Published in final edited form as:

Physiol Behav. 2008 January 28; 93(1-2): 97–109.

Feeding behavior, obesity, and neuroeconomics^{*}

Neil E. Rowland^{1,*}, Cheryl H. Vaughan², Clare M. Mathes¹, and Anaya Mitra¹

¹*Department of Psychology, University of Florida, Gainesville FL 32611-2250*

²*Department of Biology, Georgia State University, Atlanta, GA 30302-4010*

Abstract

For the past 50 years, the most prevalent theoretical models for regulation of food intake have been based in the physiological concept of energy homeostasis. However, several authors have noted that the simplest form of homeostasis, stability, does not accurately reflect the actual state of affairs and most notably the recent upward trend in body mass index observed in the majority of affluent nations. The present review argues that processes of natural selection have more likely made us first and foremost behavioral opportunists that are adapted to uncertain environments, and that physiological homeostasis is subservient to that reality. Examples are presented from a variety of laboratory studies indicating that food intake is a function of the effort and/or time required to procure that food, and that economic decision making is central to understanding how much and when organisms eat. The discipline of behavioral economics has developed concepts that are useful for this enterprise, and some of these are presented. Lastly, we present demonstrations in which genetic or physiologic investigations using environmental complexity will lead to more realistic ideas about how to understand and treat idiopathic human obesity. The fact is that humans are eating more and gaining weight in favorable food environments in exactly the way predicted from some of these models, and this has implications for the appropriate way to treat obesity.

Keywords

Behavioral economics; food intake; foraging; closed economy; weight regulation

1. Overview

Most analysts agree that the contemporary increase in body mass index, both at a cross-sectional population level and longitudinally within individuals, that is occurring in many parts of the world results from a combination of increased food intake and decreased physical activity [1]. In contrast to this observed increase, theoretical model(s) of control of food intake and body weight emphasize stability. These models are mostly biomedical in nature, meaning that physiological signals in the body and brain are hypothesized to act in a self-regulatory manner to produce an optimal or stable situation for the organism. The foundation of these models is the concept of homeostasis and body weight set point [2,3]. According to such models, if we eat more and gain weight, then several hormonal signals will act in the brain to inhibit further food seeking. Conversely, if we eat too little, the system will increase food seeking and intake,

^{*}Supported by NIH grant 1RO1 DK064712

^{*}Corresponding author. Tel: +1 352 392 0601 ext 287; fax: +1 352 392 7985 *E-mail address:* nrowland@ufl.edu (N.E. Rowland).

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

and the net result will be relative stability of body weight across time. Most of the clinical and preclinical biomedical research in this field is designed to discover or manipulate these signals with a view to a translational application to overweight humans.

The problem is the mismatch between the predictions of the model (stability of weight) and the observed situation (increment). It follows that these physiological signals relating to internal energy status are not as potent in controlling eating behavior as most models predict. Indeed, even individuals of normal and stable body weight are often employing deliberate or cognitive strategies to stay that way. These strategies include dietary restraint and exercise regimens [4] and may be considered ways to combat an environment that is hostile to weight stability - an environment that is replete with energy dense food and sedentary occupations.

It is quite unlikely that these hostile aspects of the environment will change any time soon. To date, despite the investment of billions of research dollars worldwide, the biomedical approach to the problem has not yielded spectacular results. We will develop the reasoning that this lack of success is because environmental influences, and in particular economic factors of availability and cost, have not been incorporated into the physiological models of how the brain computes food and energy balance. Thus, most of our paper does not have to do with obesity *per se*, but rather to factors that influence food intake and level of body weight maintenance. The examples that we will use are mostly from rodent studies. We will revisit the implications for human obesity at the end.

2. Behavioral economics and neuroeconomics

The discipline that has become known as behavioral economics has its roots in the law of demand which states that the consumption of or demand for a commodity decreases in a mathematically defined manner as its unit price increases [5,6]. In this usage, consumption is synonymous with acquisition or purchase and may apply to commodities as diverse as automobiles, clothes, or food. The term elasticity refers to the mathematical function or trajectory, given a particular set of conditions or market, with which demand for the commodity changes as a function of price. Currency is the form in which the price is paid and includes work, time, or exchange of goods. Accumulation of a commodity over time constitutes capital. It should be noted that at a procedural level, an economist's analysis often uses the average behavior of many consumers while most laboratory and in particular animal studies typically examine the behavior of a small number of individual subjects.

In an experimentally controlled economy, there is an interdependent relationship between price, demand and supply. **Price** in this case refers to the environmental costs such as schedules of reinforcement that relate units of behavior or effort to units of the commodity earned. **Demand** is the amount of the commodity taken by the animal over a suitable time base of observation. **Supply** is the availability of the commodity.

Economists have used such concepts widely to understand economies and consumer behavior, and it has become clear that groups of humans often do not function in an economically optimal manner, defined for example as paying the least possible unit price among an array of choices. Economic evaluation is often complicated by quality or perceived quality of goods, or too many concurrent choices [7]. The field of consumerism is the study of why people make particular choices in particular markets [8].

The study of human choice behavior, and the neurobiology thereof, has received attention in recent neuroimaging studies [9,10]. The emergent field of neuroeconomics seeks to understand the neural basis of such decision-making [11]. It is likely that the brain system(s) in this endeavor were first selected for as providing solutions to the economic problems that were present in the evolutionary times of our distant ancestors [12].

3. Motivation

Evolutionary accounts of behavior emphasize a fundamental distinction between ultimate (why) and proximate (how) mechanisms [13]. In the case of feeding, it is relatively simple to speculate on specific evolved behaviors that enhance inclusive fitness or ultimate mechanism. These include abilities to recognize and acquire food, to select a diet containing adequate specific nutrients, and to survive both feast and famine. When behaviors evolve there must be corresponding proximate mechanisms, including the ability to adapt or learn to produce the target behaviors within the lifetime of an individual of the particular species [14]. It follows that to study the biology of feeding behavior is to study proximate mechanism, arguably sculpted by ultimate mechanism.

Motivations result from neural syntheses of both internal and external conditions and they reliably precede specific actions. They may be considered part of the executive component of proximate mechanism. Epstein [15] argued that there are three characteristics or features which distinguish reflexive from motivated behavior. The first characteristic of motivated behavior is *individuation*, a concept that allows learning experiences affect future motivation of an individual through the expression of conditioned operants. The second characteristic, also learned, is *expectancy* or anticipation of goals. This gives the behavior goal-directedness. The third characteristic is an emotional or *affective* aspect. The concept of *palatability*, which may be defined as sufficiently acceptable to be consumed, is implicit in this definition of affect. We suggest that appetitive (food seeking) motivated behavior has both remote and proximate components: the remote component is foraging to increase the likelihood of food encounter [16]. Proximate components occur once food has been reached, and include costs such as handling and within-patch foraging (eg digging for worms in moist soil), as well as sensory evaluation of the food (eg palatability) that is used in part to determine whether a feeding bout is either continued or terminated.

