater food consumption when offered meals in groups rather than singly) has been reported by numerous workers (Compton and Scott, 1971; James, 1953, 1961; Ross and Ross, 1949a,b). One might speculate that this phenomenon could be an adaptation by a cooperative pack-living predator to ensure that maximum amounts of a large kill are consumed before they are lost to competing predators sharing the same ecosystem (Kruuk, 1972; Schaller, 1972). However, this hypothesis does not account for Platt and James' (1966) demonstration of a marked social facilitation of feeding among young opossums *(Didelphis virginiana),* marsupials whose adults are highly antagonistic to one another (Crandall, 1964). Social facilitation has not (to the author's knowledge) been reported as occurring among felids or domestic kittens, but its absence should not necessarily be construed as being consistent with their generally solitary hunting habits.

It must be emphasized that the foregoing discussion of social facilitation of feeding is entirely based upon observations of young animals *not* having continuous access to food (i.e., they were meal fed). Puppies tend to center their dominance relationships about the food pan when feeding is limited to discrete meals (James, 1949) to a greater extent than when they are given a continuous *(ad libitum)* food supply. Small groups of both adult dogs and cats rarely fight for possession of food that is always available, and their intakes are no higher than when they are housed individually (author's unpublished observations). The generality of the published data referring to litters, therefore, seemed to be open to question, and so we decided to look for social facilitation among adult animals accustomed to an *ad libitum* feeding regime.

The subjects were continuously monitored by a low light/infrared sensitive camera linked to a time-lapse video tape recorder (Sanyo 1360). This enabled rapid television review of infrequently occurring behaviors on replay at ×60 real-time. The dogs consisted of a litter of fully grown Miniature Poodles having continuous access to a complete, semimoist dog food (Bounce Minced Dinner), whose consumption could be calculated to the nearest gram by reference to a digitized-head scale situated within the field of the camera. A similar arrangement existed for a group of six adult cats, which were given an *ad libitum* supply of a complete dry cat food (Munchies).

Feeding visits by individual dogs or cats were recorded together with the meal size, and these could be related to the behavior of the rest of the group. The most striking feature of the results presented as cumulative intakes in Fig. 5 was the distinctly diurnal pattern of food intake by the dogs, whereas cats distributed their meals evenly throughout the 24 hr. Both species tended to take a large number of small meals (10.4 and 13.3/day, means per dog and cat, respectively), in a manner more reminiscent of the laboratory rat (e.g., Kissileff, 1970) than a predaceous carnivore. The frequency and spacing of meals in both the dogs and cats of this experiment were not much affected by the diet: meal sizes of palatable canned, semimoist, and dry foods being more or less in proportion to their caloric densities. Individual differences in meal size and frequency were apparent in both species, the most and least frequent eaters differing by a factor of more than two. Nevertheless, the suggestion by Scott (1968, p. 21) that cats are "intermittent" feeders, or stated more categorically by the same author (1971) that they are ". . . naturally occasional feeders" and "adult cats feed only once in every 24 hours or sometimes less frequently . . ." is obviously fallacious. The staple diet of all species of *Felis* is small rodents (Coman and Brunner, 1972; Ewer, 1973, p. 214), which would necessitate frequent kills providing several small meals (contrasting with feeding habits of the greater cats such as the lion or tiger, capable of taking prey larger than themselves). Interestingly, a single mouse would provide about the same number of calories as the typical meal of our laboratory cats (30 kcal).

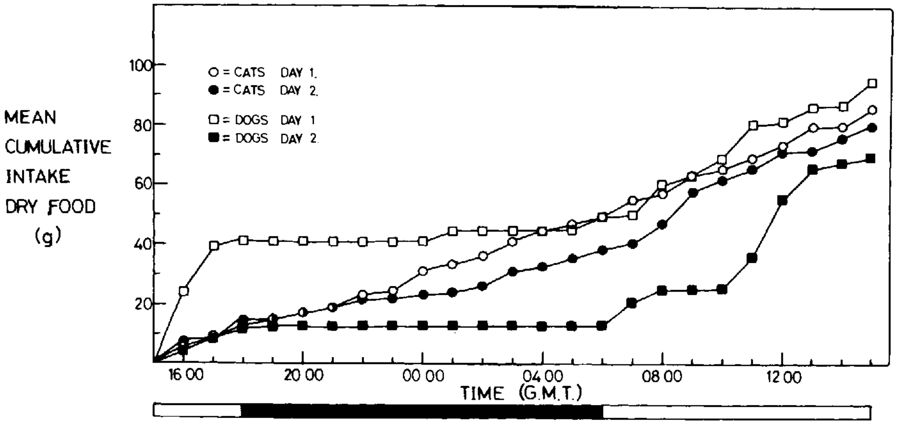

Fig. 5. 24-hr cumulative food intakes by dogs and cats. G.M.T., Greenwich mean time.

Meals were classified as being either "social" or "nonsocial" on the basis that feeding of an individual animal was or was not associated with time by the feeding of another individual. The criterion of association was that meals of two or more animals should either overlap in time or occur within 1 min of the other terminating. Of 82 dog meals and 60 cat meals observed, only 12% and 20%, respectively, were classified as social, insofar as they were associated with another animal's feeding. Less than 1% of total available time was accounted for by feeding, so it would be difficult for any single dominant animal to retain exclusive possession of the food pan (and thus give a spurious impression that feeding was an activity having little consequence for other group members). Indeed, cats were selected for these experiments on the basis of their known compatability with the rest of the group, and little fighting was observed among either the dogs or cats that might suggest food pan possession by dominant animals of the type noted by James (1949) with puppies.

EFFECTS OF PRIOR EXPERIENCE UPON FOOD SELECTION AND INTAKE

In order to satisfy their nutritional requirements, all animals must face the challenge of discriminating useful (i.e., nutritionally reinforcing) food sources from a usually more abundant array of either micronutrient-imbalanced (Harris *et al.*, 1933; Simson and Booth, 1973) or even downright toxic substances (Garcia *et al.*, 1974; Rozin and Kalat, 1971) possibly sharing many of the same sensory qualities. The learned strategies needed to overcome this challenge must doubtlessly be maintained throughout life, but feeding experiences during early development would be expected to exert particularly potent influences upon selection habits of the adult. However, the published data relevant to this issue indicate that two (apparently contradictory) feeding tendencies are established by prior dietary experiences. On the one hand, precocial birds and possibly other vertebrates are susceptible to a process that has been variously called "food imprinting" (Hess, 1964) and "fixation of food habits" (Kuo, 1967, pp. 67–72), while on the other hand, there is a tendency for laboratory raised rats (at least) to prefer foods having a novel flavor or physical characteristic (Bronson, 1966; Morrison, 1974; Welker and King, 1962; Young, 1940).* Which process is the more important for molding the food

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* Such elevated preferences for novel diets and flavors should, however, be considered in the context of a marked neophobic response of the wild rat toward novel food and fluid (Barnett, 1963), though the albino rat only exhibits a comparatively weak and transitory neophobia (Carroll *et al.*, 1975).

and prey selection habits of wild carnivores must, in the absence of quantitative data, be a matter for conjecture unlikely to justify bold cross-species generalization.

