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Dietary Control of Food Intake in Cats¹

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HIRSCH, E., C. DUBOSE AND H. L. JACOBS. *Dietary control of food intake in cats*. *PHYSIOL. BEHAV.* 20(3) 287-295, 1978. - Control of food intake was studied in adult cats with calorically diluted diets. Any changes in the physical properties of the diet led to a transient reduction in daily food intake that gradually recovered to the baseline level of intake. The cats did not increase their level of food intake on the diluted diets and lost weight. These results are discussed in relation to the feeding ecology of cats.

Caloric dilution Diet Finickiness Body weight regulation

THE relative constancy of daily energy intake despite wide variations in the taste, smell, texture and caloric density of the available food has led to widespread acceptance of the assertion that normally rats eat for calories [1, 9, 24, 39]. An increase in food intake when a basal diet is diluted with nonnutritive material has also been observed in mice [15], pigs [30], chickens [19], quail [46], goldfish [35], some ruminants [4] and some adult humans [44]. Failures to observe caloric compensation in rats [8, 24, 25, 27, 42, 45] have been attributed to deprivation induced changes in palatability [24], over-reactivity to the sensory properties of food in hypothalamic hyperphagic rats [45], or to limited access time [8]. The common feature of these explanations is that they all regard this type of regulatory failure as resulting from special circumstances.

There are, however, a growing number of instances where caloric compensation does not occur when food is available continuously to non-deprived animals. Guinea pigs [20], opossums [28], rabbits [23], cats [26], lactating rats [31], human infants [17], some adult humans [44] and some ruminants [4] all fail to show increases in food intake when the caloric density of the available diet is reduced. These observations in conjunction with many reports of overeating and excessive weight gain in mice and rats offered high fat diets [5, 16, 29, 37] raise fundamental questions about the generality of caloric compensation and its precision. Are these failures of regulation due to special circumstances or can both the successes and failures be embodied in a more general principle?

One approach to this question is suggested by recent work on the ecological determinants of feeding and

drinking patterns [12, 13, 20, 21, 22, 26]. According to the view developed in this work the relation between feeding patterns, dietary selection and body weight regulation shown by an animal is in large part a function of the ecological niche he occupies and the habitat in which he currently finds himself. The limits on the plasticity of ingestive behavior which an animal can currently display are determined by the kinds of feeding habitats that have been successfully encountered during the evolutionary history of the species. Modes of successful adjustment remain in the repertoire and are available to respond to changes in the structure of the ecosystem [7]. From this vantage point it may be possible to make predictions about the potentialities of feeding behavior in a variety of organisms. For example, straight forward predictions can be made about the carnivore's response to foods that vary in caloric density. The carnivore's nutritional problems are essentially solved once food is captured. The carnivore diet consists of animal carcasses. This food source is nutritionally balanced and is of a high, relatively constant caloric density. On this basis one would predict that carnivores should be relatively insensitive to variations in the caloric content of their food. Kanarek [26] has already shown that growing cats fail to increase bulk intake when the caloric content of their diet is reduced by 20%. The present series of experiments was designed to extend this analysis by examining the cat's response to a wide range of changes in the sensory and caloric properties of their food.

EXPERIMENT 1

Although the cat has been used in many studies

¹In conducting the research described for this report, the investigators adhered to the *Guide for Laboratory Animal Facilities and Care* as promulgated by the Committee on the Guide for Laboratory Animal Resources, National Academy of Sciences-National Research Council.

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concerned with the neural control of ingestive behavior (e.g. [3]), there is very little normative data on food intake, water intake and their interrelationships in adult cats. Experiment 1 provides such data and also examines the effect of changing the physical form of the food from hard, star-shaped pellets to a powdered mash.

METHOD

Animals

Six adult male cats and four adult female cats were used in this experiment. These cats had previously been used in a taste preference experiment that employed artificial sweeteners [6]. During the taste preference experiment the cats had been on a four hr deprivation schedule that did not influence daily food intake or body weight levels. The cats were allowed six months of ad lib access to food and water before the present experiment was begun.

