Published in final edited form as:

Behav Brain Res. 2012 June 1; 231(2): 272–278. doi:10.1016/j.bbr.2011.11.021.

Order and disorder: Temporal organization of eating

Neil E. Rowland*

Department of Psychology, University of Florida, PO Box 112250, Gainesville, FL 32611-2250, USA

Abstract

Feeding behavior is described from an evolutionary perspective, and implications for modern neurobiological studies are suggested. In particular, it is argued that meals may have evolved more for sociocultural reasons than physiological imperatives, and that biological approaches to the study of feeding episodes should adopt a more flexible model that is founded in economic or cost-benefit considerations. Specific examples of flexibility in mouse feeding behavior are given. It is further argued that the modern human food environment is so immoderate that physiological manipulations designed to restrain eating have little hope of achieving this goal.

Keywords

Evolution; Foraging; Hunter-gatherer; Eating; Meals; Mice; Obesity

1. Introduction

The early 1950s were formative years for the physiological psychology of feeding behavior. In 1954, our honoree Philip Teitelbaum defended his Ph.D. dissertation entitled “Sensory control of hypothalamic hyperphagia” and in the same year his mentor, Eliot Stellar, published his seminal paper on the physiology of motivation [1]. The previous year, Gordon Kennedy had introduced his lipostatic theory of the control food intake [2], to be followed a few months later by Jean Mayer’s glucostatic hypothesis [3]. Phil continued to work on the neural basis of feeding for another decade before moving to other problems in physiological psychology. The panorama of feeding behavior today differs in many ways from when Phil was in the field, and I will mention just two. First, there have been immense technology-driven advances including an ever-expanding appreciation of neurons, genes, epigenetics, and signal molecules. Second, there has been a substantial increase in obesity, usually measured by population mean body mass index (BMI), in humans living in most affluent societies.

One of our scientific Zeitgeists is translational research. There is strong public interest to identify biological factors linked with obesity because therapeutic manipulation of those factors might prevent or reverse obesity. For example, several genetic polymorphisms have been correlated with human obesity in genome-wide association studies [4], and these results are driving research on how those gene products affect food intake or energy expenditure, and whether they might be viable therapeutic targets. If we look beyond the allure of biomedical application, I suspect that scientists in related fields are less enthusiastic about this approach.

Behavioral ecologists and anthropologists adopt a view of feeding and energy flux through organisms (Fig. 1) in which the animal and its behavior are a complex interaction among many environmental variables. Every living species, in particular hominids, has survived periodic food shortage and famine [5,6], so our species as a whole is endowed with “thrifty” genes in relation to energy balance. The formal models from these fields view eating as opportunistic and often de-emphasize organismic or physiological factors. Given a modern human environment with many opportunities to eat, together with high quality food, a model such as that in Fig. 1 leads to the conclusion that elevated intake leading to fat storage is inevitable. In our past, it was a necessity for survival: “natural selection. . . favors individuals who can effectively store calories in times of surplus” [7]. These authors add that “Selection could not provide for the eventuality of continuous surplus because, since it had never existed, there could be no obesity and no adaptive disadvantage for those tending to become obese”.

The pace with which the incidence of obesity, including childhood obesity, has occurred in the past 25–50 years may be too rapid to be associated with genomic change, although epigenetic factors may work over a shorter time-course and some polymorphisms will underlie individual differences. These changes in gene expression could affect either physiological or behavioral traits, or both. Obesity and/or the overeating that produces it, with the exception of very rare genetic mutations, is enabled entirely by an “obesigenic” food environment. Indeed, the behavior of some individuals toward food has been likened to addiction [8]. While modern physiological and neurobiological analysis of feeding remains founded on a classic principle of homeostasis or resistance to change, there is now an appreciation that “reward” system(s) can be over-activated by highly palatable food and overwhelm intrinsic homeostatic mechanisms; instead, allostasis [9,10] may be a more appropriate descriptor.

