

Regulation of Food Intake in Monkeys: Response to Caloric Dilution¹

BARBARA C. HANSEN, KAI-LIN C. JEN AND PATRICIA KRIBBS²

Department of Physiology, School of Medicine, The University of Michigan, Ann Arbor, MI 48109

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HANSEN, B. C., K.-L. C. JEN AND P. KRIBBS. *Regulation of food intake in monkeys: Response to caloric dilution*. *PHYSIOL. BEHAV.* 26(3) 479-486, 1981.—Ability to regulate level of energy intake was studied in adult rhesus monkeys (*Macaca mulatta*) using calorically diluted diets. Twenty-four hour access to a complete liquid diet was provided via leakproof gravity feeders. The addition of water provided 4 caloric concentrations over the range of 0.5 to 1.35 kcal/ml. Average caloric intake per kg body weight was 84 ± 0.7 kcal/kg (mean \pm SE). Seven of the eight monkeys maintained a constant caloric intake by adjusting oral intake in response to randomly ordered but sustained changes in caloric density. One monkey ingested a significantly higher caloric load while receiving the highest density diet. Rates of compensation for dilution following each diet change varied widely, occurring over periods of 3 days to 2 weeks. It was concluded that individual monkeys vary significantly in the rate of adjustment to caloric dilution, and thus long term studies must be used in studying controls of feeding in monkeys.

Macaca mulatta Caloric dilution Intake regulation Liquid diet

RECENT experimental evidence combined with a reevaluation of the data of earlier reports necessitates significant modification of Adolph's [1] proposition that "within limits, rats eat for calories." The need for this restatement was first inferred by Adolph himself, and later by Booth [3] and others. It must now be stated that within limits, animals adjust not only caloric intake, but also intake of some specific nutrients, metabolic rate, activity level, and body weight in regulating energy balance [3, 16, 29, 33, 35, 36, 38, 40, 42, 46]. Furthermore, there are both inter- and intraspecies variations in the degree to which individuals adjust each parameter in response to a particular environmental or dietary alteration. In man, differences in the particular parameter which is adjusted may play a role in variations in body weight and obesity.

In seeking to determine the accuracy of the regulatory mechanisms controlling body weight, many investigators have studied the adjustment of food intake in response to variations in the nutritive density of food. Considering only those experiments (or parts of experiments) in which the ingestion of non-nutrient diluent was not limited by gut capacity or by duration of access to the food supply, the most common conclusion of previous studies has been that food intake is regulated so that body weight is maintained at a constant value or at a constantly increasing rate commensurate with normal growth. Such data have been reported for the dog [6], rat [5, 22, 29, 30, 37, 38, 39], Mongolian gerbils [20], ruminant [8, 24, 25], pig [28], chick [26,35] and man [4, 12, 48]. Some of these studies, and additional reports [13, 15, 16, 19, 23, 36, 40, 42] have, however, urged a reconsideration of this emphasis on the adjustment of intake and have

encouraged a broader approach to understanding the multiple interactions of variables involved in maintaining energy balance.

The reexamination of data from many of the past studies to integrate or infer adjustments of parameters other than intake is made difficult by a number of common problems: (1) lack of definition of "stability" of intake; (2) no standardized use of the term "caloric compensation"; (3) short-term duration of study periods (1-7 days on each dilution—usually 3 days); (4) lack of control groups for comparison of weight change and intake levels; and (5) use of different diluents, some of which were partially digestible. The present studies extend the data concerning the regulation of intake to monkeys and were designed to ascertain the degree to which monkeys compensate for caloric dilution by adjustment of oral intake, and the rate at which this compensation occurs, and to determine the degree to which changes in body weight accompany adjustments in oral intake. Because of the increasing use of monkeys in studies of gastrointestinal, endocrine, and metabolic function there is a need for specific data on the patterns of food intake in this species.

METHOD

Subjects

Eight male rhesus monkeys (*Macaca mulatta*) weighing 5.7-8.8 kg with an estimated age range of 3-9 years old were studied. Six monkeys were housed individually in cages 72×72×67 cm. The other two animals (monkeys N-1 and C-3) were restrained in primate chairs while undergoing other experiments which did not interfere with the present

¹This research was supported by NIH grant AM20493. The authors acknowledge the skillful assistance of Lynne W. Kalnasy and Barbara Sheller. Request for reprints should be sent to Dr. B. C. Hansen, Department of Physiology, School of Medicine, The University of Michigan, Ann Arbor, MI 48109.

²Now at School of Dentistry, University of Washington, Seattle, WA 98105.