Apparatus

Each cat was housed in a fiberglass cage that measured 70 cm x 55 cm x 60 cm. Purina cat chow was continuously available in a stainless steel bowl that was mounted on the front wall of the cage. Water was continuously available from a 250 ml calibrated water bottle (Wahmann Manufacturing Company, Baltimore, MD) which was mounted on the front wall of the cage adjacent to the food bowl. The cats were housed in an isolated room that was on a 12-12, light-dark cycle with the lights coming on at 7 a.m.

Procedure

Throughout the experiment the cats were allowed ad lib access to food (Purina cat chow) and water. The only manipulation that was performed was to change the physical form of the food from hard, star-shaped pellets to a powdered mash, back to pellets and then back to a powdered mash. The number of days on each of the diets and the sequence of changes were as follows: 15 days pellets, 25 days powdered mash, 15 days pellets and 10 days powdered mash. When the powdered mash was used the pellets were ground up in a Waring blender no more than 24 hr prior to use. Daily measurements of food intake, water intake and body weight were taken throughout the course of the experiment at 9 a.m. Food spillage was a problem for one of the animals. Food that was found under his cage was collected and weighed each day.

RESULTS

Figure 1 shows the changes in body weight, food intake and water intake throughout the course of the experiment. The upper panel of this figure shows that there were substantial fluctuations in body weight during the 65 days of the experiment. The largest changes in body weight were associated with the dietary transitions. The first change in diet, from pellets to powder, led to a 100 g weight loss that took a full 25 days to recover. The second transition, from powder to pellets, led to a 60 g increase in body weight within the first three days on the pelleted diet. The last transition, from pellets to powder, was associated with a small, gradual decline in body weight.

The middle panel of this figure shows that the variations in body weight were due to changes in food intake. The marked decline in food intake on Day 7 should not be

attributed to normal variation. The reduction in food intake on this day is probably due to using a fresh bag of food that differed in some way from the bag that had just been finished. (The manufacturer keeps the nutritional composition of the chow constant within the specified limits but will vary the source of the nutrients [Dr. Damon Shelton, Research Department, Ralston Purina Company, personal communication]. The food from the two bags was identical in terms of appearance, taste, smell and texture to the human observer but the possibility that the cats were able to detect a difference seems plausible in light of the marked reduction in food intake on this day.) The change in dietary texture from pellets to powder led to a pronounced reduction in food intake for nine of the ten cats. This decrease lasted for several days and then daily intake recovered to its previous level. The other cat showed a dramatic increase in food intake when the diet was switched from pellets to powder. This cat had been consuming 60 g per day on the pelleted diet and increased his daily intake to slightly over 90 g per day on the powdered diet. We do not have a suitable explanation for this cat's unusual behavior but his data are included in the group average shown in Fig. 1. The second dietary transition, from powder to pellets, led to one or two days of overeating with a subsequent return to the baseline level of intake. Again the group average is only a reflection of the behavior of nine of the cats. The cat who had shown an increase in food intake when the diet was switched from pellets to powder returned to his lower level of intake when the diet was switched back to pellets. The third dietary transition, from pellets to powder, did not influence daily intake in any of the animals. The bottom panel of this figure shows that water intake tended to parallel changes in food intake but was somewhat more variable.

The ten cats were approximately the same age but varied in sex and represented a wide range of body weights. For these reasons data for individual animals are presented in Table 1. These values are based on the last ten days of the experiment when the cats were fed the powdered chow and food and water intake were at their most stable levels. Inspection of this table reveals that the variation in these parameters was no greater in the female cats (designated by F in the table) than it was in the male cats (designated by M in the table). The body weights of individual animals are quite stable over this short time period. Individual variability in body weight rarely exceeded 1%. Food and water intake were considerably more variable, with individual coefficients of variation ranging as high as 22% for food intake and 30% for water intake. These values are somewhat higher than those reported for the rat [2], but are similar to values reported for the rabbit [11], dog [10] and pigeon [48]. In these adult cats food intake averaged about 1% of body weight (mean = 1.27%) and the average intake of water was about 250% the average intake of food (mean = 252%). Caloric intake per kg body weight averaged 42.5 kcal/kg. This value is somewhat lower than previously reported values for younger cats [18].

DISCUSSION

In addition to providing normative data on body weight, food intake and water intake the present experiment revealed two interesting findings about the control of food intake in cats. The first finding gives substance to considerable laboratory folklore concerning the finickiness of cats.