Homeostatic systems at their core are a regulated set of physiological variables or derivatives such as body weight. These systems can be revealed in controlled laboratory experiments in animals. One of the key behavioral concepts behind homeostasis is the meal: Le Magnen [11] was the first to measure and make physiological interpretation of free feeding patterns in rats. Observations like this led Smith [12] to advocate that the study of meals (*viz* their size and frequency) is *the* fundamental problem facing the behavioral neuroscience of feeding. Smith further proposed that there are both direct and indirect controls of meal size. Direct controls are the physiological changes that occur as food is consumed, such as changes in a variety of hormonal and visceral nerve signaling to the brain, whereas indirect controls are factors that modulate the sensitivity of the brain to those direct signals. These latter include environmental and organismic (e.g. deprivation state) variables. If that is true, then why has average portion size increased as people have become more obese? Although focus on when and how much is eaten at meals is an important area for analysis, Fischler and Masson [13] present an alternative perspective, namely that the disintegration of structured meals is a contributing factor to obesity. The purpose of this paper is to examine from empirical and evolutionary perspectives the significance of meals compared with non-meals. For convenience, we will treat non-meals as a single category – snacking – although this is almost certainly an oversimplification.

2. Organization of feeding in non-human primates and pre-agrarian humans

2.1. Non-human primates

Relatively detailed analysis of feeding has been performed in non-human primates in the wild as well as under laboratory conditions. In the wild, non-human primates forage extensively in groups, use primitive tools (e.g. to open nuts), engage in food sharing, but do not accumulate food. Most of their food items are small (e.g. fruits, leaves, insects, small

mammals): they have no technology for transporting these items. All of their feeding is opportunistic – an immediate consequence of locating food – and is literally hand-to-mouth. Social hierarchies may in part determine access to food [9,14,15].

Altmann [16] analyzed feeding bouts of wild howler monkeys, where a bout was defined as continuous physical contact with one food type. For all foods examined, eating within bouts was well-described by two parameter Weibull functions which describe the probability of continuing physical contact with food in time sampling interval $(n + 1)$ given that it occurred in interval (n) . As n increases, the probability declines in an orderly manner. This does not differentiate meals from snacks without imposing an arbitrary criterion. Whenever an animal stops a bout of eating of commodity A, the latency with which it may start a bout of eating commodity B will depend not only on the attractiveness (palatability) of B relative to A but also on the proximity of the two food sources and factors such as conspecific competition and risk of predation. Thus, the inter-bout interval (eventually an inter-meal interval) may be determined primarily by the environment. In the laboratory, most of these factors usually are absent or highly controlled/predictable.

Foltin [17] measured meal patterns of young adult baboons in conditions designed to emulate foraging. They were housed individually and performed operant responses (on two levers) to obtain food. One lever was appetitive so that a minimum of 30 min elapsed between the first response and a final response that activated a second (consummatory) lever. A single food item (1 g banana flavored monkey pellet, 3.3 kcal) was delivered for every 10 presses on this second lever (*viz* a fixed unit price FUP or ratio of 10). Whenever 10 min elapsed without a response on the consummatory lever, it was inactivated and a new foraging cycle was required for access to food. Thus, a meal was temporally defined by the experimenter. The baboons ate just under 4 meals per day, starting soon after room lights came on, and at about 4 h intervals—quite similar to organized meal times in many humans. This is not a true free-feeding situation: in particular the access cost on the first lever is expected to decrease meal frequency [18] and meal criterion was predetermined. Snacking was effectively precluded by imposition of this access cost which, it should be noted, has dimensions of both elapsed time and effort.

2.2. Hunter-gatherers

Molecular genetic estimates are that human ancestors split from the great apes ~5 million years ago (MYA), but it was not until ~2.5 MYA (lower Pleistocene era) that the first members of the *Homo* species appeared (*Homo habilis*, *Homo ergaster*, *Homo erectus*) along with evidence of more sophisticated tool use. Our most proximate ancestor, *Homo neanderthalis*, existed between 0.3 and 0.03 MYA and modern humans, *Homo sapiens sapiens*, appeared about 0.2 MYA. It is believed that the first large increase in hominid brain size, in *H. erectus* about 2 MYA, coincided with a radical drying of the African climate and a massive transformation of tropical forest into savannah woodlands. This climate change forced adaptations in modal diet and patterns of food acquisition and preparation [15,19]. In particular, the decline in size of post-canine teeth seen in *H. erectus* and continuing to present suggest that less food chewing was occurring due both to alterations in diet source and to preparation by cooking. The function of chewing is to reduce particle size prior to passing the food to the stomach, thereby increasing the surface area available for attack by digestive enzymes and the rate of gastrointestinal processing [20]. Modern diets require minimal chewing and so, unlike in our distant ancestors, this is no longer an obligatory rate limiting step in ingestion and digestion.