TABLE 1
COMPOSITION OF ENSURE® (PER LITER)

Protein (casein)	37.1 g
Fat (corn oil)	37.1 g
Carbohydrate (corn syrup solid)	145.1 g
Calories	1.06 kcal/ml
Vitamin A	2650 I.U.
Vitamin D	210 I.U.
Vitamin E	32 I.U.
Vitamin K	1.0 mg
Vitamin C	0.16 g
Folic acid	0.21 mg
Vitamin B1	1.6 mg
Vitamin B2	1.8 mg
Vitamin B6	2.1 mg
Vitamin B12	6.3 µg
Niacin	21.2 mg
Choline	0.53 g
Biotin	0.21 mg
Panotiothemic Acid	5.3 mg
Sodium	0.74 g
Potassium	1.27 g
Chloride	1.06 g
Calcium	0.42 g
Phosphorus	0.42 g
Magnesium	0.21 g
Iodine	0.035 mg
Manganese	0.26 mg
Copper	1.06 mg
Zinc	16 mg
Iron	9.5 mg

studies. All monkeys were housed in a constant temperature room (21–22°C) with a fixed 12-hour light-dark cycle. Water was provided ad lib 24 hr/day via a water bottle attached to the top tier of the chair.

Procedure

Monkeys were fed a complete, nutritionally adequate liquid diet (Ensure®) at a concentration of 1 kcal/ml. Fourteen percent of the energy is from protein, 31.5% from fat and 54.5% from carbohydrate. The diet composition is shown in Table 1. Twenty-four hr access to this diet was provided via leakproof gravity feeders [44]. This method was developed to provide accurate food intake data which is not generally possible using standard monkey chow. Use of a liquid diet also facilitated manipulation of caloric density in an accurate and uniform manner.

The diet was diluted with water to obtain concentrations of 1.35, 1.0, 0.75, and 0.5 kcal/ml (a range of dilution of 0–63%). In a preliminary one bottle taste acceptability study, using 4 monkeys, 3 or 4 concentrations were tested during the first hour of 14 days to compare the acceptability of the various dilutions. None of the concentrations used in this study was rejected by the monkeys and each concentration was taken in an amount not significantly different from other concentrations during the test period.

Seven monkeys received 3 of the 4 diet concentrations, given in random order and one monkey received two diet concentrations. Each caloric concentration was maintained for a minimum of 15 days and some levels were studied for

up to 60 days. The termination point for each level for each monkey was influenced by the stability of rate of weight gain and stability of feeding behavior during both baseline and dilution periods. Stability was defined by the occurrence of intakes for 3 consecutive days which varied less than $\pm 10\%$ of the mean intake for that period.

The caged monkeys were adapted to the laboratory setting for a minimum of 30 days prior to the initiation of this study. In addition to laboratory adaptation, monkeys N-1 and C-3 were adapted to a restraining chair for a minimum of 90 days. The chair restraint was necessitated by other parallel studies, and these monkeys were included in order to provide comparisons which were essential to further study of feeding controls in chronically implanted and therefore restrained animals. All monkeys were adapted to ingestion of the liquid diet at a 1 kcal/ml concentration for at least 90 days prior to the first change in diet concentration. Each monkey was weighed three times per week at the same time each morning. Liquid diet and water bottle contents were measured and feeders cleaned and refilled at the same time each afternoon. Sanitization of the feeder parts prevented diet spoilage over the 24-hour periods, and diet not taken was discarded after 24 hours. No diet preservative was necessary under these conditions.

Statistical Analysis

Analysis of variance was performed for each monkey for both volume and caloric intake. If overall F values reached significance, paired comparisons were then performed in order to locate the pair which contributed to the difference. For each concentration given longer than 15 days, the caloric intakes of the first 15 days and last 15 days were compared using Student's *t* test in order to detect change in caloric intake over time as well as the levels of steady intake during early and late periods at each concentration. Daily caloric intake and rate of weight gain of monkeys in cages and in chairs were also compared.

RESULTS

The first monkey (Q-1) was available briefly for study using only two diet concentrations; however, the remaining 7 monkeys were each studied under 3 diet concentrations, with a minimum of 15 days per concentration. Because the 1 kcal/ml diet was used as the constant diet in the present studies and as the standard diet for other experiments, periods of maintenance on this diet for the seven monkeys were extended to either 30 or 60 days. Duration of study for the other two concentrations used with each monkey was established as a minimum of 15 days, with change of diet after 15 days occurring only if stability had been established as defined by variation of less than $\pm 10\%$ around the mean for the period, over at least the last three days.