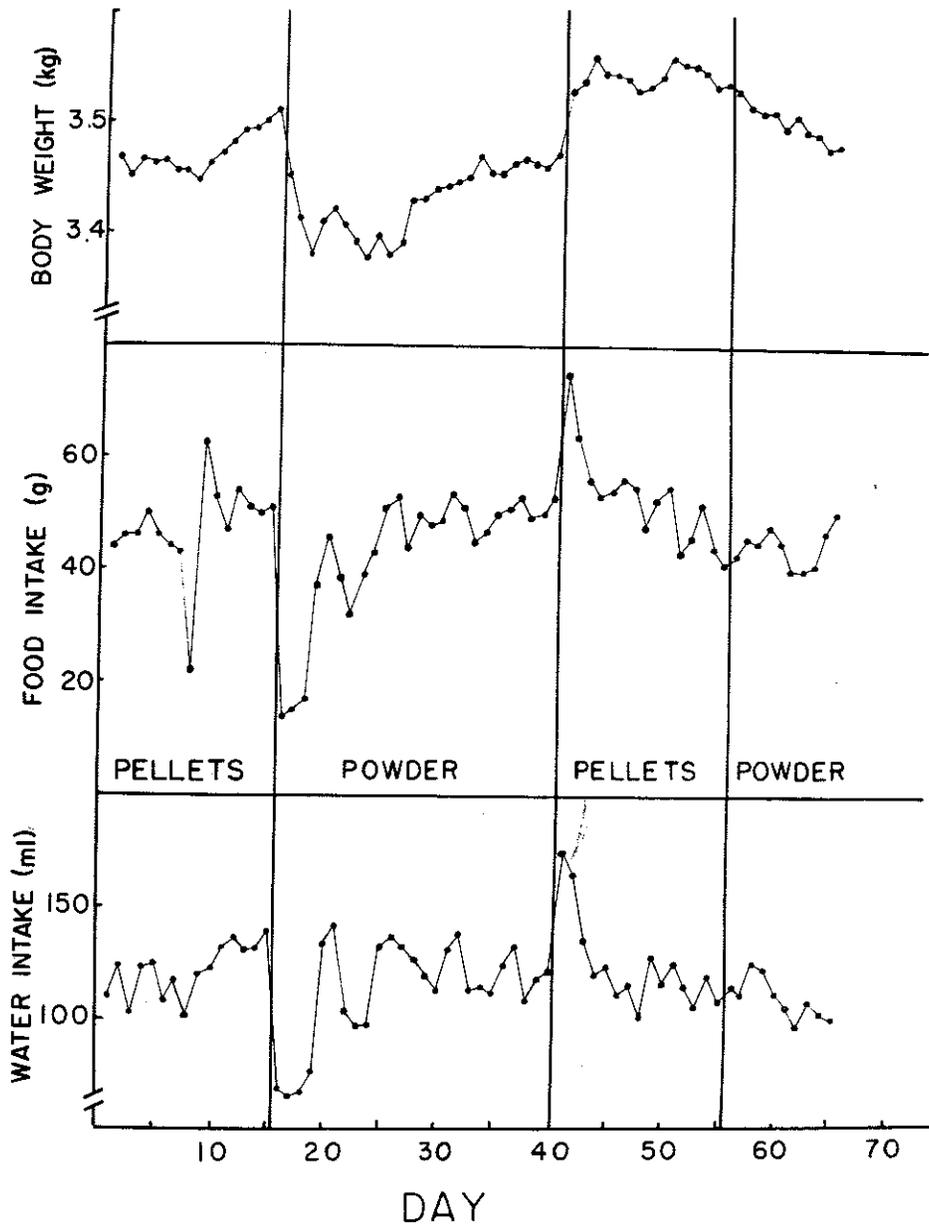


FIG. 1. Mean body weight, food intake and water intake in cats fed chow as pellets or powder.

