# Economics of food intake in mice: Energy yield of the reinforcer

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## HIGHLIGHTS

- Mice showed good caloric compensation when working for "devalued" food.
- Analysis of ranked responses in 15 min bins showed a negative logarithmic function.
- A number of food pellets earned within bins are largely independent of response cost.

## ARTICLE INFO

## ABSTRACT

One of the Zeitgeists of the field for the study of ingestive behavior is that organisms are endowed with internal self-regulatory mechanisms that ensure optimal nutrition. However, the alarming increase in the prevalence of obesity challenges us to reconsider the extent to which internal regulatory mechanisms affect food intake, especially in a free market economy. Cued by the pioneering work of George Collier and his students, we have been examining food intake (demand) in mice when the effort or price of food is manipulated. We present two new experiments in mice that investigate the effect of energy yield per unit of food earned on working for food. The first experiment shows that when the nominal energy yield of each food pellet is halved by cellulose dilution, mice show relatively inelastic calorie-related demand despite the fact the cellulose diluted diet is unpalatable. The second experiment shows that the size of the pellet reinforcer does not have a major effect on food demand except in the extreme condition of small reward and high unit price. New analyses of distributions of responding are presented which suggest that mice work for "target" numbers of food rewards with only a small influence of price or energy gain.

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## 1. Introduction

Curt Richter was the first biopsychologist to address systematically the question of amount and type of food selected and, largely on the basis of studies in rats, concluded that organisms possess powerful physiological regulatory systems which control quantity and quality of food consumed [1]. Between then and now, thousands of research papers have been published identifying hundreds of different internal signal mechanisms that affect food intake or choice. Modern theoretical accounts of feeding emphasize the complementarity of short and long term controls. Short term mechanisms implicate available energy and associated hormones that ebb and flow over the course of one or a few meals, whereas long term mechanisms implicate stored energy, in particular adipose-derived signals.

It is known that when the environment contains a variety of foods, intake in single meals is stimulated by minimizing sensory specific satiation [2]. This immediately raises questions about the strength with which the regulatory systems mentioned above can or do operate for individuals in a commodity-rich free market economy. While aspects of consumer economic choice have been modeled in the laboratory, for example using prospect theory [3] or delay discounting [4], the question of feeding over extended periods has been little-studied in particular using organisms in closed economies in which all of the food available has an imposed price.

George Collier and his students were the first to tackle this question. They characterized the amounts and patterns of a single food consumed by rats (and other species) in a closed operant behavior economy when either a procurement/access cost, or a consummatory/unit cost was imposed [5,6]. Meal size and frequency were highly sensitive to imposed access costs and to differences in caloric density of the food, but that unit price had relatively little effect on intake unless in a choice situation [5–8]. We have recently extended these protocols to mice [9,10].

In the present paper, we examine an aspect of this approach that is founded in optimal foraging theory, namely that the foraging behavior of animals should be sensitive to gross energy gain [11] for a food item (i.e., the energy derived from the food item minus the energy expended to acquire that food). We will report the results from two

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closed economy experiments in which we varied the energy yield of the food item (a small pellet) that mice received in exchange for emitting a specific number of nose pokes (the price).

In our first experiment, energy yield per pellet was altered by changing energy density. Many studies have reported the effect of dietary dilution, including the use of non-digestible fiber such as cellulose, on food intake in animals [12–14]. Many find an increase in consumption so that caloric intake is preserved until dilution is extreme. In mice, we have found one cellulose dilution study [15]: compensatory increase in intake was quantitative at low dilutions but at 50% dilution dropped to <50% of full compensation. In our study, we used 50% cellulose dilution, halving the nominal energy yield of each pellet. We hypothesize that in our study mice will show partial compensation for cellulose dilution and that the compensation will become poorer as the effort or price increases.

In our second experiment, energy yield per pellet was manipulated by altering physical size(s). Previously, using a closed economy in rats, Collier et al. [16] studied the effect of two fixed ratios (FR) of lever press operant on the daily intake of food pellets of different sizes (20, 45 or 97 mg). One of their main findings is redrawn in the left panel of Fig. 1. Consistent with conventional demand analysis, daily intake was consistently lower at the higher FR, but change in pellet size had a significant effect. This may be seen in the right panel of Fig. 1 which plots the same data using a logarithmic scale for effort or price. The data show an orderly decline in daily intake as price increases but, in the region in which the two functions overlap, the larger pellet supports ~15% higher intake. Thus, higher gross energy gain achieved by increasing energy yield of each food item modestly stimulated total energy intake. We hypothesize that in our study mice will eat more at higher energy yields per food unit or reinforcer, especially at higher price(s).