By this definition, the vast majority of contemporary laboratory research on the biological basis of food intake use protocols that test proximate motivational mechanisms because subjects are presented food without price or cost such as excursion, work, or other adversity. These protocols meet Epstein's affective criterion #3 only, and so are essentially reflexive. As a result of this focus on proximate mechanism, relatively little is known about the neurobiology of remote food motivation. It is evident that proximate or consummatory decisions cannot occur in a natural environment without prior behavior that brings the individual into contact with the commodity, such as driving to the food store.

The concept of motivational state is closely related to the term *motivating operation* [17], in turn derived from establishing operation [18], which is defined as an environmental event or stimulus condition that momentarily alters the reinforcing effectiveness of other events and the frequency of occurrence of that part of an organism's behavioral repertoire relevant to those events as consequences. For example, food deprivation may be regarded as a motivating operation that not only makes most or all foods seem more desirable but also will evoke appropriate behaviors until an acceptable (quantity and quality) food source is encountered.

The core concepts of behavioral economics are critically entwined with those of motivation. The commodity under study must have a non-zero reinforcing value, and so the price that the subject is willing to pay will depend upon the actual or expected reinforcement imparted by delivery of the commodity and/or the accumulation of capital.

4. Behavioral ecology and optimality

Animals living today possess behavioral mechanisms that were sculpted by ancestral environments to maximize inclusive fitness. Such selection must have occurred at the level of

individual genes, but those genes operate within a group or social framework and within a limited range of possible environments. Houston and McNamara [19] stated this as follows:

"Most species have evolved in environments that are much more rich and varied than are found in the laboratory... In the wild, animals may die of starvation or be killed by a predator. These possibilities do not occur in the laboratory, but the animal is presumably following rules that take these possibilities into account.....a realistic biological model must take this into account" (p.547)

Based on optimal foraging concepts [20], Houston and McNamara [19] developed a set of explicit mathematical equations to model these aspects in a virtual animal with a body size and energy storage capacity similar to a rat. In particular, they assigned numerical values to effort expended in foraging, energy gain from eating, risks of predation, and other independent variables. Without going into the mathematical details of their model, we will explain some of their results, as summarized in Figure 1. These graphs are redrawn from a specific set of parametric values applied to their equations (see legend to Figure 1), but are representative. Each panel of the graph shows how a dependent variable changes as a function of change in gross energy gain (in Watts, a unit of energy exchange per unit time) expended in foraging. For example, foraging for a food of high caloric density in a patch of high spatial density of food items would have a high gain, while foraging for a low caloric density food in a patch of low density of items would correspond to a low energy gain.

The top panel of Figure 1 illustrates that the optimal level of body energy reserves, mostly in the form of adipose tissue, increases in a curvilinear fashion with gross gain. This model contains no explicit ideal or set point for body weight. The curve instead defines a continuum of apparent set or settling points (see [3,21] for a discussion of these terms) and is determined purely by the environmental contingencies and not at all by internal factors because these latter were not modeled.

The middle panel of Figure 1 shows that the rate of intake drops by only ~15% across a 5-fold change in gross gain so may be considered relatively invariant. The bottom panel shows that the total amount of time spent foraging declines rapidly as gross gain increases, but note that the change in foraging time as gross gain increases from 25 to 50 is quite small, because more calories will need to be consumed to support the higher body reserves shown in the top panel.

Although not so designed, this model is sufficient to predict the human obesity epidemic. High gross gain equates to high caloric density, prepackaged or prepared foods of relatively low cost and minimal risk. So at a population level, people are behaving exactly as they have evolved - as optimal foragers. How can we import these concepts, founded on natural observation and model building, into the behavioral or neuroscience laboratory to address neuroeconomic issues? The rest of this manuscript is devoted to these considerations.

5. Open and closed economies

It is first important to distinguish between open and closed economies. An open economy is one in which a market condition, say working for food, is present only some of the time. This is typified in many operant psychology experiments in which animals work for a food ration during a time-limited daily session. Some time later in the day they usually receive a free ration of food that complements that earned in the session, typically to a target daily amount or body weight. Open economy experiments traditionally use some level of presession food restriction as an explicit motivating operation, and both the initiation and the termination of the meal are independent variables defined by the session parameters.

In contrast, a closed economy is one in which the commodity and its associated costs are present at all times and the subject procures all of its food under a defined set of market conditions [22-24]. In a closed economy, there is usually no explicit motivating operation, and the initiation and termination of meals are dependent variables. Most humans live in closed economies; within that context some encounters with food are essentially an open economy, such as the time available for lunch or its net cost. Many studies in humans have examined within-meal regulation, such as the effect of a preload or first course on intake of a test meal or second course [25]. However, these types of study often show carry-over effects whenever multiple meals (approaching a closed economy) have been included in the analysis [25,26].

Why is the distinction between open and closed economies important for the analysis of feeding? Smith [27] has suggested that the contemporary neuroscience of feeding considers factors influencing individual feeding episodes or meals. Open economies or daily session protocols by definition study single meals, the original interest of Skinner [28]. In contrast, Collier [29] had earlier emphasized that meal size is not the principal problem because a single meal is but a brief episode in the life of an organism, and more recently he has made this argument even more strongly [24]. Closed economies implicitly involve a sequence of meals. These two contrasting positions are not necessarily conflicting, but they may illustrate different levels at which control of meal size could occur. The experimental choice of whether to use an open or closed economy protocol determines precisely whether individual meals will or will not be a principal focus of the research. As we will review below, the economic structure of the food environment does dramatically influence meal size and frequency. This result plus the fact that food has over the course of evolutionary time frequently been an unpredictable resource suggests that the ability to accurately control meal size may not have been a strongly selected trait.

Richter [30] was the first to report meal patterns in freely-feeding rats, an essentially reflexive eating condition, but it was not until the quantitative analysis of Le Magnen [31] that an underlying theory emerged. Le Magnen made the influential observation that there was a correlation between the size of a meal and the subsequent interval to the next meal. Other investigators have not consistently found this correlation (discussed in [24]), but the basic facts that rats eat episodically and typically about 8 meals at night and 2 during the day are widely replicated. The pervasiveness of this pattern thus requires some explanation. Le Magnen suggested that meals were terminated by signals of satiation and that the intermeal interval was determined by the decay of processes of satiety to some threshold. Thus, all other factors being equal, a large meal would produce a longer period of satiety before the next meal. While few modern theoreticians make such a clear distinction between satiation and satiety, indeed it is likely that there are several temporally overlapping processes [32], we cannot simply focus on the control of meal size without regard to the sequence or context in which that meal occurs.

Most rodent models of overeating or obesity are characterized by a large meal phenotype [33,34] which implies that satiation or other control of meal size is abnormal. Because the intermeal interval typically is not abnormal, these large meals produce less duration of satiety per unit intake than in normal subjects. This is because mechanism(s) of storage seem to operate more efficiently than mechanism(s) of mobilization in hyperphagic-obese subjects; further discussion of this metabolic aspect is beyond the scope of this review.

6. Simulating foraging costs

Collier and his colleagues [35] have distinguished two types of economic cost in foraging - procurement and consummatory. **Procurement cost** is often similar to travel effort and/or time, that we have termed remote appetitive behavior [16], and is the time and effort needed to locate a food item or patch. **Consummatory cost** is the effort expended within the patch - for example,

digging for food items, sucking nectar, opening seeds, or catching small but abundant prey. The distinction between these two costs may be blurred in some situations, but for analytical and for many practical purposes they appear to be separable. We will now discuss the impact of these two types of costs on behavior of animals. The relationship of these costs to the environment of humans will be discussed later.