Experiment 1 revealed that cats are extremely sensitive to changes in the sensory properties of their food. This sensitivity was seen indirectly in the dramatic reduction in food intake on Day 7 when a fresh bag of food was used. This sensitivity was also evident when the texture of the food was changed from pellets to powder. This dietary change induced a complete anorexia in some animals and a substantial increase in food intake in one cat. Both reductions in food intake are probably best viewed as neophobic responses [36]. This interpretation is suggested by the eventual return of food intake to baseline values and the complete attenuation of this response the second time the diet was switched from pellets to powder. As previously mentioned we do not have a suitable explanation for the behavior of the cat that showed an increase in food intake

when the diet was switched from pellets to powder but even this atypical response is consistent with an emphasis on finickiness in cats.

The second interesting finding in this experiment was that over a relatively brief time period the magnitude of variability in the intake of the various nutrients is no greater in cats than in other animals [2, 10, 11, 48]. Over longer time periods Randall and his coworkers [32,33] have reported rhythmic oscillations in body weight and food intake in cats and have attempted to relate these rhythms to underlying physiological events.

EXPERIMENT 2

The high, relatively constant caloric density of the

TABLE 1
INTERRELATIONS BETWEEN FOOD INTAKE, WATER INTAKE, CALORIC INTAKE AND BODY WEIGHT UNDER AD LIB CONDITIONS IN THE CAT

Cat No.	Body Weight		Food Intake (g)		Water Intake (ml)		Ratio of Food Intake to Body Weight		Caloric Intake per kg BW		Ratio of Water Intake to Food Intake	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
F1	1813	± 13.8	28.0	± 6.41	61.0	± 10.78	0.0153	± 0.0034	52.0	± 10.1	2.27	± 0.63
F3	2489	± 11.9	24.8	± 3.35	55.0	± 16.73	0.0099	± 0.0013	33.1	± 12.2	2.22	± 0.61
F6	2152	± 22.3	44.0	± 8.66	78.6	± 20.80	0.0204	± 0.0041	68.4	± 13.1	1.78	± 0.34
F8	2463	± 23.5	28.1	± 5.15	78.8	± 20.62	0.0113	± 0.0020	37.6	± 6.0	2.64	± 0.41
M2	3565	± 23.6	44.6	± 8.65	115.7	± 15.15	0.0124	± 0.0023	41.0	± 8.1	2.69	± 0.72
M4	3500	± 38.8	40.6	± 5.21	130.9	± 30.19	0.0115	± 0.0014	38.9	± 5.4	3.20	± 0.58
M5	5941	± 32.5	71.9	± 8.97	219.3	± 38.99	0.0121	± 0.0015	40.0	± 5.0	3.08	± 0.62
M7	4283	± 39.3	34.7	± 3.80	81.1	± 17.68	0.0080	± 0.0008	25.9	± 3.1	2.32	± 0.43
M9	3382	± 25.0	37.1	± 11.35	91.0	± 18.53	0.0109	± 0.0033	36.2	± 10.8	2.61	± 0.72
M10	5437	± 27.4	87.6	± 9.26	215.5	± 37.14	0.0160	± 0.0016	53.2	± 6.0	2.45	± 0.37
Group Mean	3501		44.1		112.3		0.0127		42.5		2.52	
Mean SD	25.81		7.08		22.6		0.0021		7.90		0.55	
Mean Coefficient of Variation	0.0086		0.171		0.215		0.169		0.16		0.22	

carnivore diet raises the interesting question as to whether feeding behavior in the cat under laboratory conditions is sensitive to variations in the energy content of the available diet. Kanarek [26] has previously shown that at a 20% level of celluloflour dilution two growing female cats failed to show an increase in food intake. Skultety [41] has also observed that adult cats fail to reduce food intake over long time periods when the caloric density of the diet is increased. The present experiment extends Kanarek's [26] observations over a wider range of dilutions and employs kaolin as the diluent because several lines of evidence suggest that cellulose can be metabolized by animals other than ruminants [20,47].

METHOD

Animals

The ten cats that were used in Experiment 1 were also used in the present experiment. They were divided into two groups of three males and two females that were matched as closely as possible on the basis of body weight. The average starting weight for the two groups was 3423 g and 3471 g.

Apparatus

The housing and maintenance conditions were the same as in Experiment 1.

Diets

Powdered Purina cat chow (3.36 kcal/g) was used as the basal diet. Four levels of kaolin dilution were used; 10% (3.02 kcal/g), 20% (2.69 kcal/g), 30% (2.35 kcal/g) and 40% (2.02 kcal/g).