Furthermore, whenever possible, periods on each diet were extended to 30, 45, 60 days so that we might obtain data concerning longer term changes, and the degree to which initial achievement of stability, as defined above, was sustained. Comparisons of mean intake made between data obtained only on the first 15 days at each concentration level did not differ significantly from comparisons using the longer periods, although in 4 instances of diet changeover intake reached the defined stability, but still showed trend at 15 days. Longer periods permitted more detailed study of within diet day to day and week to week variations. We have also examined separately the last five day period on each diet

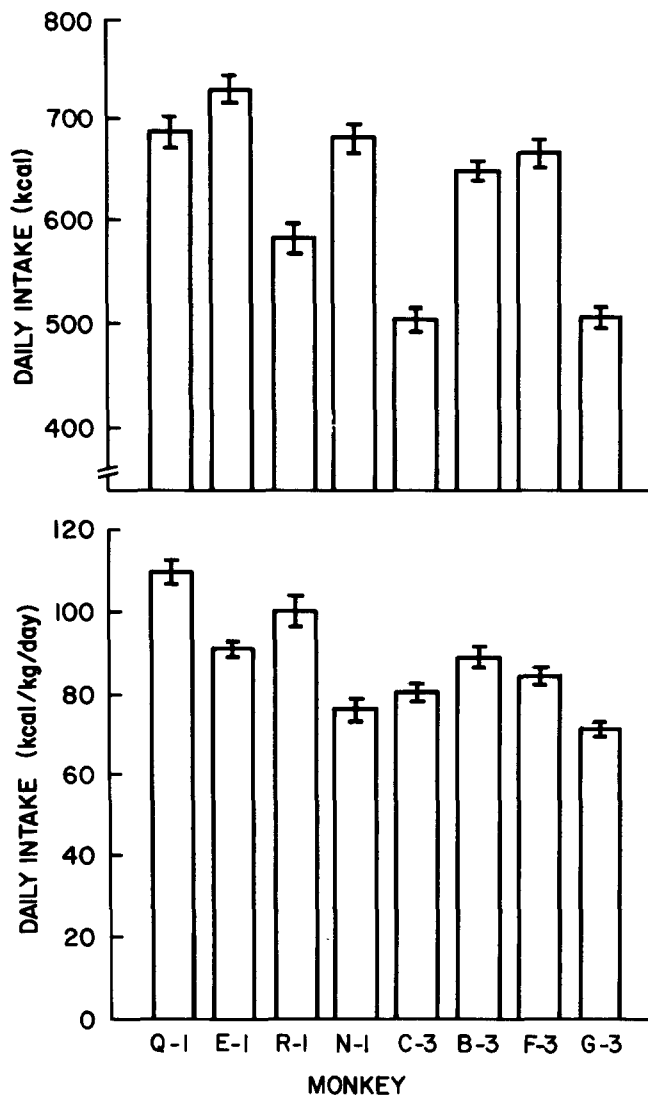


FIG. 1. Daily caloric intake (upper panel) and daily caloric intake per kg body weight (lower panel) of eight monkeys. Number of days per monkey ranged from 15 to 60 days (total days=795).

concentration, and again found no differences from the conclusions based on the longest period available for each diet concentration (Table 2). All monkeys at all diet concentrations reached the defined degree of stability within less than 15 days of the transfer to a new diet, and degree of stability did not increase with longer periods on the diets.

Normal Daily Caloric Intakes

Data from the eight monkeys totaled 795 days. The mean daily caloric intake for all monkeys including all concentrations was 621 ± 3.33 kcal (mean \pm SE, range: 448–759) and the average caloric intake per kg body weight was 84 ± 0.7 kcal/kg (range: 63–119). Figure 1 (upper panel) indicates the daily mean caloric intake for each monkey, and the lower panel shows caloric intake per kg of body weight by monkey. Six of the 8 monkeys averaged 70–90 kcal/kg intake per day. The two monkeys exceeding 90 kcal/kg were the two smallest monkeys (5.7 and 6.1 kg). The rates of weight gain for these 8 monkeys over 4 different diet concentrations ranged

from 0 to 0.24 kg/week which were within the ranges seen in normally growing monkeys.

The caloric intake per kg body weight did not differ between the two chaired and the six caged monkeys, confirming prior studies of within animal comparisons of chaired vs. caged food intake. These two chair-restrained monkeys (N-1 and C-3) showed a drop in weight initially after chairing, as is generally observed during chair adaptation, however, both weight and intakes returned to normal levels within two weeks of chairing and prior to the initiation of the present studies. Thus, the results obtained from the two chaired monkeys were combined with those obtained from the caged monkeys for the purposes of analyses of the precision of regulation or oral intake.

No difference in water intake was observed during any of the diet concentration periods.