There is no evidence for a food acquisition model other than hunter-gatherer prior to primitive agriculture some 0.01 MYA. At that time, some populations became increasingly managers of food resources while others remained hunter-gatherers, or a hybrid [21]. Some

relatively pure populations of hunter-gatherers still exist today although most are affected by modern society. Winterhalder [22] has described four defining features of these populations, of which the most important for the present discussion is underproduction of food and absence of material accumulation. There is no evidence of food storage for over 90% of hominin history, through *H. neanderthalis*, whereas a wide range of food storage strategies have evolved with *H. sapiens*. These strategies are dictated entirely by the environment—the types of foods present and their seasonal availability. For example, peoples indigenous to Arctic regions have a diet almost entirely of animal source foods, and so preservation of meat garnered in the summer has been pivotal to their survival during the harsh winter. In contrast, peoples indigenous to equatorial regions have abundant fruits and grasses with small seasonal variability, and their tendency to preserve and store food is much less developed. No single set of strategies can be considered better or more adaptive than another [23]. In contrast to apes, most hunter-gatherers were and are central place foragers: they have a hub (e.g. village) to which the benefits from hunting and gathering are transported [22,23]. If food storage occurred at a central location, there would have to be rules for when and how much was disbursed, by and to whom. This process would have imparted a meal structure of sorts, either at family or community levels, and the extent to which a central food store was not raided “illegally” may be an early manifestation of dietary restraint [9].

During the last 100 years, several studies of the last hunter-gatherer populations were made, and led to some general conclusions [7]. First, there is wide variation in the food habits of the various populations that reflect, in part, different indigenous food sources. The term hunter-gatherer does not imply any set of behaviors, but rather the extraordinary adaptiveness of these populations. Second, hunter-gatherer populations always experience periodic food shortages or famine; this may be seasonably predictable or due to unforeseen circumstances [5,6]. Robust feeding and accumulation of fat during times of surplus are crucial behavioral and physiological capacities for most if not all species. Third, hunter-gatherers typically spend only 3–4 h per day foraging: they have been characterized as the original affluent society and, paradoxically, the “advance” of agriculture was sometimes associated with poorer nutrition [5]. Energy expenditure of hunter-gatherers is not extreme: their average metabolic rate has been estimated to be $<2\times$ basal [24]. One of the strategies by which this is accomplished is that when food is plentiful they forage over a large area and are very selective eaters, but when food is scarce they are less selective and forage in proximate areas resulting in energy savings. In contrast to a prevalent view that modern humans expend much less energy in physical activity than their ancestors, these data suggest this discrepancy may not be as high as might be imagined.

Brown and Konner [5] review data showing at a population-wide level that until very recently females carried substantially more body fat than males, especially in subcutaneous depots. This has been related to reproductive success in an energy-uncertain environment: the cost of gestation is ~ 300 kcal/day and lactation is higher at ~ 500 kcal/day early postpartum up to ~ 1000 kcal/day at 1 year. Brown and Konner [5] suggest that 15–20% of body weight as fat would be a suitable buffer against food shortage for reproductively active women. Many modern epoch hunter-gatherers breastfeed their infants for several years, and they do not become pregnant again until they have finished nursing the previous infant [6]. Brown and Konner [5] present ethnographic evidence that, in at least 80% of 58 primitive societies surveyed, plumpness and large hips and legs were considered markers of female beauty. Such beauty would not occur without diversion of food resources. Perhaps women were better able to replenish body stores in times of plenty, and more speculatively may be susceptible to offers of “extra food”—perhaps the analog of dessert or snacks in today’s world. If true, this would occur despite the fact that the principal female gonadal hormone, estradiol, decreases food intake in laboratory settings. The large sociocultural basis for this sex difference also should be emphasized: until ~ 200 years ago, obesity was a sign of health

or wealth and was much more prevalent in the rich. This remains the case in countries with lower average wealth and incidence of obesity, but in affluent countries such as the USA it is the lower socioeconomic classes that are more obese and the difference tends to be greater in females than males. In these cases, food security may be an additional issue leading to the accumulation of exogenous as well as endogenous stores [25].