6.1. Consummatory costs

Most open economy experiments investigate consummatory costs such as the schedules of reinforcement with which behavioral scientists are familiar. These include:

Fixed ratio (FR): the price of each food unit is fixed (eg number of responses)

Variable ratio (VR): the mean price of each food unit is constant, but the actual cost of each item varies around that mean. An FR is a VR with zero variance around the mean.

Progressive ratio (PR): successive food items within an episode of feeding become progressively more costly. An FR is a PR with zero increment from the initial value.

Both the VR and PR mimic essential aspects of foraging within a patch. In the case of a VR, not only may the food items in a real patch be of variable effort to obtain but they may also vary in size and nutritional quality. In either event, the net energy yield per response is variable. Many patches have a finite number of food items and it follows that successful foraging will deplete a patch so that successive items are harder to find; this is simulated by a PR. What happens when these concepts are applied to a closed economy?

6.1.1. Consummatory costs and demand—The first closed economy laboratory study of which we are aware is that of Logan [36]. His work predated the theoretical distinction between open and closed economies and the development of optimal foraging theory, and Logan instead used the term *free behavior situation*. Rats were housed continuously in operant chambers in which the force on a lever, the FR, and the reward size could be varied independently. The results from a condition in which water was subject to a series of fixed prices, but a food ration of 12 g/day was available at no cost (and was presumably consumed entirely) are redrawn in Figure 2. It may be seen that daily water intake was a negative exponential function of FR, a linear negative function of lever force, and a positive exponential function of unit reward size. It is striking that rats would work hard to obtain about 12 ml of water per day, which at the imposed food ration was close to the estimated minimum water need for digestion of this dry food, ~1 ml/g [37]. Logan's result shows that rats consume in excess of this minimum need only in easy conditions. We found a similar result in rats with free access to water of low palatability (quinine added) [38]. In economic terms, demand for the commodity is relatively inelastic until either the price becomes high or if it is less palatable or attractive.

Hursh and colleagues [39] conducted a more systematic analysis of cost-benefit ratios. In their protocol, **Unit price of food** = (FR × lever force)/(reinforcer size × probability of delivery). The control condition was considered 1 pellet, 1.0 probability, and low force. Rats under high cost conditions (double the force and probability of delivery=0.5) showed more rapid decline in demand as FR increased than those under standard or low cost conditions (Figure 3, left panel). But when unit price of food was plotted against demand, a single curve fit all eight of the conditions studied (two levels each of force, reinforcer size, probability of reinforcement) (Figure 3, right panel). These data demonstrate that rats use an energetically based cost-benefit computation that is independent of the constituent factors underlying unit price. In this context, unit price becomes equivalent to gross energy gain, as in Houston & McNamara's analysis (Figure 1).

Hursh et al [39] noted that these demand curves could be used to reinterpret traditional psychobiological findings such as hyperphagia after ventromedial hypothalamic lesions. If the primary effect of such lesions were to reduce the value of the reinforcer, it is predicted that the animals would overeat at low cost but show a precipitous decline as the cost increased. If as discussed above, cost includes palatability as well as calories, then this prediction fits the observed behavior of these rats [40] quite well.

6.1.2. Consummatory costs, meal parameters, and body weight—In a landmark paper, Collier, Hirsch and Hamlin [35] applied the concept of optimality to the interpretation of operant data in a closed economy. In their consummatory cost condition, rats were required to emit a FR lever press for each small pellet of nutritionally complete food in a closed economy. After several days to achieve stability at one FR, rats were advanced to a higher FR. Their principal results are redrawn in Figure 4, panels A-C. The number of meals per day (a meal was operationally started with a single press and ended after 10 min of no pressing) was ~27/day at the lowest FR and dropped to about half that number at the highest FR. Meal size increased slightly across this range, but at no point was particularly large. The drop in meal number was not fully offset by the increase in meal size, so that total food intake dropped by ~40% across the range of FRs imposed, defining a demand function. This demand function is thus determined mainly by a change in the number of meals initiated without change in meal size. It should be noted that the duration of meals must increase with FR (it takes longer to emit more responses) and so the within meal feeding rate, equivalent to gross gain in Figure 1, decreases proportionally.

Bauman [41] used a modification of Collier's protocol but, because higher consummatory FRs are necessarily associated with longer inter-pellet intervals and longer meal durations, he used an additional time manipulation. In this variation, rats had to press once on a lever to initiate an obligatory time delay after which a single press on a second lever would deliver a food pellet. The delays were determined on an individual basis to emulate the inter-pellet intervals during an initial standard procurement FR study. Bauman found that the number of pellets earned per day changed as a function of the delay with precisely the same relationship as the estimated delays associated with FRs in the initial study. Thus, elapsed time rather than effort *per se* is a critical dimension in demand and, by inference with Collier's study [35], on number of meals initiated. A similar conclusion was derived from a study of delays in a procurement cost protocol [42], and this result will be discussed later.

Peck [43] extended Collier's analysis to examine the effects on body weight. He found that as food demand decreased with increasing FR, female rats maintained a progressively lower body weight, decreasing in a curvilinear fashion from ~320 g at FR4 to ~250 g at FR256. This dynamic change of ~20% in weight was presumably mostly in (white) adipose tissue and so may reflect ~40% loss of energy reserves, which corresponds very well to the dynamic range of reserves in Houston & McNamara's model (Figure 1A). Peck found similar results when, instead of varying the effort to obtain food, food was made less palatable through addition of quinine sulfate. Thus, as we mentioned previously for bitter fluids [38], decreased palatability functionally alters demand in the same way as increased price. A similar type of interaction of palatability and effort has been noted by Ackroff and Sclafani [44].

6.1.3. Implications for inclusive fitness—In section 3, we mentioned ultimate mechanisms, so it is appropriate to ask whether these effects of cost on food intake and body weight have implications for inclusive fitness. Perrigo [45] studied female *Mus* and *Peromyscus* mice that were subjected to a FR of wheel revolutions to trigger delivery of each small food pellet. Separate groups were given different FRs ranging from 0 (*ad lib*, no effort) to 275. After a period to establish normal or baseline behavior, the mice were mated and the effects of FR condition on body weight and survival of the offspring were followed. The results

from the *ad lib* groups and from groups with FR near the middle of the range studied (FR=175) are shown in Table 1.

During the baseline period, the FR175 mice ate about 10% less than the corresponding *ad lib* groups and as a result either lost or failed to gain weight. This is consistent with the model in Figure 1 where FR175 would decrease gross energy gain relative to *ad lib*. During lactation, food intake rose progressively, reaching ~230% of baseline in the *ad lib* groups. In *Mus*, the FR175 group showed only a small increase in food intake, and they cannibalized pups so that only about two survived per litter but these were of relatively normal weight at the end of lactation. In *Peromyscus* the FR175 group more than doubled food intake but not to the levels of the *ad lib* group and, although all of the pups survived (~6 per litter), they were markedly underweight. Thus, the foraging cost on the mother reduced her inclusive fitness because either the number or the vigor of the offspring was adversely affected. While the mechanism differed between species, this study validates the important principle that changes in food price will have implications at a population level.