Effects of Diet Dilution: Adjustment of Caloric Intake

Figure 2 shows the mean daily caloric intake for each dietary concentration for each experimental period including intakes prior to reaching stability. Diet concentrations were administered randomly, however, they are arrayed here by concentration for ease of comparisons. Table 2 summarizes these daily caloric intakes and allows comparison to respective volume intakes of the 8 monkeys on the different diets. Paired comparisons of the volume intakes showed that except for one monkey G-3, the volume intake was significantly increased as the diet was progressively diluted. Monkey G-3 did not show any change in volume intake between diets of 1.35 kcal/ml and 1.0 kcal/ml concentrations. Since volume of intake was generally adjusted in the appropriate direction for changes in caloric concentration, 7 out of 8 monkeys maintained a stable caloric intake. Monkey G-3 increased his caloric intake by 30% and 41% ($p < 0.01$) on the 1.35 kcal diet when compared to the 1.0 and 0.5 kcal diet, respectively.

The relative stability of the caloric adjustment was even more apparent when data were plotted in kcal/kg/day (Fig. 3), thus adjusting for overall change in body weights over the extended experimental periods. When the body weight was included in the calculations, only one monkey, G-3, ingested significantly fewer calories on the most dilute diet compared to the other two concentrations. Therefore, over the range of 0.5 to 1.35 kcal/ml, and given continuous access to the diet for 24 hours/day, monkeys generally regulated their intake to maintain a stable kcal/kg intake, as shown in Fig. 4 for one monkey. Three day moving averages were used in order to smooth a day to day variation.

Although higher diet concentrations were sometimes accompanied by the higher variation in daily caloric intake, no consistent difference in variability was found between concentrations.

Effects of Diet Dilution: Rate of Weight Gain

Intake was not the only parameter that was adjusted during changes in diet caloric density. The differences between Figs. 2 and 3 reflect both the gradually increasing body weight to be expected over time, and adjustments of body weight in response to caloric concentration and varied caloric intakes, possibly including both metabolic and activity level changes.

Figure 5 indicates the high variability in rate of weight change and intake. For the sake of clarity, data from only 3 monkeys were presented in this figure. Each symbol repre-

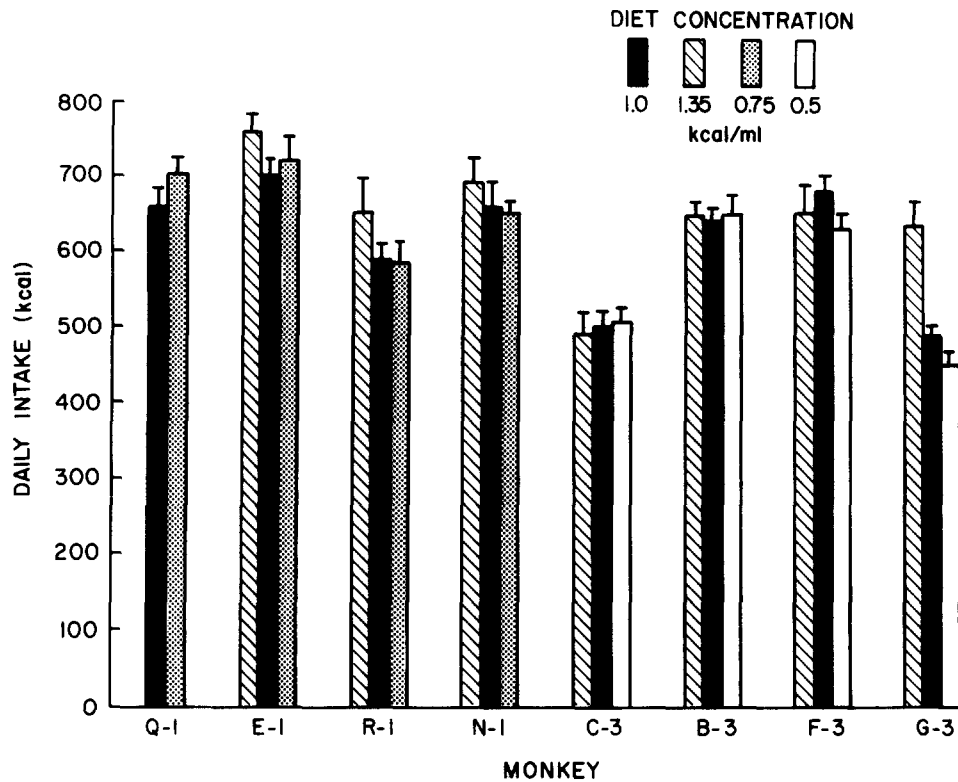


FIG. 2. Effects of caloric concentration of diet on caloric intake of monkeys (Mean \pm SE). Diets were administered in random order.