Procedure

The control group was fed the powdered Purina cat chow throughout the course of the experiment. The experimental group was fed this diet for the first ten days and were then presented with the four diluted diets in order of increasing dilution. Each diluted diet was available for ten days. Following testing at the 40% level of dilution the experimental group was returned to the undiluted diet for an additional five days of measurement.

RESULTS

Figure 2 shows a progressive decline in body weight for

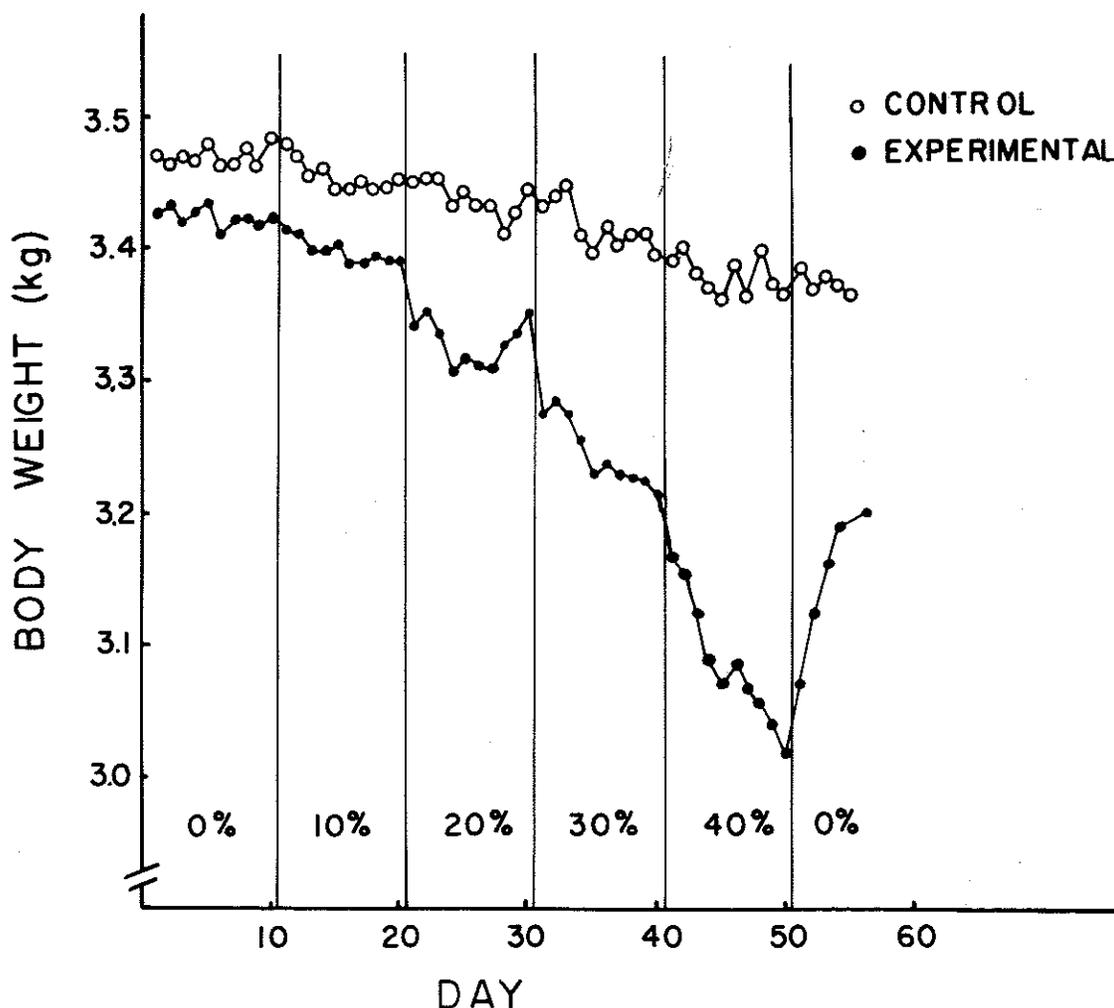


FIG. 2. Mean body weight of experimental and control groups.