6.2. Hoarding

Another behavior that is dependent upon proximate foraging is hoarding, which occurs when animals elect to cache or accumulate capital (food) instead of eating it [46]. Food restriction, and perhaps more generally food insecurity, promotes hoarding [47]. Hoarding when food is readily available can be regarded as a way of avoiding to pay higher prices in the future. This may be a conscious act in humans but we cannot infer that animals are anticipating their environment; instead, we favor the interpretation that it reflects an evolutionarily selected trait.

Bartness and colleagues have examined foraging in a species well-known for hoarding, Siberian hamsters. The hamsters live in a two compartment closed economy environment in which a lower 'burrow' is connected via a tube to an upper cage. There, food pellets may be earned from a dispenser contingent on running a fixed number of revolutions in a wheel. Once obtained, animals then have the choice of eating the food in the top compartment, or putting it in their pouches to return to the burrow and form a food hoard. This arrangement is advantageous for separating distal and proximate components of appetitive behavior.

Increases in imposed foraging effort in Siberian hamsters results in decreased food intake, food hoarding and foraging [48]. Compensation for increased energy demands are handled similarly to what has been shown for rats (Figure 1B). The simulation of a depleted patch (eg a fast) in this closed economy asks how energy demands for foraging may change when there is no input of metabolic fuels. It has previously been shown that hamsters increase hoarding preferentially to food intake following a fast [49,50]. Foraging was measured after a fast and at a relatively low foraging effort (FR10) hoarding was significantly higher than at a high effort (FR200) while food intake was unchanged [49]. This suggests that optimal energy levels are influential in hoarding as well as food intake that occurs while foraging.

Cerebroventricular injection of the orexigenic peptide, AgRP, increased the amount of food consumed and hoarded, but the stimulatory effect on hoarding occurred at doses lower than those that increase food intake [51]. Similar results were found with acute injection of two other orexigenic agents, peripherally- injected ghrelin [52] and centrally-injected NPY [53].

In a quite different protocol, Whishaw & Kornelser [54] found that rats with ibotenic acid lesions of the nucleus accumbens showed abnormal hoarding (carrying food to store it) while their consummatory behavior (carrying food to eat it) was normal. This suggests that neural circuits for appetitive and consummatory behaviors are at least partially separable [55].

6.3. Procurement costs in foraging

In Houston & McNamara's model (Figure 1), it is irrelevant whether the effort expended in foraging is in either consummatory or procurement categories, or a combination. But to the animal, the distinction seems to be extremely important.

6.3.1. Collier's studies—Collier and colleagues were the first to compare procurement and consummatory costs [35]. Their consummatory results were discussed above (Figure 4, panels A-C). In their original procurement protocol, completion of a lever press FR opened a door and gave the rat access to a large bowl of food from which it could eat as much as it chose for no additional cost. However, when the rat stopped eating for 10 min, the door was closed and a new FR was needed to gain access to the food. The results from this protocol are shown in Figure 4, panels D-F. As procurement cost increased the number of meals per day decreased, and meal size increased almost reciprocally so that total intake remained constant, except at the highest ratio. This result of marked flexibility of meal size stands in marked contrast to the inflexibility of meal size in the consummatory protocol (Figure 4, panels A-C). It should be noted that at low procurement costs, the meal number (~10) and size (2-3 g) approximate typical meal patterns of *ad lib* feeding rats with a comparable food [30,31].

Mathis, Johnson and Collier [42] examined the effect of a time delay rather than lever press effort in procurement. In this study, rats were required to press a procurement lever only once, but delays ranging from 0 to 163,840 s (~46 hr) were then imposed before access to the food bowl was granted. Each delay was in effect for a minimum of 7 days. At a delay of 1 s, rats took essentially a free feeding pattern, *viz* ~9 meals per day of 2-3 g. At a delay of 21 min, meal number was halved to ~4-5 per day, and meal size doubled so that total intake was unchanged. The authors noted that rats required ~20 min to complete FR640 and so comparison with the results in Figure 4 (panels D,E) suggests that the effect of an equivalent delay on meal number was less than predicted by procurement cost alone. Thus, both time and physical effort appear to contribute to the change in meal patterns with procurement cost.

Collier, Johnson & Mathis [56] conducted a study in which procurement was contingent upon either turning a running wheel a criterion number of times to activate a consummatory lever, or a separate procurement lever. In both cases, the effort to either turn the wheel or depress the lever was varied across a 64-fold range. Increasing effort on the procurement device slowed the procurement rate because rats rested during ratio runs, but had very little effect on meal pattern which was instead determined mainly by the actual procurement ratio. In both cases, time seemed to be the major cost to the animal, greater than physical effort.

These demonstrations that time is at least as important a cost factor as effort are, in retrospect, perhaps not surprising. For small animals the actual metabolic cost incurred in moving through their environment may be as little as 1% of total energy expenditure [57]. Additionally, time spent foraging may increase the risk of predation (simulated also in Houston & McNamara's model [19]) and we will now consider this briefly.

6.3.2. Time and predation—Fanselow et al [58] examined whether a simulated danger of foraging would have a similar effect to effort on procurement in rats. Completion of a procurement lever press ratio caused a cue light to extinguish at which time each press on the same lever delivered food pellets. After 4 min without a pellet, the system reset. They ran several baseline procurement ratios with the same effect on meal number and size reported above (Fig 4, panels D,E). An unsignaled brief (1 s) foot shock was then programmed at variable intervals, averaging less than once per h. The animals could avoid this mild shock by staying in an insulated nesting area, but whenever they came to the lever for food there was this small risk of shock. In all procurement conditions, rats reduced the number of meals during the shock phase by about 50% compared with baseline. For example, at a procurement ratio

of 32 in their second experiment, rats took an average of 5.7 meals per day under baseline and 2.0 meals during the shock phase. This was not simply a response to shock, because in another phase of this experiment, the rats were given 30 shocks in a separate chamber, but they still took 5.7 meals in the foraging environment. Further, they showed that by staying in their nest box, rats avoided all but about 2-3 of the scheduled shocks. Thus, the introduction of a temporally uncertain but rare aversive event caused the animals to substantially reduce the number of excursions (meal number) but increase the duration of stay at the food (meal size), exactly as would have been observed with a further increase in procurement cost alone. Thus, other motivational variables (in this case risk avoidance), like effort, can almost completely override controls of meal size that are apparent in an *ad lib* food world.

6.4 Travel between patches

In a real world economy, both consummatory costs and procurement costs occur, but there usually is more than one alternative location or patch for foraging. The **matching law** is a statement of how organisms allocate their consummatory behavior between two patches differing in reinforcement density. The simplest form of the law is $B1/B2 = r1/r2$, where $B1$ and $B2$ represent the behavior allocated to patches 1 and 2, and $r1$ and $r2$ are the relative prices for the (same) reinforcer in the two patches. A more general form of that equation [59] is:

$$\text{Log } B1/B2 = s \text{ log } r1/r2 + \text{log } b$$

where s is a sensitivity factor and b is a bias in favor of one or the other food alternative, for example differences in palatability.