TABLE 2
CALORIC AND VOLUME (ml, MEAN \pm SE) INTAKE FOR VARIOUS DILUTIONS OF DIET

Monkey No.		1.35 kcal/ml	1.0 kcal/ml	0.75 kcal/ml	0.5 kcal/ml	<i>p</i> *
Q-1	volume		663 \pm 24.2 (n=15) [†]	940 \pm 29.4 (n=30)		<0.0001
	kcal		663 \pm 24.2	705 \pm 22.0		n.s.
E-1	volume	565 \pm 18.7 (n=30)	700 \pm 25.2 (n=30)	964 \pm 39.0 (n=30)		<0.0001
	kcal	763 \pm 25.3	700 \pm 25.2	723 \pm 29.2		n.s.
R-1	volume	484 \pm 25.2 (n=15)	590 \pm 23.7 (n=30)	769 \pm 36.7 (n=30)		<0.0001
	kcal	653 \pm 47.5	590 \pm 23.7	576 \pm 27.5		n.s.
N-1	volume	520 \pm 21.7 (n=45)	677 \pm 32.1 (n=30)	874 \pm 19.1 (n=15)		<0.0001
	kcal	693 \pm 29.5	677 \pm 32.1	656 \pm 14.3		n.s.
C-3	volume	368 \pm 20.5 (n=15)	504 \pm 16.0 (n=60)		1019 \pm 37.3 (n=30)	<0.0001
	kcal	497 \pm 27.7	504 \pm 16.0		510 \pm 18.6	n.s.
B-3	volume	483 \pm 11.5 (n=45)	647 \pm 14.5 (n=60)		1306 \pm 50.7 (n=15)	<0.0001
	kcal	653 \pm 15.5	647 \pm 14.5		653 \pm 25.4	n.s.
F-3	volume	488 \pm 26.5 (n=60)	688 \pm 17.7 (n=60)		1270 \pm 32.9 (n=45)	<0.0001
	kcal	658 \pm 35.5	688 \pm 17.7		636 \pm 16.3	n.s.
G-3	volume	472 \pm 22.7 (n=30)	493 \pm 11.1 (n=60)		908 \pm 26.0 (n=60)	<0.0001
	kcal	642 \pm 30.2 [‡]	493 \pm 11.1		454 \pm 13.0	<0.01

*Significance level for F test.

[†]Number of days tested.

[‡]1.35 vs 1.0, *p*<0.01; 1.35 vs 0.5, *p*<0.01; 1.0 vs 0.5, not significant.

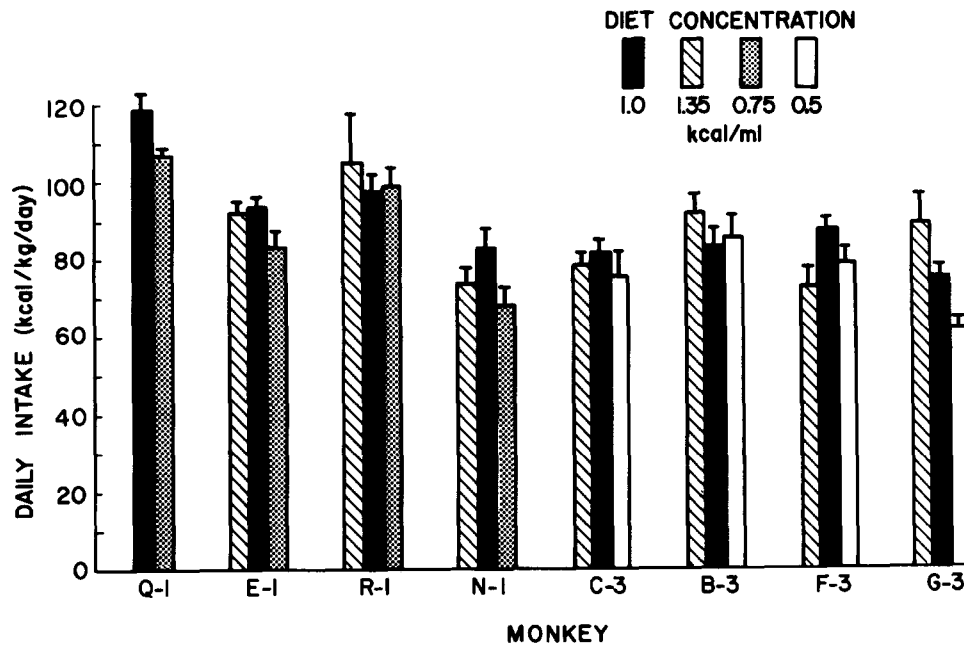


FIG. 3. Effects of caloric concentration of diet on daily caloric intake per kg body weight of monkeys. (Derived from same data as Fig. 2 corrected for mean body weight at each concentration.)