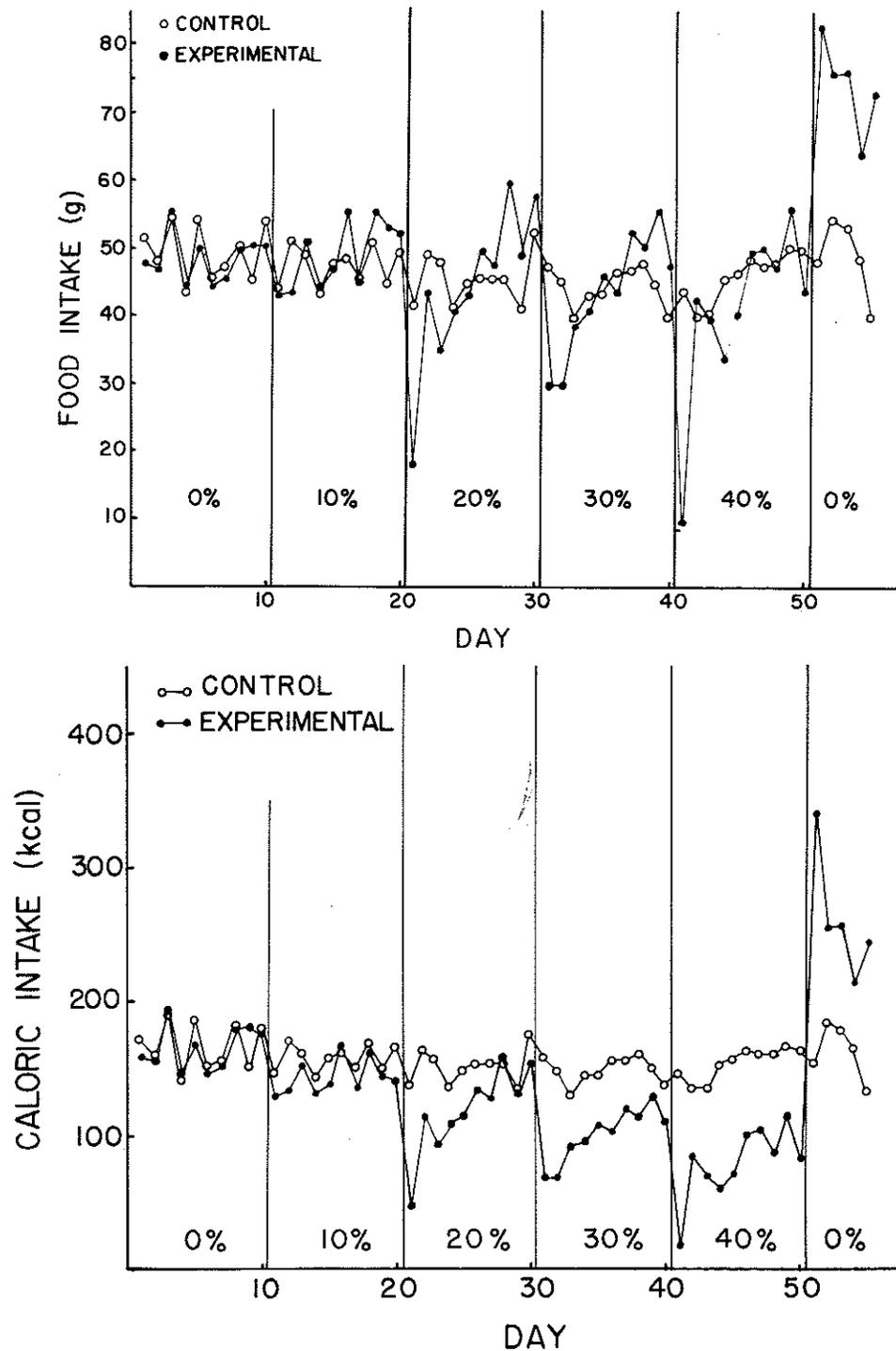


FIG. 3. Mean food intake and caloric intake of experimental and control groups.

the experimental animals on the diluted diets. In each ten day period the degree of weight loss was inversely proportional to the caloric density of the available diet. Weight loss averaged 31 g, 40 g, 132 g and 196 g at the four levels of dilution. When the experimental animals were returned to the undiluted chow there was a substantial increase in body weight and more than 50% of the original weight loss was recovered during this five day period.