The view of the hunter-gatherer as a central place forager does not discount the likelihood that some fraction of foraged food was eaten at the time it was encountered (*viz*, snacking). This might have been especially true in children who were included in gathering from an early age—and some amount of snacking was likely to have been tolerated. The much more recent advent of agrarian societies has probably sharpened the rules of meal structure. The critical aspect of this argument is that meals are NOT an intrinsic biological property of *H. sapiens*, but are instead are a product of social and economic imperatives.

3. Social structure and eating

3.1. The significance of meals

The previous section ended with the perhaps controversial suggestion that meals and meal patterns may not be physiologically or intrinsically programmed, but are instead sociocultural conveniences that served adaptive functions such as food sharing and socialization. The more recent developments of job specialization and token economies, in which some individuals are doing daily jobs unrelated to food acquisition and instead earn goods or tokens that they can exchange for food, led to additional rules about when a workforce could and could not interrupt work to eat. There have been and continue to be substantial cultural differences in this regard [13]. But as with hunter-gatherers, no one pattern (of meals) is obligate.

Fischler [13] examined food patterns in late 20th century “Western” human societies. Two of the nations that he studied, the USA and France, seem to occupy opposite poles of a spectrum. In France, meals remain a strong social organizing force, both in the home and when eating out. In the USA, a significant amount of eating occurs outside of formal meals and often in solitude. Fischler also notes that regions with social geography similar to France have highly organized social eating etiquette and quite low incidences of obesity, while regions with more individualized and less rule-guided eating have the highest rates of obesity. It is argued that this “anomie” – a breakdown of social rule – may be enabling obesity [13]. This is a correlational argument that perhaps would not satisfy a natural scientist, but it does provide a focal point for thinking about how or why obesity has higher incidence in some post-industrial and relatively affluent nations but not in others. Obviously, there may be other factors including the relative cost of food and different preferred foods, such as social facilitation of eating [26]; I will focus on the direct environmental factors.

3.2. Control of meal size

The control of meal or portion size is a major concern, because people tend to eat all of what they are served or self-served, and factors such as plate or utensil size have a significant effect [27,28]. In the USA, portion sizes have doubled in the past 20 years, driven by a free market economy and the fact that the food ingredients are only a very small part of the cost to the consumer. It costs very little more to serve a large compared to a small portion or meal, and restaurant patrons may feel they are getting more for their money if they buy from the vendor with the largest portion size. Thus, to maintain market share, competing restaurants may be engaged in a battle of escalating portion size. When confronted with the fact that large portions are fueling obesity, the corporate defense is that people have the choice to eat only part of what they are served. While that is true, most people evidently are unable to exercise the requisite dietary restraint. It seems instead that a type of opportunistic

feeding is at work: “if it’s there, eat it because that’s the biological program”. At the extreme, restaurants with all you can eat fixed price menus let the consumer set their own meal size. Even in this context, portion size may be influenced by this social milieu: if everyone is selecting and eating large portions, the likelihood for another individual to conform by also taking a large portion will be high.

3.3. Snacking

These considerations show that meal size is not under strong biological control. What about the second facet of overeating, increased snacking? In the USA, food has become ubiquitous, often in conjunction with other American passions such as spectator sports and automobiles. Most gas stations now sell food or snacks, car repair shops or washes have food machines, and every car is now equipped with places to put food or drink, often calorie-laden. In fact, any time people are sitting around – often alone – feeding is facilitated. More insidiously, much of the time spent at our computers while engaged in non-workplace activities (gaming, social media) are times for snacking and, in part to accommodate this, some fast food delivery restaurants now operate all night. Of course, we cannot blame the restaurants for enhancing their business –they are catering to a consumer demand for snacking. Fischler might agree that this is a manifestation of the anomie of eating. I go further and suggest that the loosening of social restraints reveals an underlying and biologically natural opportunistic or hunter-gatherer mode of eating out of which meals were developed as social necessities to overcome the disorder of eating from hand-to-mouth. Is there any evidence to support this suggestion that snacking may be the biologically natural mode of eating? This evidence would not be found in archaeological or ethnographic records, so to answer this I will turn to laboratory and mainly rodent studies. The skeptical reader may argue that a rodent may be incapable of hunter-gatherer decisions, and at one level that is certainly true; what I will show in the next section is that rodents do make simple food decisions and it is legitimate to study those to inform our understanding of human behavior, but without explicitly invoking the term “animal model”.