## 2. Methods

### 2.1. Experiment 1: cellulose dilution

#### 2.1.1. Animals and procedure

Male CD-1 mice ~6 mo of age and with an initial weight of ~40 g lived (except for 1 h servicing per day when they were in holding cages) and obtained all of their food in standard test chambers (Med Associates) we have described before [10]. The chambers were illuminated on the same light schedule (lights on 0700–1900). Completion

of a designated number of nose pokes (the fixed unit price, FUP) delivered a food pellet to an adjacent food trough. Animals were free to accumulate nose pokes without any time limit. Nose pokes and pellet deliveries were recorded in 15 min bins for each 23 h session. Water was freely available from a sipper spout.

One group of eight mice received a 45 mg standard nutritionally complete grain-based pellet (Test Diet 5TUM: ~3.2 kcal/g) for each completed FUP. Mice in the second group of eight received a 45 mg pellet manufactured to contain 50% by weight of non-digestible cellulose (Test Diet catalog #1815596-380: ~1.6 kacl/g). To avoid neophobia, all mice were presented the cellulose-diluted pellets in jars in their home cages for a few days prior to study. After initial adaptation, mice were studied for four consecutive days each at FUP (5, 10, 25, 50,100, 200). Pellet intakes were corrected for spillage retrieved each day from the pan below the trough. Corrected intakes, expressed as weight eaten per day, were averaged for each mouse across each FUP block.

### 2.2. Experiment 2: pellet size and number

The general procedures were as for Experiment 1, with the following differences. The subjects were 24 male C57BL/6 mice ~6 mo of age with an initial weight of ~45 g, divided into three groups of eight. Each group was designated to receive different amounts of food upon completion of each FUP (1 × 20 mg, 2 × 20 mg, 1 × 45 mg), all standard grain-based diet (3.2 kcal/g). An incrementing series of FUP (5–100) was imposed, four days each, followed by two days at FUP200.

### 2.3. Data analysis

In addition to standard parametric analyses by ANOVA for the effects of FUP and diet type, intakes of each mouse across the demand series were fit to an essential value [17] or exponential demand function $\log Q = \log (Q_0) + k \, (e^{-\alpha P} - 1)$ where $Q$ is the mean quantity of food consumed per day, $P$ is the concurrent unit price, and $k$ is a constant ($= 3$) scaling factor. This analysis provides two parameters: $Q_0$ is intake extrapolated to zero cost, and $\alpha$ is elasticity or the curvature of the function. Low $\alpha$ values indicate less elasticity of demand and greater essential value ($1/\alpha$) [17].

To investigate in detail the temporal distribution of effort, and in particular whether the highest FUPs imposed ceiling rates on food acquisition, additional analyses of the responses per 15 min bin will be
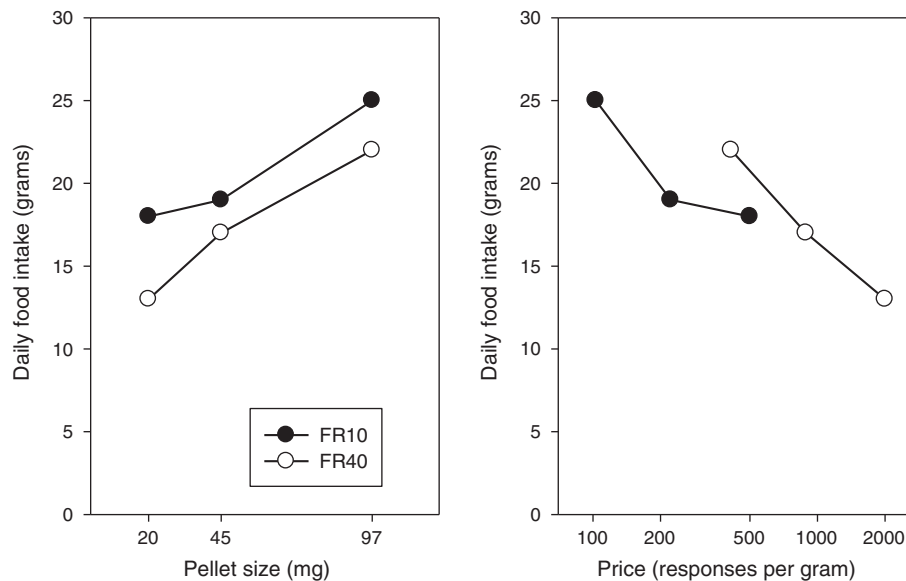


Fig. 1. Effect of pellet or reinforcer size on intake in rats working for food, compiled from data in Collier et al. [15]. The left panel shows mean daily intake at one of two unit prices (FR 10 or 40 lever press responses per pellet) as a function of pellet size. The right panel shows the same data expressed as lever press responses per gram of food obtained (symbols as in left panel).