The upper panel of Fig. 3 shows that during the periods of dietary dilution the food intake of the experimental animals was quite variable but in no instance was there evidence of an increase in caloric intake that was proportional to the degree of kaolin dilution. At the 10% level of dilution there were no discernible changes in food intake. At the higher levels of dilution food intake followed a similar pattern during each ten day period. Each dietary

transition, from a more concentrated to a less concentrated diet, led to a substantial decrease in food intake during the first day or two of the new diet. This was followed by a gradual recovery to the control level of intake and in some instances food intake over the shot the control value on the last day or two of the period.

However, the bottom panel of this figure shows that although there was a tendency to increase food intake towards the end of each ten day period there were only a few days when the caloric intake of the experimental group was equal to the caloric intake of the control group. In general the reduction in caloric intake was directly related to the degree of dietary dilution. The last panel of the upper and lower portions of Fig. 3 shows that bulk was not a limiting factor. When the experimental group was returned to the undiluted diet food intake almost doubled. Even on the most dilute diet a considerably smaller increase in food intake would have been sufficient to maintain a constant level of caloric intake.

Water intake in both groups tended to be more closely related to the amount of solids ingested rather than to caloric intake.

DISCUSSION

The results of this experiment suggest that adult cats are relatively insensitive to the caloric properties of their food. Over a wide range of dilutions these cats tended to maintain a relatively constant level of bulk intake. This led to a decrease in caloric intake and a substantial weight loss. The tentative nature of this conclusion is based on the observation that at levels of dilution above 10% the cats showed a marked reduction in bulk intake each time a more dilute diet was introduced and in each instance bulk intake eventually recovered to the control level. It is conceivable that if a longer period of time had been allowed on each of the diets caloric tracking would have been observed. The tendency towards overeating at the end of the 20% and 30% dilution periods supports this possibility. However, two lines of evidence suggest that the failure of these cats to maintain a constant level of caloric intake is not an artifact of limited exposure to a novel diet. Animals which show caloric compensation tend to exhibit an adjustment in food intake fairly rapidly [1,43]. For example, in the rat, Snowdon [43] has shown that adjustment for dilution occurs by the sixth meal of the day. In addition, Kanarek [26] has shown that with a 20% level of dilution cats fail to increase food intake over a two month period of exposure. Similarly, Skultety [41] has noted that cats fail to decrease food intake over a period of 200 days when a calorically denser diet was offered.

Another possible explanation for the failure of these cats to show caloric adjustment is that the diluent makes the diet less palatable and these animals compromise energy intake rather than consume large quantities of a poor tasting diet. The finickiness seen in Experiment 1 would certainly support this interpretation. If an explanation based on low palatability was correct one would expect bulk intake to be inversely related to the level of adulteration. This type of relation between the level of kaolin dilution and intake was clearly not observed and would seem to rule out the possibility that the failure to maintain caloric intake was due to the poor taste of the diets.

GENERAL DISCUSSION

These observations reveal that cats are very sensitive to changes in the sensory properties of their food but their feeding behavior does not appear to be responsive to changes in the caloric properties of their food. If these results are viewed from a homeostatic perspective one would be inclined to add the cat to a growing list of animals that fail to show proportional adjustments in food intake following caloric dilution and proceed with an analysis of the variables that underlie this regulatory failure. Conversely when these results are viewed from an ecological perspective a more coherent picture may emerge.

Animals occupy a wide diversity of feeding niches and have developed feeding strategies for exploiting specific food items to meet their caloric and nutritional requirements [7, 13, 34, 38]. These feeding strategies can be roughly divided into three categories: herbivorous, omnivorous and carnivorous. Each of these strategies can be described in terms of the availability, nutritional quality and caloric density of the usual food sources. An examination of these feeding strategies that focusses on caloric density provides a framework for interpreting the results of this experiment.