Working with dogs, cats, and Mynah birds, Kuo (1967) reported that surprisingly "fixed" food preferences could be induced in all three species by raising them from birth on distinctive diets. Great difficulty must have been encountered in feeding day-old puppies and kittens on these diets without any supplementation by mothers' milk, but Kuo does not mention any mortalities among his subjects. We have conducted a number of studies with puppies and kittens along similar lines to those of Kuo, except that they were introduced to fixed diets at weaning rather than from birth. The results are consistently at variance with Kuo's, in that the adult animals never developed an enhanced preference for their rearing diet, but rather they preferred to eat a novel alternative.

In the first experiment, two groups of five 6-week-old Basenji puppies were assigned to one of two different experimental dry dog foods (P and R/CC) which they received as their sole diet for the ensuing 16 weeks. All grew satisfactorily during this period. At the age of 22 weeks they were allowed a choice of the two diets in their usual individual feeding boxes in morning and evening meals over ten consecutive days. The results (Fig. 6) indicate a marked preference for the novel dry diet on the first day

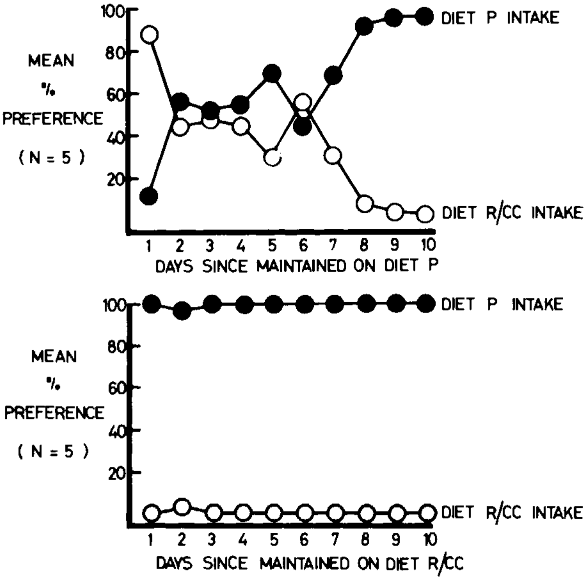

Fig. 6. Preference of Basenji puppies for novel dry foods.

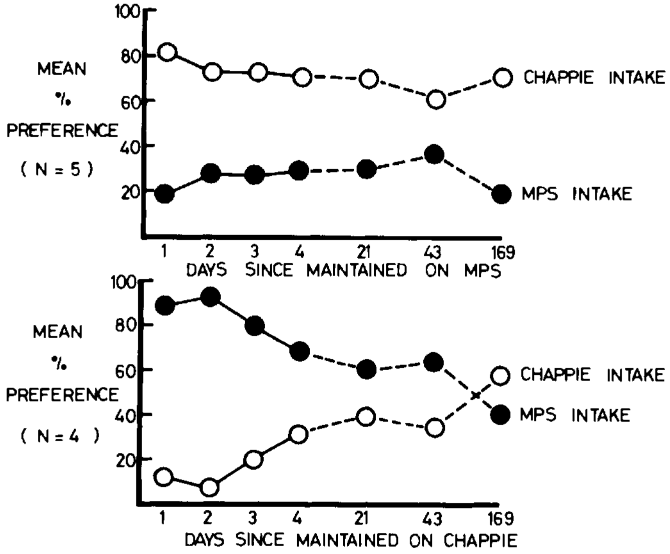

Fig. 7. Preference of Terrier puppies for novel canned foods.

($p < 0.01$, between-groups comparison), which for the group previously maintained on diet P declined on subsequent tests. In contrast to these diet P dogs, those reared on R/CC exclusively preferred diet P on all tests. This reversal of an initial preference (induced only by long established exclusive feeding) is consistent with Young's (1940) now classic observation of a similar phenomenon in rats, since we had previously established that diet P was more palatable than R/CC among dogs naive to both diets.

A second experiment with puppies was conducted with a different breed (nine West Highland White Terriers) and more palatable diets (Chappie versus Kal Kan M.P.S.) than in the experiment reported above. Prefeeding of the diets was again maintained for 16 weeks, followed by 12 consecutive preference tests conducted over 4 days, and further tests after 3, 6, and 24 weeks. Both the Chappie- and M.P.S.-reared dogs showed a consistent preference for the novel diet. The data in Fig. 7 were broken down by analysis of variance, and showed significant ($p < 0.001$) differences between the two diet groups.

Experiments with kittens have yielded comparable results. Twenty-four weanling kittens were assigned to three groups, to be fed exclusively either C26 chicken variety, C26 liver variety, or Whiskas (all palatable canned cat foods). The two groups of C26-reared kittens had precisely reversed initial preferences after the 16-week maintenance period. However, unlike the puppies in the second experiment, the kittens' initial preference for the novel variety quickly decreased across time so that the groups did not significantly differ from one another after the second and subsequent days' preference tests (Fig. 8a). This outcome was consistent with our prior expectations that the two varieties were equally palatable.

The kittens prefed Whiskas were allowed the choice of Whiskas and Kitekat (the novel food) over 40 days as shown in Fig. 8b. Again, the latter was initially preferred ($p < 0.05$), but after 10 days the more palatable Whiskas assumed the usual preference advantage ($p < 0.01$) that is observed among naive cats (author's unpublished observations).