When travel time is simulated with a changeover delay or other effort to get from one patch to another, overmatching is consistently observed, in which $s > 1$ and the organism spends more time in the denser environment than is predicted by the simple matching law [60-62]. This may be understood if travel time is regarded as adding to the overall price of the commodity. This in turn means that procurement costs will influence the behavior in response to imposed consummatory costs. This possibility has been examined with a protocol in which concurrent procurement and consummatory costs were imposed on rats [63]. In this situation, such an interaction was indeed observed, and the optimality of the strategy in terms of unit price depended on the relative magnitudes of procurement and consummatory costs.

7. Toward a neurobiology of foraging

There are several problems with optimal foraging or laboratory simulations thereof, not least including an adequate definition of the term *cost* at a physiological and/or neural level. We have reviewed above that there is no simple solution – the type of effort, time expended, and likelihood of danger are among the cost factors that profoundly affect the behavior of rodents. Another problem is that these studies often entail several months to study a few subjects, especially in a closed economy where the each subject may occupy a valuable test chamber continuously. However, there have been few systematic attempts to streamline these protocols into a form that would be suitable for neurobiological investigation.

7.1. Brief protocols

A closed economy consummatory cost study in rats by Raslear et al [64] showed that as little as one day is necessary to achieve stable performance in rats. In their first study, rats were run through seven FRs (ranging from 1 to 360) for 24 h each, and the sequence was repeated four times consecutively. The demand curves were identical for all four replications. In a second study, the FRs were presented in random rather than ordered sequence, and the results were similar. Thus, demand curves in short term studies are similar in form to those generated over

a longer time frame. This in turn means that rats adapt their behavior very rapidly upon changing schedules.

We (Atalayer & Rowland, unpublished data, 2007) have recently found a similar result in CD-1 mice subjected to incrementing consummatory FRs. The mice were studied for four days at each FR, and the total intake and meal patterns were acquired each day. Neither intake nor meal number showed significant differences between the first and fourth day at each FR. These results, along with Raslear's, suggest that at least for consummatory costs, only a few days of data are necessary at each condition. This observation increases the availability of these closed economy protocols for neurobiological investigation.

7.2. Pharmacologic approaches

The effect of drug treatments on foraging can best be studied using a within-subject design with a baseline set of conditions and then one or more drug conditions. This has been used in short session open economy studies, for example examining the acute or chronic effect of a drug on the break point for food in FR or PR schedules [65,66], usually with food restriction as a motivating operation.

To adapt this to the closed economy non-deprivation situation requires that the drug must be present at pharmacologically relevant concentrations throughout each session, often 24 h. Some drugs may have long enough actions to be studied over periods of several hours [67,68], but many have actions that decay quite rapidly and so daily injection is not a viable solution. Such drugs could be administered continuously, for example by implanted osmotic minipump [69], slow release implant, or from an external source via a catheter, or in the latter case in an episodic fashion. West et al [70] were among the first to use such an infusion (of cholecystokinin in free feeding rats), with the result that total food intake did not change but meals were smaller and more frequent. With the exception of the work by Foltin [67], none have used an economic protocol, and in Foltin's study the subjects (baboons) were working in a 2 h/day access schedule with post-session supplements, rather than a true closed economy.

We have examined this principle recently using sodium appetite as a model motivated behavior in rats [71]. Completion of a procurement FR (1,80 or 300) on one lever moved a spout into reach from which the rat could lick NaCl solution, and the same costs on a second lever delivered water. Whenever 5 min elapsed without a lick the tube was retracted and new procurement effort was required. Under baseline conditions, rats consumed approximately equal amounts of water and NaCl at hypotonic (0.04M) or isotonic (0.15M) concentrations, but avoided hypertonic (0.4M) NaCl and instead took mostly water. After the baseline period, rats received daily subcutaneous injections of deoxycorticosterone acetate (DOCA) in oil. This provides a sustained release of the synthetic steroid into the circulation and is known to be associated with a robust and sustained sodium appetite under cost-free conditions [72]. During the DOCA phase the intake of all concentrations of NaCl increased, as did the number of bouts initiated per day. The number and size of bouts in both baseline and DOCA phases were related to the procurement cost, similarly to the case for food (cf Figure 4). This shows that a chronic physiological change that induces an appetite under free access conditions also causes orderly changes in behavioral strategies for procurement of NaCl.

7.3. Genetic approaches

Rather than manipulation of physiology through the use of hormones or other agents, foraging protocols lend themselves to analysis of genetic differences using between-subjects designs. Because most of the relevant spontaneous and targeted mutations are in mice, we needed to validate this foraging model in mice which, with the exception of Perrigo's study [45] cited previously, have not been used widely in operant tasks.

We initiated this line of inquiry using the leptin-deficient C57BL/6 (B6) obese mouse (Lep^{ob}; formerly known as *ob/ob*) and their normal (wild type) littermates [73]. In this study, obese and lean female B6 mice were housed continuously in a two lever operant chamber with water freely available. One lever was designated the foraging or procurement lever, and a cue light indicated the availability of this lever. Completion of a procurement FR (in six phases of the study, ranging from 5 to 480) activated the consummatory lever, also cued with a light. A fixed consummatory cost (5 or 10 presses) delivered a 20 mg food pellet. As in the Collier protocols described above, mice could eat as much as they elect to eat at any time during the 23.5 h daily session, but whenever 10 min elapsed without a food delivery, the consummatory lever was inactivated and control reverted to the procurement lever. The results are shown in Figure 5. Like rats, mice took decreasing numbers of meals per day as procurement cost increased, and with a reciprocal increase in meal size. The obese mice took larger meals than lean mice at the lower procurement ratios, but as the meal sizes rose at the higher procurement costs, the difference between the two genotypes was no longer evident. This may be due to a ceiling effect on meal size. The obese mice ate about 30% more than lean mice throughout the study, and both groups maintained their daily caloric intake across all ratios examined. Thus, leptin is not a critical signaling molecule in determining meal patterns across procurement conditions.

We then examined another obese model, mice with targeted deletion (knockout, KO) of the melanocortin type 4 receptor gene (MC4R) [74]. The procedure was similar to that described for the *ob/ob* mice but, unlike in that model, neither the KO mice nor their wild type controls conserved food intake across a wide range of procurement costs. Thus, while both genotypes decreased their number of meals per day from 5-6 at the lowest procurement cost to 3 at the highest, their mean meal size did not double, and so their intake fell by about 25% from the lowest to highest ratios. Additionally, the MC4RKO mice were not hyperphagic relative to the wild types and as a result lost substantial weight during each phase of the experiment. *Ad libitum* feeding between phases allowed these animals to regain the lost weight, presumably through overeating. Thus, compared with B6 mice, the wild type control mice (of a mixed 129/B6 background strain) showed elasticity of food demand under these conditions and the KO mice were not hyperphagic even at the easiest ratios.