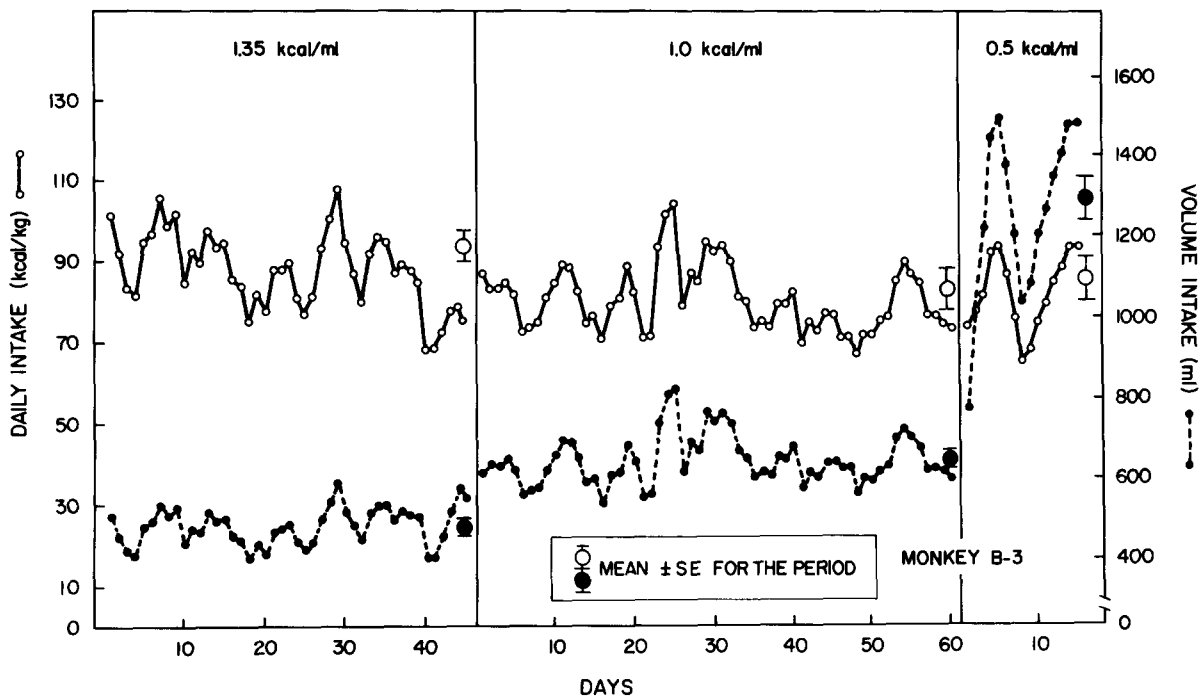


FIG. 4. Three day moving average of volume intake (●---●) and caloric intake (○—○) of monkey B-3 during the entire experimental period.

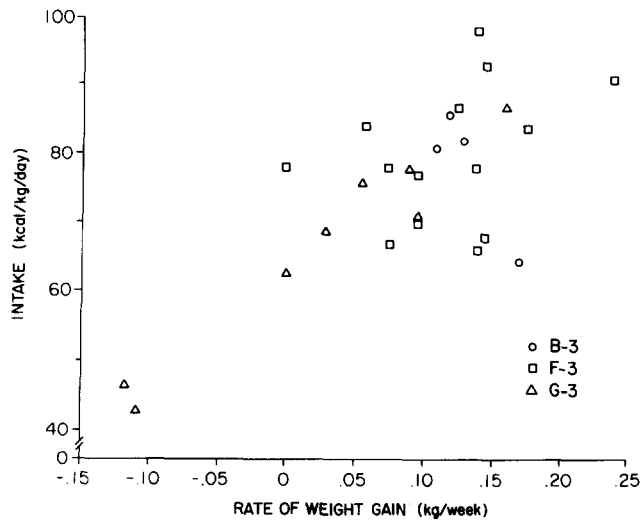


FIG. 5. Rate of weight gain with varied intake levels for three monkeys. Every symbol represents a separate period of stable intake for one monkey. ("Stable" was defined as day to day variation of less than 10%.) Each period was at least 10 days duration.

sents a period of stable intake of at least 10 days' duration. These data also indicate the wide range of intakes which produced the same rate of weight gain in a single monkey. For example, monkey F-3 gained weight at a rate of 0.140–0.146 kg per week over an intake range of 66 to 98 kcal/kg per day, or 394 to 815 calories per day under constant laboratory conditions. These differences were not explained by changing body weight, and are therefore not due solely to the decrease in basal metabolic rate which accompanies increasing body size.

Figure 6 depicts the daily food intake (kcal/kg) and rate of weight gain (kg/week) at different body weights for all monkeys (except G-3). Monkeys reduced the number of calories ingested per kg of body weight as body weights increased, but nevertheless, maintained approximately the same average rate of weight gain.