4. Laboratory rodent studies

4.1. Adaptation of meal frequency and size

One of the important advances in the laboratory study of food intake was the recording of spontaneous meal patterns in laboratory rats by Le Magnen and Devos [11]. He categorized rats’ feeding into episodes (meals) and applied temporal criteria for separating one meal from the next. Such criteria have been questioned and modified over the years, but the fundamental idea that a continuous temporal stream of essentially digital events (*viz* taking food or not taking food in each appropriately small time interval) can and should be organized into meals has not been questioned [29]. As a Frenchman, Le Magnen lived in a society and epoch in which meals were highly structured social events and fast food had not yet made an appearance. The fact that *ad libitum* fed rats took on average 10 meals per day of standard grain-based food was taken to be a reflection of the physiological make-up of the rat. And that view persists today. In general, behavioral neuroscientists try to “reverse engineer” brain systems from behavior: but if the behavior is inaccurately conceived or described, there will be a critical flaw in that analysis.

One of the voices of opposition to the “meal dogma” was that of George Collier. In a seminal paper, Collier et al. [30] showed that the number of meals taken per day by rats was determined almost exclusively by the cost of access to that meal and not by the unit price once food was reached. Meal size was reciprocally determined by the meal number and not by any internal regulator of meal size (Fig. 2). Collier went on to show this effect in several species, my laboratory has extended this to mice [31–33], and this is consistent with the

earlier discussion (Section 2) of Foltin's [17] result on meal number in primates using a high access cost. At a high access cost, rats turn into 2 meal per day eaters, quite different from Le Magnen's ad lib pattern. In Collier's case, and in our mice, the cost (in responses on a device such as a lever) is only a few minutes of responding. We believe, consistent with Collier, that both 2 and 10 meal patterns of feeding (and all of the intermediate steps) are natural for a rodent—they reflect optimal or near-optimal solutions of episodic fueling in different environments. In accordance with a common nomenclature of nutritionists and ecologists, the 10 meal per day rat may be better viewed as a "grazer" or snacker rather than a true meal eater.

4.2. Of mus and homo

There is a very large discrepancy in ad libitum meal numbers reported in the relatively few published studies using mice [33]. When this analysis was first made, I suggested that differences in the microenvironment of feeding (e.g. height of the feeder, type of food) might be responsible; this could be articulated more generally as subtle differences in the effort to procure food. In the operant behavior situation that we have used in my lab, mice work for 20 mg pellets of nutritionally complete food and we find that meal number is very sensitive to the temporal meal-defining criterion applied [31,32]. In part, that is because some of the feeding episodes, especially at night, have relatively low local eating rates separated by significant pauses, hence the sensitivity to criterion. A typical pattern of eating is shown in Fig. 3: this appears to be more a pattern of grazing rather than meal taking, and so forcing the analysis of data into meals may not be a true reflection of the intrinsic organizational unit(s) of behavior. The pattern shown in Fig. 3 is completely consistent with a detailed analysis of home cage activities in mice by Tecott and his co-workers [34]: mice are almost continuously active for several hours at a time during the night, and feeding occurs only as short bouts within that prolonged activity period. Given this propensity to graze, at least in mice for part of the night, we asked what would happen if we forced mice to become meal eaters, perhaps recapitulating the socialization of eating in man.