We considered that this might be due to a decreased food motivation in the KO mice, and to test this we introduced a PR for the consumption cost, but without a procurement phase [75]. PR schedules are frequently used to assess motivation for drugs or food, typically in short sessions. To adapt this to a closed economy protocol we introduced a reset interval: following cessation of responding (the break point) for 20 min, the PR schedule reset to one. Since the first few pellets in each meal are the cheapest, the optimal strategy to avoid work under these conditions would be to take many small meals. In this condition, MC4RKO mice were hyperphagic and did so by taking larger meals – that is they incurred about double the mean price per pellet of their wild type counterparts. Thus, there does not seem to be a motivational deficit in these animals. The reasons that the KO mice were hyperphagic in this protocol but not the procurement cost protocol are not clear at this time. One possibility concerns the different timing of the costs imposed by these protocols, before a meal in the procurement protocol but during a meal in the consumatory PR protocol. These data suggest that there are indeed genetic differences that are amenable to (neuro)economic analysis.

8. Relevance to obesity

It should now be evident that increased environmental cost of food produces decreased consumption and as a result decreased body energy or fat content. What sort of environment produces obesity? Rats fed even standard food for a lifetime become obese and live shorter lives relative to those with partially restricted food (see [76] for discussion). One implication

of this is that ad libitum feeding produces a sub-optimal animal and calls into question whether any ad libitum regimen, whether it be with chow or with palatable energy dense diets designed to produce even more overeating or weight gain, is a meaningful norm against which to study biologically programmed or optimal regulation.

An example more directly relevant to foraging is a study of three troops of baboons in the Amboseli National Park, Kenya [77]. One troop had for many years incorporated the use of menu items from a dumpster at a tourist lodge, while the other two troops were exclusively wild-feeding. When captured for isotope dilution analysis of body fat content, dumpster-using females had a mean 23.2% body fat, compared with 1.9% in the wild-feeding troops. Body length was comparable. The effects were similar in direction, but less dramatic, in males. The estimated food intake of the troops was identical, so the principal contributing factor to relative obesity appeared to be lower energy expenditure mostly in the form of locomotion to procure that food. This result, in which decreased energy expenditure and increased body fat content produced no decrease in food intake again reveals the inadequacy of a physiological control system for body weight in the face of a (self-selected) toxic food environment.

These examples lead to the immediate question of what aspects of the environment would produce a healthy restructuring of the balance between food intake and energy expenditure? Hill and his colleagues [78] are actively advocating that changes in public policy need to be developed to stem the epidemic of obesity spawned by our toxic food environment. We have reviewed evidence that animals eat less when effort has to be expended to procure food, but the converse is also true, that animals eat more when food is available at little or no cost. There are at least three facets to this concept of availability as it applies to human society.

The first is that food production systems have become so efficient in many countries that most people have abundant, safe, tasty and often energy-dense food available at an affordable price in their local market. This probably encourages food hoarding – impulsive food buying that is not related to a current need and often in excess of any conceivable need before the next scheduled visit to the market [47]. Once it's in the home, it may be irresistible.

The second is related to the fact that the proportion of meals consumed outside the home has been steadily increasing and is projected to increase still further. In restaurants, you tend to eat what is put in front of you – portion size and number of courses or options, not hunger, largely determines the amount eaten [79]. Additionally, all-you-can-eat fixed price restaurants are not uncommon in the USA, and this predictably encourages eating more because portion size has no imposed limit.

The third is the increase in non-meal eating, or snacking. Many workplaces now have snack vending machines or trolleys that offer a variety of often high calorie snacks and beverages. And many group meetings - business or social - include obligatory snacks.

This paints a picture of a food environment in which the constraints of cost and availability that have been present throughout our evolutionary past have been substantially eliminated. Without these natural constraints, the physiological systems for many individuals seem to be inadequate to maintain balance.

8. Concluding remarks

Basic tenets of behaviorism demonstrate that the environment plays an important role in modulating behavior, including feeding and body weight regulation. It is apparent the food environment has changed compared to that in which contemporary species evolved, slowly until the last 100 years, but since then and in particular in the past 50 years at an accelerated

pace. This accelerated change correlates closely with the alarming increase in the incidence of obesity in humans.

In this review, we have provided theory and examples of the influence of economic factors on food intake in animal models. These models, particularly in closed economies, predict increased consumption and increased body weight when the price is low and/or quality is high. In fact, humans are behaving like perfect optimal foragers in their new food-replete environment, and this has ethical implications for ways in which treatments for obesity should be viewed. These closed economy protocols, which have clinical and predictive validity, have to date been used very little in neurobiological investigation of food intake. Examples given show the utility of these protocols in the analysis of pharmacological and genetic factors. Neuroeconomic decision-making concepts need to be incorporated into our understanding of the quantitative and qualitative aspects of food procurement and intake; these offer a view that in which homeostatic-type mechanisms are subordinate to economic principles, but also allow integration with systems that currently are articulated as mediating reward or reinforcement.

9. References

- Hill JO. Understanding and addressing the epidemic of obesity: an energy balance perspective. *Endocr Rev* 2006;27:750–61. [PubMed: 17122359]
- Berthoud HR. Multiple neural systems controlling food intake and body weight. *Neurosci Biobehav Rev* 2002;26:393–428. [PubMed: 12204189]
- Harris RBS. Role of set-point theory in regulation of body weight. *FASEB J* 1990;4:3310–8. [PubMed: 2253845]
- Vogels N, Westerterp-Plantenga MS. Categorical strategies based on subject characteristics of dietary restraint and physical activity, for weight maintenance. *Int J Obes* 2005;29:849–57.
- Hursh SR. Economic concepts for the analysis of behavior. *J Exp Anal Behav* 1980;34:219–38. [PubMed: 16812188]
- Hursh SR. Behavioral economics. *J Exp Anal Behav* 1984;42:435–52. [PubMed: 16812401]
- Wansink B. Environmental factors that increase the food intake and consumption volume of unknowing consumers. *Annu Rev Nutr* 2004;24:455–79. [PubMed: 15189128]
- Dagevos H. Consumers as four-faced creatures. Looking at food consumption from the perspective of contemporary consumers. *Appetite* 2005;45:32–9. [PubMed: 15921822]
- Tom SM, Fox CR, Trepel C, Poldrack RA. The neural basis of loss aversion in decision-making under risk. *Science* 2007;315:515–8. [PubMed: 17255512]
- Padoa-Schioppa C, Assad JA. Neurons in the orbitofrontal cortex encode economic value. *Nature* 2006;441:223–6. [PubMed: 16633341]
- Glimcher, PW. *Decisions, Uncertainty and the Brain: The Science of Neuroeconomics*. MIT Press; Cambridge MA: 2003.
- Sherry DF. Neuroecology. *Annu Rev Psychol* 2006;57:167–97. [PubMed: 16318593]
- Mayr E. Cause and effect in biology. *Science* 1961;134:1501–5. [PubMed: 14471768]
- Sober, E.; Wilson, DS. *Unto Others*. Harvard University Press; Cambridge MA: 1998.
- Epstein, AN. Instinct and motivation as explanations for complex behavior. In: Pfaff, DW., editor. *The Physiological Mechanisms of Motivation*. Springer-Verlag; New York: 1982. p. 25-58.
- Rowland, NE.; Mathes, CM. Appetitive and consummatory aspects of food intake in rodents. In: Harris, RBS.; Mattes, RD., editors. *Appetite and food intake: behavioral and physiologic considerations*. Taylor & Francis; in press
- Tapper K. Motivating operations in appetite research. *Appetite* 2005;45:95–107. [PubMed: 16046245]
- Michael JL. Distinguishing between discriminative and motivational functions of stimuli. *J Exp Anal Behav* 1982;37:149–55. [PubMed: 7057126]
- Houston AI, McNamara JM. The value of food: effects of open and closed economies. *Animal Behav* 1989;37:546–62.