To summarize, we have found that massed feeding of a single nutritionally balanced diet to young dogs and cats induces a transient depression of its relative palatability. This outcome is not unique to young animals, since novel foods are also favored by adult cats (Hegsted *et al.*, 1956) and dogs (author's unpublished observations). The concept of "oral satiety"

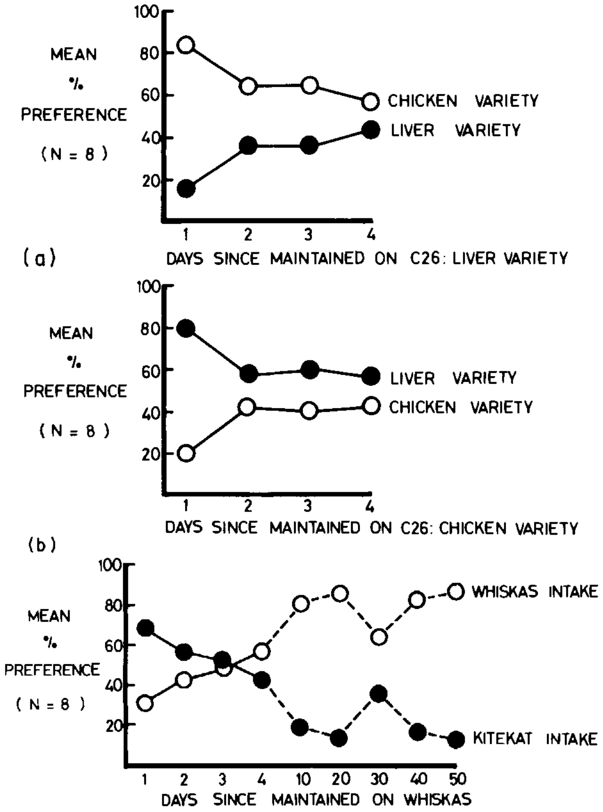

Fig. 8. Preference of kittens for novel canned foods.

TABLE I

Influence of Meal Frequency and Between-Meal Variety upon Caloric Intake of Cats

Diet	Caloric intake (kcal/day)
Fed once per day	
Whiskas	227
Sam	181
Kitekat	224
Average	211
Fed three times per day, same diet	
Whiskas–Whiskas–Whiskas	401
Sam–Sam–Sam	287
Kitekat–Kitekat–Kitekat	236
Average	308
Fed three times per day, different diets	
Whiskas–Sam–Kitekat	435
Sam–Kitekat–Whiskas	508
Kitekat–Whiskas–Sam	413
Average	452

(Le Magnen, 1971) is probably relevant in this context. Thus, both dogs and cats can be induced to increase the duration and size of their meals by successive presentations of three distinctively different diets, compared to any regularly replenished single diet (author's unpublished observations). Similar effects due to regular variation in flavor of rat diets were reported by Le Magnen (1956).

A demonstration of how presentation of contrasting diet types can enlarge total daily caloric intakes of cats is illustrated by the data in Table I. Twenty-seven cats were assigned in equal numbers to one of three groups on the basis of best match for age, sex, body weight, and prior food intakes.

Each group of nine cats was itself subdivided into three sets of three, which were then fed one of the diets or diet combinations indicated in Table I. Over three consecutive days, each set of three cats experienced all of the three diets or diet combinations. Data from this modified factorial design was treated to an analysis of variance. Highly significant diet and group effects ($p < 0.001$) can be attributed to enlarged caloric intakes of cats fed three times per day (46% greater than single-meal feeding), which was still further increased among those cats offered a succession of *different* diets over three meals on the same day.

The doubling in caloric intake (from 211 to 452 kcal/day) associated with providing both increased feeding opportunities and between-meal variety confirms what has already been stated about the plasticity of the regulatory mechanisms over food intake. Clearly, stimulus change or sensory contrast is an important factor affecting a diet's acceptance, which can doubtlessly be attributed to change along more than one dimension and within more than any one sensory modality. The particular role of olfaction as a determinant of a diet's palatability and its contrast with diets having a different odor are explored in the next section.

OLFACTORY INFLUENCES OVER INGESTIVE BEHAVIOR

It is our everyday human experience that the "normal" appreciation of food can be greatly affected by our sense of smell (Henkin *et al.*, 1971). Perhaps experimenters have been deterred from "discovering" the obvious, or is it that they are still slaves to the misconception that "taste" is synonymous with "flavor" and odor provides just a little something extra? There are certainly methodology difficulties associated with studying the relationship between olfaction and feeding, but it is hoped that the present chapter will show that many of them can be overcome by the simple expediency of dissociating the food itself from odors introduced through or over the food via a clean airstream.

Previous studies exploring the relationship between food palatability and odors can be criticized on the grounds that the supposed "odor" was actually incorporated into the test water or diet (e.g., Simson and Booth, 1973; Soane and Clarke, 1973; Le Magnen and Tallon, 1968). This raises the possibility that the introduced "odor" might be perceived via a nonolfactory route, as by direct absorption through the roof of the oral cavity (Kare *et al.*, 1969) or by alteration to the taste of the ingested food or water (Doty, 1975, p. 397).

Olfactory deficits induced by lesions or surgical removal of the olfactory bulb (Kovach and Kling, 1967; Larue and Le Magnen, 1972) also make for problems of interpretation since destructive intervention of the nervous system may produce unwanted secondary effects additional to anosmia (Whitten, 1956). The same can be said of techniques intended to effect a more specific interference with the sense of smell, as by irrigation of the olfactory mucosa with zinc sulphate (Alberts and Galef, 1971) or procaine hydrochloride (Doty and Anisko, 1973).

If surgical or chemical destruction of components of the olfactory system does not provide the methodology with which to make unambiguous demonstrations of the role of odors in feeding behavior, then such severe

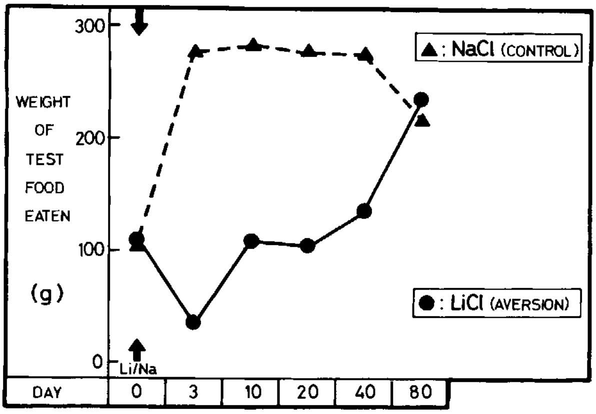

Fig. 9. Mean intakes of canned meat by cats, demonstrating dietary aversion learning.

impositions upon the animals' welfare are difficult to defend upon purely scientific grounds (Ryder, 1975). We have, therefore, adopted an alternative approach in which food-derived odors or the volatile components of a flavor are localized in their presentation to the animal by being suffused over or through a pelleted dry cat food. A three-part series of studies will be described in this section which demonstrates a crucial role of olfaction in establishing the palatability of food for the domestic cat. Thus, odors can (a) mediate the recognition of a diet to which a learned aversion has been formed, (b) direct selection of one food over an alternative that differs only by odor quality, and (c) both initiate and sustain feeding.