The caloric density of the diet appeared to affect the rate of weight gain for certain monkeys. The average rate of weight gain was highest at higher caloric density and slightly lower on the most diluted diet, the majority of monkeys maintained a rate of weight gain of approximately 0.10 kg/week across stable periods of intake on all diets. Only one monkey (G-3) dropped his rate of weight gain to zero at the most diluted diet when his intake also dropped. Three monkeys gained weight faster than the rest at 1.35 kcal concentration and one monkey gained more than others at 1.0 kcal concentration. All monkeys slowly gained weight over the entire experimental period, as is expected for *Macaca mulatta* in this age range. The yearly rate of weight gain was considerably lower than that observed during periods of stable intake, such that a body weight gain of approximately 1.5 kg/year was most commonly observed.

Effects of Diet Dilution: Rate of Adjustment to Change

The rates of adjustment by monkeys to changes in caloric density of a liquid diet are both complex and variable. These adjustments of oral intake volume are affected by (1) the

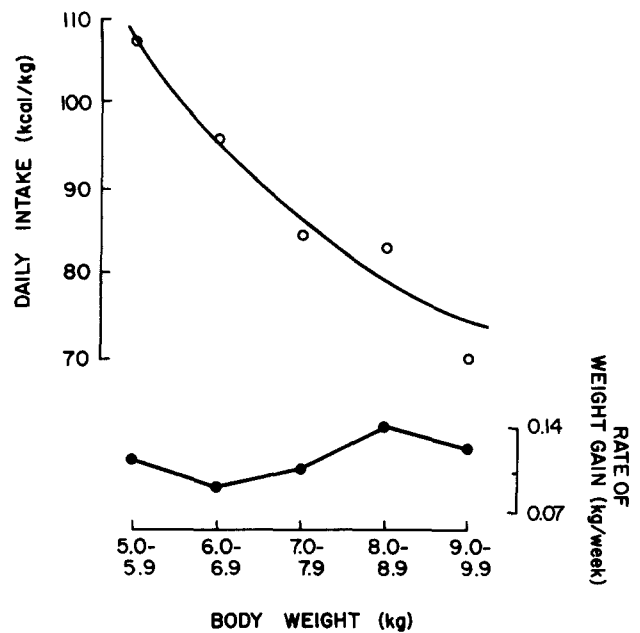


FIG. 6. Comparison of body weight with caloric intake per day and rate of weight gain per week (N=8 monkeys).

direction of the change (i.e., toward more dilute, or toward more concentrated diets), (2) the stringency of the test of "stability" or "compensation", (3) the degree to which the shift has produced concomitant changes in rate of weight gain, and (4) the length of time considered for each level of dilution.

For most monkeys, a shift toward a more concentrated diet (i.e., from 0.5 kcal/ml to 1.0 or 1.35 kcal/ml or from 1.0 to 1.35 kcal/ml) resulted in a brief period of overeating lasting one to several days followed by a return to baseline caloric intake. Conversely, caloric intake on the first day or two after a shift to a more dilute diet tended to be low, and the adjustment period was often prolonged to two weeks. With greater differences between the caloric concentrations of two diets in adjacent periods, both the time for adjustment and the variability were greater. Return of intake to stable caloric levels for all dilution shifts occurred by the end of the second week.

DISCUSSION

Monkeys, either caged or chaired, adapted rapidly and well to the liquid diet used in the present study. Rates of growth were comparable to those reported previously for monkeys on a chow diet [10, 11, 43]. Stools were formed and diarrhea rarely occurred and, if present, it was transient. Thorough daily cleaning of the feeding tubes prevented the diet from spoilage.

Daily caloric intake for all four diet concentrations varied from 63 to 119 kcal/kg for the 8 monkeys. Since the body weights of these monkeys varied from 5.7 to 8.8 kg, and it has been reported that caloric intake per kg of body weight decreases as body weight increases [11], it was therefore expected that a wide range of caloric intakes would be observed.

All monkeys gained weight during the experimental period as is normal for monkeys in this age range. Weight gain was higher for some monkeys at higher concentrations

and slightly lower on the most diluted diets. No growth failure on diluted diets was observed in the present study, in contrast to the findings of Kerr *et al.* [21]. Monkeys fed a milk diet in Kerr's laboratory evidenced significant growth failure, although all nutrient intakes were near normal levels. The authors attributed their growth failure to excess water turnover or metabolism. Monkeys on the milk diet may, however, have been experiencing the symptoms of gastrointestinal disturbances of lactase deficiency, and thus increasing diarrhea due to the lessened ability to hydrolyze lactose to glucose and galactose as has been previously described in monkeys [47]. The diet used in the present studies (Ensure®) was lactose free.