The herbivore's diet is characterized by foods of a low, relatively constant caloric density. The monogastric herbivores partially compensate for the low caloric density of their foods by large volume intakes and selective feeding [7]. The complex and lengthy digestive processes of the ruminant herbivores and their symbiotic relationship with anaerobic bacteria enables them to partially compensate for the low caloric density of their foods by efficient extraction of energy from their fibrous food sources. The energy stores of both monogastric and ruminant herbivores are also buffered by a large reservoir of undigested and partially digested food. The contents of the ruminant's four stomachs accounts for as much as 20% of their body weight. In monogastric herbivores the cecum serves this function. The properties of their foods, feeding behaviors and digestive systems raises the interesting possibility that feeding behavior in herbivores is not directly influenced by the energy content of their food and these animals should not show adjustments in food intake when the energy content of their diet is varied. In reviewing the data on dietary dilution in ruminants Baile and Forbes [4] emphasize that food intake in these herbivores is sensitive to variations in the caloric content of their diets when bulk is not a limiting factor. However, careful examination of the many studies they cite reveals many instances where caloric compensation does not occur in ruminants even when concentrated feeds are used. In relation to omnivores the range of dilutions that ruminants respond to is rather limited. In monogastric herbivores the available evidence shows no instances of successful caloric adjustment. Guinea pigs [20], opossums [28] and rabbits [23] all fail to increase their food intake when their diet is diluted. The evidence for caloric compensation in herbivores is far from compelling. The preceding analysis is not meant to suggest that feeding behavior in all herbivorous species is insensitive to the caloric content of their food, but rather that this ability is not necessarily a fundamental requirement of a herbivorous feeding strategy. Depending on their past and current feeding niches some herbivores may be able to adjust intake to caloric density but for other herbivores their feeding patterns and digestive processes provide alternative mechanisms for the regulation of energy balance.

The omnivores are characterized by an opportunistic feeding strategy that allows a wide choice of habitats. Their food varies widely in caloric and nutritional value. One implication of this variability is that the feeding behavior of the omnivore should be very sensitive to variations in caloric density and must compensate for the deficiencies or excesses of the current food source by adjusting the kind and amount of food that will be eaten in the next several meals. Beginning with Adolph's [1] classic observation that rats adjust their food intake to maintain a constant level of caloric input there are now a large number of reports that corroborate this observation in a variety of omnivores including mice [15], goldfish [35], chickens [19], quail [46], pigs [30], gerbils (Kanarek, unpublished observations) and some adult humans [44]. However, there are instances where perfect caloric tracking does not occur in omnivorous species. Human infants [17], some adult humans [44] and lactating rats [31] fail to show precise caloric tracking on diluted diets. Similarly there are many strains of rats [5, 16, 29, 37] and mice [16] that develop obesity on high fat diets. These failures appear to be the exception for omnivorous species.

The carnivorous feeding strategy is characterized by foods of a high, relatively constant caloric density and bulk intake can accurately gauge caloric intake. On this basis one could speculate that a calorie sensing mechanism would be lacking or sluggish in these animals. The present results in conjunction with the findings of Skultety [41] and Kanarek [26] lend credence to this idea. Domestic cats do

not appear to be sensitive to the caloric content of their food. The limited data on other carnivorous species tends to support this idea. Janowitz and Grossman [25] found that dogs fail to compensate completely for caloric dilution and even when there was a tendency for food intake to vary with the nutritive density of the diet the response was extremely sluggish or transient.

Janowitz and Grossman [25] only allowed their dogs a 45 min period of access to food a day. This procedure has led to the interpretation that the failure of these dogs to adjust food intake was due to deprivation induced changes in palatability [24]. Jacobs and Sharma [24] attempted to support this interpretation by showing that three dogs with 24 hr access to food increased their intake when the diet was diluted with cellulose. When these same dogs were restricted to a limited meal there was a reduction in bulk intake. Careful examination of their data (Fig. 7, p. 1092) shows a sustained increase in food intake in only one dog on the diluted diet and even this increase does not appear to exceed the range of variation on the undiluted diet. Cowgill's [14] data on caloric adjustment in dogs fed a high fat ration is no more compelling. These observations indicate that the feeding behavior of carnivores is relatively insensitive to the energy content of their diet. These failures to control food intake in the regulation of body weight are consistent with the feeding niche of carnivores and emphasize how ecological considerations about patterns of feeding and diet selection can provide a framework for understanding this apparent regulatory failure.

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