Demonstration of Dietary Aversion Learning*

Most readers will be familiar with the phenomenon of "bait shyness" in rats and other vertebrates, induced as a result of temporal association between sickness and a characteristically flavored diet or drink (see reviews by Garcia *et al.*, 1974; Rozin and Kalat, 1971). The experiment to be described demonstrates this phenomenon in cats.

Sixteen cats were assigned to two groups of eight on the basis of matched sexes and body weight. On the first day of the experiment (Day 0, Fig. 9) they were all individually fed 100 g of an experimental meat-based canned diet (M, based mainly upon cow lungs). The cats' normal maintenance diet was a complete dry cat food, so that M was quickly eaten because it was both palatable and novel. Immediately after they had fin-

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* These studies of dietary and odor aversion learning were conducted while the author was a visiting scientist at the Monell Chemical Senses Center, Philadelphia.

ished eating, one group (aversion) was given lithium chloride (1% body weight of a 0.15 N solution, as in Nachman and Ashe's 1973 study with the rat). The other (control) group was treated with an equimolar solution of sodium chloride.

After two days' maintenance on the dry food, all cats were again offered M to appetite, as also on the tenth, twentieth, and fortieth days of the study. Figure 9 shows mean intakes of M during their six meals.

Analysis of variance (between groups, days 3–80) revealed a significant ($p < 0.001$) depression of intake by the aversion group of M, but not of their usual maintenance diet. Cats in the control group ate meals of M that were three times larger than aversion cats' meals of the same diet, whereas both groups continued to eat the maintenance dry cat food as before. Comparisons of intakes on each of days 3, 10, 20, and 40 confirmed that the dietary aversion was sustained for a period in excess of 1 month after only a single exposure to the U.C.S. (LiCl). By day 80, the two groups ate equally large meals of M. However, this interval of between 40 and 80 days probably does not encompass the time limit for retention of a dietary aversion, since the learned response would have suffered interference (or M-acquired properties of "learned safety") in five meals when M was offered (see Rozin and Kalat, 1971, p. 477). Nevertheless, the generality of the phenomenon of dietary aversion learning has been extended to include the cat on the basis of the results from this experiment. One could speculate that this ability might have a parallel in nature, serving to protect wild felids from repeated ingestions of prey or organs of prey that might induce gastric distress. The widely reported avoidance of insectivorous rodents by predaceous carnivores (e.g., Macdonald, 1977; Pearson, 1966) might be an example of aversion learning occurring under natural conditions. Garcia *et al.* (1974) and Chapter 13 of this volume have reported that aversions to mutton can be induced in coyotes by lithium chloride with a consequent reduction in their predation of sheep.

Influence of Odors upon Food Selection and Food Avoidance

There is some controversy as to whether rats can use olfactory stimuli to sustain a learned dietary aversion. Garcia *et al.* (1974) failed to find any diminution of the ability of "anosmic" rats to form an aversion to apple juice, and Barnett, Cowan, and Radford (1975) came to the same conclusion after finding that wild *Rattus rattus* made anosmic by the zinc sulphate method (Alberts and Galef, 1971) still avoided millet treated with poisonous zinc phosphide. However, in the Garcia *et al.* study one could argue that the most salient cue available to form the basis of an aversion to apple juice would be an acid taste. Where an easily discriminable or unusual odor is paired with a poisoning episode, quite effective aversions to the odor can be learned (Lorden *et al.*, 1970; Supak *et al.*, 1971). Furthermore, pairing an odor with a flavored water supply can then provide the basis for a learned odor-aversion being generalized to the flavored liquid (Domjan, 1973; Taukalis, 1974), which certainly hints strongly that odors have a more important role in "setting the hedonic tone of food" than is suggested by Garcia *et al.* (1974, p. 828).

The influence of odors upon food selection has been studied in our laboratory by arranging a simple two-choice preference situation (Hegsted *et al.*, 1956) of two food bowls, each fitted with a perforated base through which an airstream (3 liters/min) could be passed. If one of the airstreams is bubbled through homogenized meat, the aroma can be transferred by the airstream to the food. Ten cats were tested for preferences of their usual dry diet, either odorized by an airstream that had been bubbled through M, or just suffused with the clean carrier airstream. Reference to the data for days 1 + 2 in Fig. 10 shows that their average preferences were 87% in favor of the M odor. Two groups of five cats were then matched on the basis of their equal preference for M odor. Both were *fed* M on day 3; one was treated with LiCl (aversion) and the other with NaCl (control), as in the previous experiment. A succession of preference tests between air and M odor followed on days 5–10, and the results are presented as 2-day means from alternated bowl positions (because of the need to control for idiosyncratic bowl biases).

On day 5 there was a *total* avoidance by all cats in the aversion group of the M-odorized food, but an 80% preference by controls. This avoidance of the M odor was not quite so marked on the sixth and succeeding days, though intakes of the odorized food were never more than half that of the

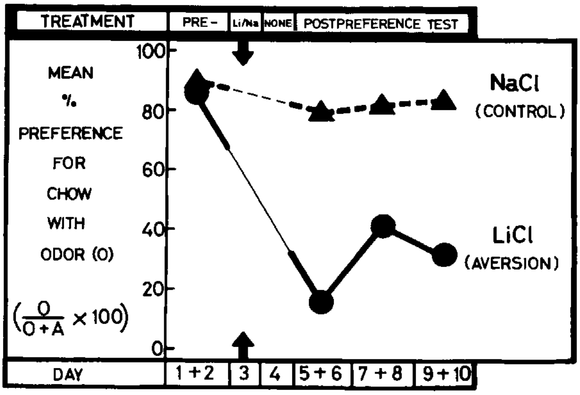

Fig. 10. Dry food/odor preferences of cats, demonstrating odor toxicosis learning.

control group (overall days, $p < 0.001$). The total food intakes by the two groups was rather similar (aversion: 16.8 g/meal, controls: 17.4 g/meal), so that the main effect of the M odor was to *direct* selection.