20. Schoener TW. Theory of feeding strategies. *Annu Rev Ecol System* 1971;2:307–43.
21. Davis JD, Wirtshafter D. Set points or settling points for body weight?: A reply to Mrosovsky and Powley. *Behav Biol* 1978;24:405–11. [PubMed: 743072]
22. Timberlake W, Peden BF. On the distinction between open and closed economies. *J Exp Anal Behav* 1987;48:35–60. [PubMed: 3625103]
23. Collier GH, Johnson DF, Hill WL, Kaufman LW. The economics of the law of effect. *J Exp Anal Behav* 1986;46:113–36. [PubMed: 3760748]
24. Collier G. A functional analysis of feeding. *Adv Study Behav* 2005;35:63–103.
25. Rolls BJ, Pirraglia PA, Jones MB, Peters JC. Effects of olestra, a noncaloric fat substitute, on daily energy and fat intakes in lean men. *Am J Clin Nutr* 1992;56:84–92. [PubMed: 1609767]
26. de Castro JM. In search of the structure of a function: the eating behavior of free-living humans. *Nutrition* 2007;23:374–7. [PubMed: 17331703]
27. Smith GP. The controls of eating: a shift from nutritional homeostasis to behavioral neuroscience. *Nutrition* 2000;16:814–20. [PubMed: 11054585]
28. Skinner BF. Drive and reflex strength. *J Gen Psychol* 1932;6:22–37.
29. Collier GH. Satiety: an ecological perspective. *Brain Res Bull* 1985;14:693–700. [PubMed: 3928096]
30. Richter CP. Animal behavior and internal drives. *Quart Rev Biol* 1927;2:307–43.
31. Le Magnen, J. Advances in studies on the physiological control and regulation of food intake. In: Stellar, E.; Sprague, JM., editors. *Prog Physiol Psychol*. 4. Academic Press; New York: 1971. p. 203–61.
32. Blundell JE, Halford JC. Regulation of nutrient supply: the brain and appetite control. *Proc Nutr Soc* 1994;53:407–18. [PubMed: 7972155]
33. Castonguay TW, Upton DE, Leung MB, Stern JS. Meal patterns in the genetically obese Zucker rat: a reexamination. *Physiol Behav* 1982;28:911–6. [PubMed: 7100292]
34. Moran TH, Katz LF, Plata-Salaman CM, Schwartz GJ. Disordered food intake and obesity in rats lacking cholecystokinin A receptors. *Am J Physiol: Regulat Integ Comp Physiol* 1998;274:R618–25.
35. Collier GC, Hirsch E, Hamlin PH. The ecological determinants of reinforcement in the rat. *Physiol Behav* 1972;9:705–16. [PubMed: 4655163]
36. Logan, FA. The free behavior situation. In: Levine, D., editor. *Nebraska Symposium on Motivation* 1964. University of Nebraska Press; Lincoln NE: 1964. p. 99–128.
37. Rowland N, Nicolaidis S. Metering of fluid intake and determinants of ad libitum drinking in rats. *Am J Physiol* 1976;231:1–8. [PubMed: 961847]
38. Rowland NE, Flamm C. Quinine drinking: More regulatory puzzles. *Physiol Behav* 1977;18:1165–70. [PubMed: 928538]
39. Hursh SR, Raslear TG, Shurtleff D, Bauman R, Simmons L. A cost-benefit analysis of demand for food. *J Exp Anal Behav* 1988;50:419–40. [PubMed: 3209958]
40. Powley TL. The ventromedial hypothalamic syndrome, satiety, and a cephalic phase hypothesis. *Psychol Rev* 1977;84:89–126. [PubMed: 322184]
41. Bauman R. An experimental analysis of the cost of food in a closed economy. *J Exp Anal Behav* 1991;56:33–50. [PubMed: 1940762]
42. Mathis CE, Johnson DF, Collier G. Procurement time as a determinant of meal frequency and meal duration. *J Exp Anal Behav* 1995;63:295–311. [PubMed: 7751834]
43. Peck JW. Rats defend different body weights depending on palatability and accessibility of their food. *J Comp Physiol Psychol* 1978;92:555–70. [PubMed: 98538]
44. Ackroff K, Sclafani A. Palatability and foraging cost interact to control caloric intake. *J Exp Psychol: Animal Behav Proc* 1999;25:28–36.
45. Perrigo G. Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. *Animal Behav* 1987;35:1298–1316.
46. Bartness, TJ.; Day, DE. Food hoarding: a quintessentially anticipatory appetitive behavior. In: Fluharty, SJ.; Grill, HJ., editors. *Prog Psychobiol Physiol Psychol*. Academic Press; New York: 2003. p. 69–100.

47. Dodd DK, Stalling RB, Bedell J. Grocery purchases as a function of obesity and assumed food deprivation. *Int J Obes* 1977;1:43–7. [PubMed: 617107]
48. Day DE, Bartness TJ. Effects of foraging effort on body fat and food hoarding in Siberian hamsters. *J Exp Zool* 2001;289:162–71. [PubMed: 11170012]
49. Day DE, Bartness TJ. Fasting-induced increases in food hoarding are dependent of the foraging-effort level. *Physiol Behav* 2003;78:655–68. [PubMed: 12782221]
50. Borer KT, Rowland N, Mirow A, Borer RC, Kelch RP. Physiological and behavioral responses to starvation in the golden hamster. *Am J Physiol: Endocrinol Metab Gastrointest Physiol* 1979;236:E105–E112.
51. Day DE, Bartness TJ. Agouti-related protein increases food hoarding more than food intake in Siberian hamsters. *Am J Physiol: Regulat Integ Comp Physiol* 2004;286:R38–R45.
52. Keen-Rhinehart E, Bartness TJ. Peripheral ghrelin injections stimulate food intake, foraging, and food hoarding in Siberian hamsters. *Am J Physiol: Regulat Integrat Comp Physiol* 2005;288:R716–R722.
53. Day DE, Keen-Rhinehart E, Bartness TJ. Role of NPY and its receptor subtypes in foraging, food hoarding, and food intake by Siberian hamsters. *Am J Physiol: Regulat Integrat Comp Physiol* 2005;289:R29–R36.
54. Whishaw IQ, Korneliser RA. Two types of motivation revealed by ibotenic acid nucleus accumbens lesions: dissociation of food carrying and hoarding and the role of primary and incentive motivation. *Behav Brain Res* 1993;55:285–95.
55. Berridge KC. Motivation concepts in behavioral neuroscience. *Physiol Behav* 2004;81:179–209. [PubMed: 15159167]
56. Collier G, Johnson DF, Mathis C. The currency of procurement cost. *J Expl Anal Behav* 2002;78:31–61.
57. Garland T. Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am Natur* 1983;121:571–87.
58. Fanselow MS, Lester LS, Helmstetter FJ. Changes in feeding and foraging patterns as an antipredator defensive strategy: a laboratory simulation using aversive stimulation in a closed economy. *J Exp Anal Behav* 1988;50:362–74.
59. Baum WM. On two types of deviation from the matching law: bias and undermatching. *J Exp Anal Behav* 1974;22:231–42. [PubMed: 16811782]
60. Aparicio CF. Overmatching in rats: the barrier choice paradigm. *J Exp Anal Behav* 2001;75:93–106. [PubMed: 11256869]
61. Baum WM, Aparicio CF. Optimality and concurrent variable-interval variable-ratio schedules. *J Exp Anal Behav* 1999;71:75–89. [PubMed: 16812893]
62. Pliskoff SS, Fetterman JG. Undermatching and overmatching: The fixed-ratio changeover requirement. *J Exp Analysis Behav* 1981;36:21–7.
63. Johnson DF, Triplehorn J, Collier G. The effect of patch depletion on meal patterns in rats. *Anim Behav* 1993;46:55–62.
64. Raslear TG, Bauman RA, Hursh SR, Shurtleff D, Simmons L. Rapid demand curves for behavioral economics. *Anim Learning Behav* 1988;16:330–9.
65. Higgs S, Barber DJ, Cooper AJ, Terry P. Differential effects of two cannabinoid agonists on progressive ratio responding for food and free-feeding in rats. *Behav Pharmacol* 2005;16:389–93. [PubMed: 16148443]
66. LeSage MG, Stafford D, Glowa JR. Effects of anorectic drugs on food intake under progressive-ratio and free-access conditions in rats. *J Exp Anal Behav* 2004;82:275–92. [PubMed: 15693523]
67. Foltin RW. Effects of dietary and pharmacological manipulations on appetitive and consummatory aspects of feeding in non-human primates. *Appetite* 2005;45:110–20. [PubMed: 15951055]
68. Zorrilla EP, Inoue K, Valdez GR, Tabarin A, Koob GF. Leptin and post-prandial satiety: acute central leptin more potently reduces meal frequency than meal size in the rat. *Psychopharmacology* 2005;177:324–35. [PubMed: 15609069]
69. Rowland NE. Effect of continuous infusions of dexfenfluramine on food intake, body weight and brain amines in rats. *Life Sci* 1986;39:2581–6. [PubMed: 2432374]