In view of the generally consistent compensation for caloric dilution seen in these monkeys, further consideration of previous studies of other species is warranted. A number of reported modifications in methods of maintenance of energy balance among various subjects above and beyond the simple adjustment of oral intake have been described. Such changes have included the increase or decrease of body weight to a new level [1, 29, 35, 36, 40, 42], change in the rate of weight gain for growing animals [2, 3, 16, 26, 35, 36, 38, 40], and change in the kcal/kg body weight ingested while maintaining a constant weight pattern, suggesting unmeasured changes in activity or metabolic expenditure [4, 16, 32, 36, 46]. Some species, such as guinea pigs and opossum never compensated for dietary dilution [13,23].

Because adjustments to changes in diet dilution are multiply determined, and because these factors are often excluded from discussions of caloric compensation, it is difficult to compare our data from monkeys with earlier reports of other species. Generally, however, it appears that monkeys resemble rats [1, 5, 15, 16, 29, 38, 39, 41] and gerbils [20] in that they can maintain a relatively constant caloric intake or caloric intake per kg of body weight. At the other end of the scale are dogs, cats, guinea pigs and opossum, which were reported to be very sluggish in compensating for caloric dilution or never achieved compensation [13, 14, 16, 23].

Hirsch *et al.* [14] hypothesized that animals' eating habits, food seeking strategies, as well as their responsiveness to sensory (taste) stimuli are developed according to their feeding niches. Animals which experience diets which vary widely in caloric density may have developed a sensitive calorie-detecting system while those who usually have very narrow ranges of food choice may have failed to develop such fine adjustments. Cats and dogs are carnivorous, and thus daily food is usually high in protein and caloric content. Volume plays a larger role in regulating their intake than does caloric density. The calorie-detecting system may be less developed in these animals, thus leading to failure to adequately increase the volume intake in the face of caloric dilution. On the other hand, rats, gerbils and monkeys, and even man, usually face a wide range of edible food in the natural situation. For monkeys, these foods include high caloric nuts and low caloric fruits and leaves. In order to avoid caloric deficiencies or excesses, these animals may have become particularly sensitive to the caloric content, allowing adjustments in the amount eaten in every meal. Nevertheless, some deficiency in caloric compensation has been observed in these animals. One monkey G-3 in the present experiment, lactating rats [30], adult rats on high fat diets [17,34] and humans [18, 40, 45]

have not always shown this precise caloric regulation of intake.

Another factor affecting caloric compensation is the variability of the intake, and potential changes in variability with diets of different caloric density. Among monkeys the variability of intake was not correlated with the level of diet dilution, a finding which concurred with an earlier study in humans [4]. In other species, however, the variability of intake has been associated with the caloric concentration of the diet. Smith, Pool and Weinberg [36], studying rats, found the highest variability with the most concentrated diet and the lowest with the most diluted diet. In contrast, Van Hemel and Myer [42] found that variability in caloric intake of quails increased with increasing dilution.

Studies of humans have not permitted the "blind" long-term studies that would permit detection of possible "types" of people differentiated according to the dominant type of adjustment to diets of varying caloric density. Jordan's 2 human subjects failed to increase their volume intake of diluted Metrecal in order to compensate for the dilution [18]. No body weight records were reported on these 2 subjects; hence, it is difficult to identify whether subjects used other means of adjusting to compensate for short term dietary dilution. Spiegel [40], based on caloric intakes and body weight changes, reported three types of human subjects: "regulators", "questionable", and "non-regulators". It is highly likely, in view of the present study, that metabolically these human subjects behaved similarly to our monkeys who showed wide ranges of caloric intake over which a stable weight pattern could be maintained. The mechanisms involved probably include changes in both activity and expenditure of energy, and may involve as yet not understood processes such as those falling under the term "luxusconsumption" [27].

As with humans, patterns of compensation among monkeys varied, sometimes occurring within a day or two, and at other times taking one week or more. The two to five-day periods for compensation found by Spiegel [40] were similar to that in monkeys, although we would infer that longer periods sometimes are necessary in both species.

In another study of humans, Campbell *et al.* [4] did not report the rate of adjustment of intake, but stated that subjects did not always compensate perfectly for changes in caloric density. Details are not available for further analysis of these findings, although they apparently fit the pattern of the present study and that of Spiegel [40].

In summary, although both rats and monkeys compensate well to diet dilution, some species differences in regulation are apparent. It is possible that in rats the appropriate adjustment of caloric intake to maintain an incremental pattern of body weight is the primary parameter regulated in the control of energy balance. Quail represents the other extreme, in that they apparently regulate body weight precisely to the availability of nutrients [42]. Monkeys, like rats, are capable in many cases of precisely integrating changes in body weight, body composition, activity, and metabolic efficiency to regulate energy balance. The data on dogs and cats showed that they do not fit the rat model (primarily adjusting intake) or the quail model (primarily adjusting body weight). Such species differences may be important in understanding the mechanisms by which caloric intake is regulated, and they require further consideration.

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