The Initiation of Feeding by Odors

If one recalls that M was itself a novel diet for the cats used in these studies, one could argue that its odor provided the basis for an enhanced "palatability response" toward their familiar maintenance food. However, a more parsimonious explanation would be that the M odor had reinforcing properties not connected with its presentation around the dry food (cf. Long and Tapp, 1967, 1968) and may not contribute much to its perceived palatability. Thus, the odor may just have attracted investigation (and so, physical movement) by the cats toward its source around the food, and thereby biased intake in favor of the nearest bowl. Many other classes of olfactory stimuli will initiate investigation (Doty, 1972, 1975), but in the context of social and sexual selection rather than feeding behavior. Interestingly, a study by Shumake, Thompson, and Bullard (1973) demonstrated that rats will greatly increase their entries and occupation times of the one arm of a four-arm maze suffused with a food odor. Although these authors did not present the odor in the same context as food, it was probably affected by the rats' motivation to find food since hungry rats were significantly more responsive than satiated rats.

After demonstrating an influence of odors upon food selection, the relevant question seemed to be whether food-derived odors can initiate and sustain consumption of a diet that would not otherwise be eaten. This was investigated in two experimental situations. The first utilized meal-fed cats, which were introduced one at a time into an observation cage to be fed their regular dry diet. The second situation permitted long-term (13-hr) observation of groups of cats, always provided with an *ad libitum* supply of food and whose behavior could be recorded by time-lapse video tape (see section on social factors affecting ingestive behavior). Both methods have proved suitable for evaluating the ingestion stimulatory qualities of odors derived from highly palatable foods.

The results of two experiments will be presented here, to illustrate this action of odors. Working with 20 cats usually fed individual meals, we have consistently found that both the duration and size of the meals can be increased by blowing a succession of "attractive" food odors through their maintenance diet after satiety or voluntary termination of feeding. Figure 11 illustrates one aspect of the results from an experiment in which a continuous airstream (3 liters/min) was substituted by the odor of M, after the cats had stopped eating during both of the preceding phases of the

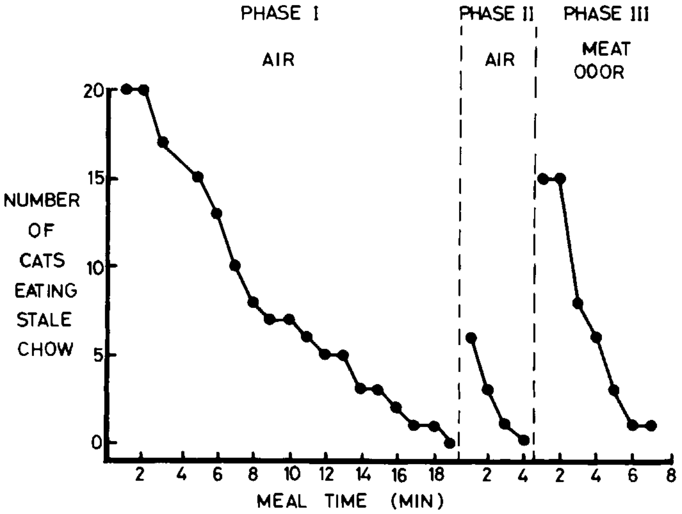

Fig. 11. Duration and incidence of feeding during single free access meals of cats, showing modification by the odor of a palatable canned meat diet.

meal. A "phase" consisted of the time during which the cat ate its food, plus an additional time-out of 60 sec after feeding ceased.

M-odor provoked a rapid revival of interest in the food, to the extent that eating recommenced in 15 of the 20 cats. If total food consumption of each cat is rated as 100, then the proportions eaten during the three consecutive phases AIR–AIR–M ODOR were on the average 45–17–38. This profile of food consumption has been significantly altered ($p < 0.01$) from the pattern obtained in control experiments run as a consecutive sequence AIR–AIR–AIR (65–22–13).

An essentially similar odor-mediated phenomenon was demonstrated to initiate and sustain bouts of feeding among nine cats having 24-hr access to dry cat food. In this experiment alternating half-hour sessions of AIR and ODOR derived from cooked rabbit meat (a highly preferred food item for the cat) were presented. Both the number of meals and food consumption were significantly increased by the rabbit odor (Fig. 12). This substantially altered pattern of food intake emphasizes that odors do indeed contribute to the hedonic tone of food (i.e., its palatability) in a way that is closer to the conceptualization suggested by Le Magnen (1971) than that of Garcia *et al.* (1974).

We have only recently begun to extend the methodology described here for cats to dogs. Preliminary results indicate that odors are equally influential over patterns of food selection and intake in this species. The profi-

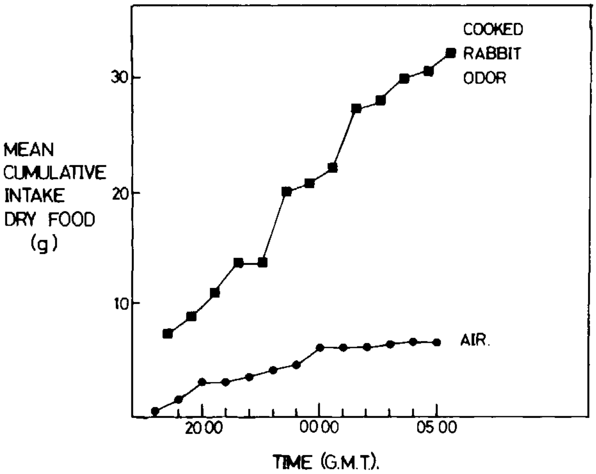

Fig. 12. Mean cumulative intakes of dry cat food during alternating half-hour presentations of air and odor over the food. G.M.T., Greenwich mean time.

ciency of the dog in olfactory detection tasks has been extensively studied in both an applied and scientific context (Moulton and Marshall, 1977). From naturalistic studies, it is evident that wolves also possess a highly developed olfactory sense, employed as both a means for receiving odor signals from conspecifics and detecting and trailing prey (Mech, 1970). Other authors mention the use made by canids of olfactory cues for detecting prey (e.g., Macdonald, in press, for the red fox *Vulpes vulpes*), but few reports on other families of carnivores (including the Felidae) are to be found in the literature. It is obvious that many more comparative studies are needed before the significance of the results reported here can be extended to the circumstances facing pet or feral dogs and cats, let alone the truly wild carnivores. However, sufficient evidence exists to surmise that olfaction is intimately involved in the processes of both prey location and close evaluation of food by many more than just the two species described here.