70. West DB, Fey D, Woods SC. Cholecystokinin persistently suppresses meal size but not food intake in free-feeding rats. *Am J Physiol: Regulat Integr Comp Physiol* 1984;246:R776–87.
71. Colbert CL, Rowland NE. Sodium preference and appetite in rats in an operant protocol. *Physiol Behav* 2005;83:715–21. [PubMed: 15639156]
72. Fregly MJ, Rowland NE. Role of renin-angiotensin- aldosterone system in NaCl appetite of rats. *Am J Physiol: Regulat Integr Comp Physiol* 1985;248:R1–R11.
73. Vaughan CH, Rowland NE. Meal patterns of lean and leptin-deficient obese mice in a simulated foraging environment. *Physiol Behav* 2003;79:275–9. [PubMed: 12834799]
74. Vaughan CH, Moore MC, Haskell-Luevano C, Rowland NE. Meal patterns and foraging in melanocortin receptor knockout mice. *Physiol Behav* 2005;84:129–33. [PubMed: 15642615]
75. Vaughan C, Moore M, Haskell-Luevano C, Rowland NE. Food motivated behavior of melanocortin-4 receptor knockout mice under a progressive ratio schedule. *Peptides* 2006;27:2829–35. [PubMed: 16930774]
76. Rowland NE. Food or fluid restriction in common laboratory animals: balancing welfare considerations with scientific inquiry. *Comp Medicine* 2007;57:149–60.
77. Altmann J, Schoeller D, Altmann SA, Muruthi P, Sapolsky RM. Body size and fatness of free-living baboons reflect food availability and activity levels. *Am J Primatol* 1993;30:149–61.
78. Hill JO, Peters JC, Wyatt HR. The role of public policy in treating the epidemic of global obesity. *Clin Pharmacol Ther* 2007;81:772–5. [PubMed: 17314927]
79. Wansink B. Environmental factors that increase food intake and consumption volume of unknowing consumers. *Annu Rev Nutr* 2004;24:455–79. [PubMed: 15189128]

FIGURE 1.

Optimal energy reserves (kJ, top panel), optimal intake rates (Watts, middle panel), and optimal proportion of time spent foraging (bottom panel) as a function of gross energy gain while foraging (Watts). Data redrawn from Figures 7,8 and 9 of Houston & McNamara [19] for a closed economy with the specific model parameters, basal metabolic rate = 2.5W, foraging metabolic rate=7.5W, plus 0.0005 W/kJ body reserves.

FIGURE 2.

Results from Logan's [36] closed economy study in which rats were lever pressing on various FR schedules for water reinforcement. A free 12 g food ration was given daily. The top panel shows how the demand for water increased with unit reinforcer size. The middle panel shows the demand for water decreased as a function of increasing unit cost, but became inelastic at higher FRs. The lower panel shows that increasing the relative effort expended to press the lever had a relatively small effect on demand.

FIGURE 3.

Median daily response output (left panel) and food demand (45 mg pellets earned per day; right panel) in rats studies under 8 different unit price conditions, where the Unit price = (fixed ratio $\times$ lever weight)/(pellets per reinforcement $\times$ probability). The left panel shows 3 of the 8 conditions, the standard (1 pellet per reinforcement, probability 1.0, lever force 0.265N), a lower cost (2 pellets per reinforcement, probability 1.0, force 0.265N), and the highest cost studied (1 pellet per reinforcement, probability 1.0, force 0.53N). On the right, food demand is plotted against consummatory cost; all 8 groups fell on or near the single function that is shown. Intake is well conserved at relatively low costs, but drops precipitously as cost becomes high. Data redrawn from Figures 2 and 3 of Hursh et al [39].

FIGURE 4.

Effect of various consummatory costs (panels A-C) and procurement costs (panels D-F) on mean number of meals per day (A,D), mean meal size (B,E) and total lever presses emitted (C,F). Derived from data in Collier, Hirsch & Hamlin [35].

FIGURE 5.

Mean number of meals per day decreases and mean meal size increases as procurement fixed ratio (PFR) increases in lean and obese (*ob/ob*) mice. The consummatory cost for each pellet was 5 presses at low PFR and 10 at the higher PFRs. Redrawn from [73].

TABLE 1

Mean daily food intake and litter parameters in female *Mus* and *Peromyscus* in an economy in which food pellets were available either freely or for a cost (FR175; wheel turn).

	<i>Mus</i> No cost	<i>Mus</i> FR175	<i>Peromyscus</i> No cost	<i>Peromyscus</i> FR175
Baseline Food intake (g/day)	5.6	5.1	4.7	4.2
Food intake (g/day) lactation*	12.5	7.0**	11.5	10.0**
Pup weight (g)*	7.5	7.2**	9.0	5.5**
Fraction pups surviving*	60%	33%**	100%	100%

Data from Tables I & II and Figures 1 & 2 of Perrigo [44]. Shown are means of N=8-11/group.

* Measures from day 18 postnatal (end of lactation).

** FR175 group significantly different from *Ad lib* condition.