While the role of olfaction in feeding behavior has been emphasized in this paper, this is not intended to suggest that gustatory influences are any less significant. Indeed, an enormous literature attests to the ease with which the palatability of both foodstuffs and liquids can be modified by alteration along one of the dimensions of taste (e.g., Bartoshuk *et al.*, 1975; Carpenter, 1956; Kitchell and Baker, 1972), making further discussion of this point in relation to dogs and cats unnecessary. Little, if any, sound experimental data exist on taste or odor preferences of carnivores that exploit contrasting food sources, and which could form the basis for a comparative ecological model of sensory control over feeding behavior. It seems unlikely that this situation will be remedied in the foreseeable future, since it is mainly the so-called "pest" species that presently attract much attention, and regrettably that is often with the objective of developing more effective media with which they may be baited and destroyed.

REFERENCES

Alberts, J. R., and Galef, B. G. (1971). Acute anosmia in the rat. A behavioral test of a peripherally-induced olfactory deficit. *Physiol. Behav.* **6,** 619–621.

Anderson, R. S. (1974). Obesity in the dog and cat. *Vet. Annu.* pp. 182–186.

Barnett, S. A. (1963). "A Study in Behaviour," pp. 28–33, Methuen, London.

Barnett, S. A., Cowan, P. E., and Radford, G. G. (1975). Peripheral anosmia and the discrimination of poisoned food by *Rattus rattus* L. *Behav. Biol.* **13,** 183–190.

Bartoshuk, L. M., Jacobs, H. L., Nichols, T. L., Hoff, L. A., and Ryckman, J. J. (1975). Taste rejection of nonnutritive sweeteners in cats. *J. Comp. Physiol. Psychol.* **89,** 971–975.

Bernston, A. A., and Hughes, H. C. (1974). Medullary mechanisms for eating and grooming behavior in the cat. *Exp. Neurol.* **44,** 255–265.

Booth, D. A. (1972). Caloric compensation in rats with continuous or intermittent access to food. *Physiol. Behav.* **8,** 891–899.

Bronson, A. (1966). Evidence of the lack of influence of early diet on adult food preference in rats. *J. Comp. Physiol. Psychol.* **62,** 162–164.

Carpenter, J. A. (1956). Species differences in taste preferences. *J. Comp. Physiol. Psychol.* **49,** 139–144.

Carroll, M. E., Dinc, H. I., Levy, C. J., and Smith, J. C. (1975). Demonstrations of neophobia and enhanced neophobia in the albino rat. *J. Comp. Physiol. Psychol.* **89,** 457–467.

Coman, B. J., and Brunner, H. (1972). Food habits of the feral house cat in Victoria. *J. Wildl. Manag.* **36,** 848–853.

Compton, J. M., and Scott, J. P. (1971). Allelomimetic behavior system: Distress vocalisation and social facilitation of feeding in telomian dogs. *J. Psychol.* **78,** 165–179.

Crandall, L. S. (1964). "*Management of Wild Animals in Captivity.*" Univ. of Chicago Press, Chicago, Illinois.

Domjan, M. (1973). Role of ingestion in odor-toxicosis learning in the rat. *J. Comp. Physiol. Psychol.* **84,** 507–521.

Doty, R. L. (1972). Odor preferences of female *Peromyscus maniculatus bairdi* for male mouse odors of *P.m. bairdi* and *P.leucopus noveboracensis* as a function of estrous state. *J. Comp. Physiol. Psychol.* **81,** 191–197.

Doty, R. L. (1975). Determination of odor preferences in rodents: Methodological review. *In* "Methods in Olfactory Research" (D. G. Moulton, A. Turk, and J. W. Johnston, Jr., eds.), pp. 395–406. Academic Press, New York.

Doty, R. L., and Anisko, J. J. (1973). Procaine hydrochloride olfactory block eliminates mounting in the male golden hamster. *Physiol. Behav.* **10,** 395–397.

Ewer, R. (1973). "The Carnivores." Cornell Univ. Press, Ithaca, New York.

Garcia, J., Hankins, W. G., and Rusiniak, K. W. (1974). Behavioral regulation of the milieu interne in man and rat. *Science* **185,** 824–831.

Harris, L. J., Clay, J., Hargreaves, F. J., and Ward, A. (1933). Appetite and choice of diet.

The ability of the vitamin B deficient rat to discriminate between diets containing and lacking the vitamin. *Proc. R. Soc. London, Ser. B* **113,** 161–190.

Hatton, G. I. (1975). Ingestive mechanisms and behaviours. *In* "The Behaviour of Domestic Animals" (E. S. E. Hafez, ed.), pp. 73–107. Baillière, London.

Hegsted, D. M., Gershoff, S. N., and Lentini, E. (1956). The development of palatability tests for cats. *Am. J. Vet. Res.* **17,** 733–737.

Henkin, R. I., Schechter, P. J., Hoye, R., and Mattern, C. F. T. (1971). Idiopathic hypogeusia with dysgeusia, hyposmia, and dysomia. *J. Am. Med. Assoc.* **217,** 434–440.

Hess, E. H. (1964). Imprinting in birds. *Science* **146,** 1128–1139.

Jacobs, H. L., and Sharma, K. N. (1969). Taste versus calories: Sensory and metabolic signals in the control of food intake. *Ann. N.Y. Acad. Sci.* **157,** 1084–1125.

Jalowiec, J. E., Panksepp, J., Shabshelowitz, H., Zolovick, A. J., Stern, W., and Morgane, P. J. (1973). Suppression of feeding in cats following 2-deoxy-D-glucose. *Physiol. Behav.* **10,** 805–807.

James, W. T. (1949). Dominant and submissive behavior in puppies as indicated by food intake. *J. Genet. Psychol.* **75,** 33–43.

James, W. T. (1953). Social facilitation of eating behavior in puppies after satiation. *J. Comp. Physiol. Psychol.* **46,** 427–428.

James, W. T. (1961). Relationship between dominance and food intake in individual and social eating in puppies. *Psychol. Rep.* **6,** 478.

Janowitz, H. D., and Grossman, M. I. (1949). Some factors affecting the food intake of normal dogs and dogs with esophagostomy and gastric fistula. *Am. J. Physiol.* **159,** 143–148.

Jones, A. F., and Hamilton, F. (1971). "The World Encyclopedia of Dogs." World Publ. Co., New York.

Joshua, J. O. (1970). The obese dog and some clinical repercussions. *J. Small Anim. Pract.* **11,** 601–606.

Kanarek, R. B. (1975). Availability and caloric density of the diet as determinants of meal patterns in cats. *Physiol. Behav.* **15,** 611–618.

Kare, M. R., Schechter, P. J., Grossman, S. P., and Roth, L. J. (1969). Direct pathway to the brain. *Science* **163,** 952–953.

Kissileff, H. (1970). Free feeding in normal and "recovered lateral" rats monitored by a pellet-detecting eatometer. *Physiol. Behav.* **5,** 163–173.

Kitchell, R. L., and Baker, G. G. (1972). Taste preference studies in domestic animals. *In* "Nutrition Conference for Feed Manufactures: 6" (H. Swan and D. Lewis, eds.), pp. 158–202. Livingstone, Edinburgh.

Kovach, J. K., and Kling, A. (1967). Mechanisms of neonate suckling behaviour in the kitten. *Anim. Behav.* **15,** 91–101.

Kruuk, H. (1972). "The Spotted Hyena: A Study of Predation and Social Behavior." Univ. of Chicago Press, Chicago, Illinois.

Kuo, Z. Y. (1967). "The Dynamics of Behavior Development, An Epigenetic View." Random House, New York.

Larue, C. G., and LeMagnen, J. (1972). The olfactory control of meal pattern in rats. *Physiol. Behav.* **9,** 817–821.

Le Magnen, J. (1956). Hyperphagie provoquée chez le rat blanc par altération du méchanisme de satiété périphérique. *C. R. Seances Soc. Biol. Ses. Fil.* **150,** 32.

Le Magnen, J. (1971). Advances in studies on the physiological control and regulation of food intake. *Prog. Physiol. Psychol.* **4,** 203–261.

Le Magnen, J., and Tallon, S. (1968). Préférence alimentaire du jeune rat induit par l'allaitement maternal. *C. R. Seances Soc. Biol. Ses Fil.* **162,** 387–390.

Long, C. J., and Tapp, J. T. (1967). Reinforcing properties of odors for the albino rat. *Psychon. Sci.* **7,** 17–18.

Long, C. J., and Tapp, J. T. (1968). An apparatus for the assessment of the reinforcing properties of odors in small mammals. *J. Exp. Anal. Behav.* **11,** 49–51.

Lorden, J. F., Kenfield, M., and Braun, J. J. (1970). Response suppression to odors paired with toxicosis. *Learn. Motiv.* **1,** 391–400.

Macdonald, D. W. (1977). On food preference in the red fox. *Mamm. Rev.* **7,** 7–24.

Mayer, J., and Thomas, D. (1967). Regulation of food intake and obesity. *Science* **156,** 328–337.

Mech, L. D. (1970). "The Wolf" Nat. Hist. Press, Garden City, New York.

Mech, L. D. (1975). Hunting behavior in two similar species of social canids. *In* "The Wild Canids. Their Systematics, Behavioral Ecology and Evolution" (M. W. Fox, ed.), pp. 363–368. Van Nostrand-Reinhold, Princeton, New Jersey.

Morrison, G. R. (1974). Alterations in palatability of nutrients for the rat as a result of prior tasting. *J. Comp. Physiol. Psychol.* **86,** 56–61.

Moulton, D. G., and Marshall, D. A. (1977). The performance of dogs in detecting α-ionone in the vapor phase. *J. Comp. Physiol.* **110,** 287–306.

Nachman, M., and Ashe, J. H. (1973). Learned taste aversions in rats as a function of dosage, concentration, and route of administration of LiCl. *Physiol. Behav.* **10,** 73–78.

Nagamachi, Y. (1972). Effect of satiety center damage on food intake, blood glucose and gastric secretion in dogs. *Am. J. Dig. Dis.* **17,** 139–148.

Pearson, O. P. (1966). The prey of carnivores during one cycle of mouse abundance. *J. Anim. Ecol.* **35,** 217–233.

Platt, J. J., and James, W. T. (1966). Social facilitation of eating behavior in young opossums. I. Group vs. solitary feeding. *Psychon. Sci.* **6,** 421–422.

Ross, S., and Ross, J. G. (1949a). Social facilitation of feeding. *J. Genet. Psychol.* **74,** 97–108.

Ross, S., and Ross, J. G. (1949b). Social facilitation of feeding behavior in dogs. II. Feeding after satiation. *J. Genet. Psychol.* **74,** 293–304.

Rozin, P., and Kalat, J. W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychol. Rev.* **78,** 459–486.

Ryder, R. D. (1975). "Victims of Science: Use of Animals in Research." Davis Poynter, London.

Schaller, G. B. (1972). "The Serengeti Lion: A Study of Predator-Prey Relations." Univ. of Chicago Press, Chicago, Illinois.

Scott, P. P. (1968). The special features of nutrition of cats with observations on wild Felidae nutrition in the London Zoo. *Symp. Zool. Soc. London* **21,** 21–36.

Scott, P. P. (1971). Dietary requirements of the cat in relation to practical feeding problems. *Pap. Small Anim. Nutr. Workshop, Univ. Ill. Coll. Vet. Med., 1971.*

Shumake, S. A., Thompson, R. D., and Bullard, R. W. (1973). An automated odor test for rats. *Behav. Res. Methods & Instrum.* **5,** 279–282.

Siegel, P. S. (1957). The repetitive element in the diet. *Am. J. Clin. Nutr.* **5,** 162–164.

Simson, P. C., and Booth, D. A. (1973). Olfactory conditioning by association with histidine-free or balanced amino acid loads in rats. *Q. J. Exp. Psychol.* **25,** 354–359.

Skultety, F. M. (1969). Alterations of caloric intake in cats following lesions of the hypothalamus and midbrain. *Ann. N.Y. Acad. Sci.* **157,** 861–874.

Smith, G. P., and Epstein, A. N. (1969). Increased feeding in response to decreased glucose utilization in the rat and monkey. *Am. J. Physiol.* **217,** 1083–1087.

Soane, I. D., and Clarke, B. (1973). Evidence for apostatic selection by predators using olfactory cues. *Nature (London)* **241,** 62–63.

Sudakov, K. V., and Rogacheva, S. K. (1963). The afferent and efferent activity of the gastric fibers of the vagus nerve during fasting and after taking food. *Fed. Proc., Fed. Am. Soc. Exp. Biol.* **22,** T306–T310.

Supak, T., Macrides, F., and Chorover, S. (1971). The bait shyness effect extended to olfactory discrimination. *Commun. Behav. Biol.* **5,** 321–324.

Taukalis, H. K. (1974). Odor aversions produced by long CS–US delays. *Behav. Biol.* **10,** 505–510.

Toates, F. M., and Booth, D. A. (1974). Control of food intake by energy supply. *Nature (London)* **251,** 710–711.

Welker, W. I., and King, W. A. (1962). Effects of stimulus novelty on gnawing and eating by rats. *J. Comp. Physiol. Psychol.* **55,** 838–842.

Whitten, W. K. (1956). The effect of removal of the olfactory bulbs on the gonads of mice. *J. Endocrinol.* **14,** 160–163.

Young, P. T. (1940). Reversal of food preferences of the white rat through controlled prefeeding. *J. Genet. Psychol.* **38,** 129–164.

Young, S. P. (1944). "The Wolves of North America," Part I. Am. Wildl. Inst., Washington, D.C.

DISCUSSION

Doty: Did I understand you correctly: once an animal has had an early experience of a food, and was then switched to another which was novel, it preferred the novel alternative for a long period of time? In other words, an imprinting occurs.

Mugford: If one must use the term imprinting, it could be described as a form of negative imprinting whose effect upon food selection is usually only transient. However, in the experiment with West Highland White puppies, the effect seemed to be more persistent—up to 6 months.

Doty: But these effects were due to early feeding experiences.

Mugford: Not necessarily, since the puppies would all have had some contacts with a diversity of solid foods up to the age of 8 weeks when they were weaned. Thus, they would share the same diet as their dam prior to joining the experiment. We have worked with adults and obtained exactly the same potentiation of interest in the new food. Sometimes the effect is transient, at other times more long lasting, depending upon the relationship between palatability of the familiar and novel foods. The effects are particularly transient if the familiar food is more palatable than the unfamiliar food.

Rogers: I would like to describe some observations we have made of kittens and purified diets, which they normally will not accept very readily. If you take an adult cat and give it a purified diet containing specified amino acids, it may take from 2 to 4 weeks before it will eat properly. If the same diet is given to young kittens, they will accept it quite readily, eat, and grow. Now, after we have had kittens on this diet for a couple of months we have changed them to a regular kibble for 6 months. On the first re-presentation of the amino acid diet to the now adult cat, it is readily accepted. We thought that this was interesting because it demonstrates how acceptance of a generally unpalatable diet can be improved by prior feeding during early life.

Mugford: This is indeed a most interesting observation.

Moskowitz: I have two questions. First, in your data on eating speeds of dogs you showed a combination of two foods, Chum and Mick, which seemed to show an intermediacy rather as Senseman had suggested before with the two kinds of food for his slugs. Is there an algebra whereby you could predict the rate of eating as a function of the initial rate of the two components, or is it just plain intermediate?

Mugford: The initial rates are highly correlated with the overall rate.

Moskowitz: Well, do you think it is possible to predict the rate of the mixtures in varying combinations if you knew the initial rates of consumption of the two or three components?

Mugford: I would think that it would be possible to do so, because the responses are extremely stable for particular individuals and are characteristic of each diet studied.

Moskowitz: I know that in humans you cannot predict the hedonic response to a mixture of odors; only the hedonic responses of each component. My second question concerns this very interesting novelty effect. If you watch human children, there is a period at which they will accept almost anything, then they grow into a period of recalcitrance when they will not accept anything that they do not know, and then as they get still older they diverge into adventurous eaters and normal eaters; along two completely different paths. Some people like anything new while others will never eat anything new. Have you any observations in animals analogous to this situation in humans?

Mugford: Our data do not support the notions of either dietary imprinting or neophobia for the dog or cat. However, we have really only worked with young animals of less than 4 years of age. It is conceivable, though improbable, that animals in their dotage may change their selection strategies in the way you have suggested occurs among humans.

Pangborn: Do cats and dogs eat differently in a group compared to a solitary situation?

Mugford: No, with qualifications. The surprising outcome of our observations with mature animals was that the timing, duration, and frequency of meals was similar when several individuals were compared to the same animals living as a compatible group. Much depended upon the social relationships between members of the group, and obviously one could select a pair of dogs in which one was always dominant and aggressive toward the other. In such a situation, food intake by the subordinate would decline.

Garcia: We have done a number of taste and odor studies, and the problem is one of telling whether the animal is tasting the odor. This really is a problem, especially since animals can make such incredibly subtle taste discriminations. Does that bother you as much as it bothers me?

Mugford: Yes, it does bother me, especially since in many studies that I have cited, as Soane and Clarke (1973) the odorant was incorporated into the diet at fairly high concentrations, making it quite likely that it could have been detected via a nonolfactory route. In our experiments, absorption of an airborne odor onto dry food, having a moisture content of only 8%, would probably be minimal. It would seem to me to be more parsimonious to hypothesize that there may be an olfactory mediation at work, rather than absorption prior to gustatory reception.

Garcia: Well, the problem is that when we used anosmic animals they showed no loss in ability to discriminate the poisoned food—absolutely none. In fact, most of the time they were a little better than the ones having senses of both taste and smell.

Mugford: Surely, one would expect the animals to be attending to the most salient cue emanating from the food. In the case of the experiment where you were using apple juice (see main text, Garcia *et al.*, 1974) the overwhelming sensation was probably acid, i.e., taste. Doubtlessly, animals make the best of a situation in which they are challenged by the need to avoid poison, and accomplish protective strategies of food discrimination by employing more than any single sensory modality.

Sato: In the experiment with Basenjis, what was the difference between diets offered to the two groups?

Mugford: They contained different ingredients and were manufactured by different processes, so they would be expected to differ along several sensory dimensions.

Sato: Is there a possibility that nutritional factors were involved in the switch from one diet to the other?

Mugford: I think that this might have been the case, except that in all of the experiments I have just reported, the animals grew well and at rates appropriate to the particular breed. In sustaining adequate growth, the diets were presumably nutritionally balanced and not lacking in an essential micronutrient.

Sato: Have you done any chemical characterization of the rabbit odor which might explain its attractiveness?

Mugford: Meat aromas are all of immense chemical complexity, so we have not fractionated or identified compounds in the odor of rabbit meat that might change cats' feeding behavior.