In this protocol, food access was restricted to a fixed number of opportunities per day (4, 8, or 16) spaced evenly between late afternoon and early morning to emulate the time at which mice normally do all of their eating. The duration of access was adjusted reciprocally to the number of opportunities such that all groups received a total of 160 min access in a 24 h period (Fig. 4). Access was signaled by a light above a nose poke manipulandum, and mice then had the opportunity to earn food pellets at either low or high fixed unit price (FUP: 2 or 25 responses in separate study phases). Three findings are of note. First, the overall intake was the same in all 3 opportunity groups, and was ~50% lower at FUP25 than at FUP2. This is a significantly bigger drop in intake at FUP25 compared with FUP2 than the small decline we have observed at the same costs under continuous access conditions [31]. Second, the 16 and 8 opportunity groups took food in only ~50% and 75% of all opportunities, respectively. Thus, at FUP25, mice electively decreased intake rather than eat in all of the opportunities. Last, even at the relatively extreme condition of 4 opportunities and FUP25, mice spent only a fraction of each meal time actually responding and eating at high rates. The maximum meal size observed in this protocol was ~1 g, but in other studies using palatable desserts we find non-deprived mice can eat ~2 g in 30 min [35]. It appears that calories consumed, time since the last meal, and overall intake do not fully account for meal sizes when mice are forced to eat meals. At even moderate costs the mice self-restrict because of the imposed meal structure, and relatively independently of organismic variables such as body mass or its derivative signals.

5. Quo vadis omnivores?

A decade ago, in an insightful summary of the career contributions of George Collier, Smith [36] noted that Collier's analysis "emphasized feeding patterns as strategies adopted to deal with ecological challenges rather than as expressions of metabolic repletion and depletion" and that "Collier's robust and quantitative behavioral results are ripe for physiological analysis". Implicitly, Smith [36] and more recently Power and Schulkin [9], while acknowledging that meal patterns per se are not very meaningful tools with which to study physiology, nonetheless anchor their physiological correlates in controls of meal size. Smith [36] argued that one of the critical gaps in knowledge omitted from Collier's works is the time course with which animals adapt their feeding patterns as the environment changes. In our own studies, we find that adaptations are often complete within one 24 h cycle, and this is consistent with earlier work by Raslear et al. [37]. This might seem rapid to a typical operant behaviorist who waits weeks or months for a behavior to stabilize, but it would not be surprising to a behavioral ecologist who might argue that when the environment changes behavior has to change quickly: slow adapters may not survive. To stay within a framework of direct and indirect controls of meal size, then it is parsimonious to focus on (at least) two types of indirect controls—those that work over a very short time frame (minutes to hours) and those that work over a longer period (hours to weeks). Physiological depletion of energy stores would be a long term modulator, and these are fairly easy to manipulate in the laboratory. The short term modulators include chemical factors like taste but also environmental events such as feeding opportunities. One of the ideas I have woven throughout this paper is that humans are opportunistic foragers and eaters. The sight or smell of food is biologically programmed to grasp our attention—an instantaneous and indirect control that requires an instantaneous decision on whether to eat or not to eat (or buy). The food industry preys upon this basic biological mechanism to draw us to their products.

Power and Schulkin [9], in their insightful analysis of the evolution of obesity, consider both health-related and sociocultural costs of obesity. Consistent with our view, they emphasize that obesity is a natural product of today's obesogenic food environment. They argue that there are many paths to obesity and likewise there will be many approaches to prevent or reverse obesity. Health care costs are consuming a rapidly increasing fraction of gross domestic products of free market economies, much of the increase coming from debilitating obesity-related problems such as diabetes, cancer, and stroke. This is an unsustainable trajectory. Treatment of obesity is indeed urgent but, from our foregoing analysis and extrapolating from Galbraithian economics, overconsumption is a consequence of a society that becomes affluent by artificially stimulating demand in excess of need. The path ahead for the behavioral scientist, then, must include an acute awareness of the environmental factors that currently will surely overwhelm most if not all physiological inhibitors of eating that we can devise. That is, physiological controls can be effective in conditions that enable them to be operative; unless and until those conditions are met, the translation of research in the field will be marginal.

Finally, to return to our honoree, it would be idle for me to speculate what line of research Phil Teitelbaum might choose if he were entering a food motivation laboratory today. I am sure he would hold true to one of his tenets that he told me countless times during his years at UF (and eventually I heard): to wit, a reductionist approach to a problem without immediate resynthesis is an empty endeavor. This has certainly had an influence on my evolution as a scientist and the same principle was passed to younger generations via the undergraduate course entitled "Integrative Physiological Psychology" that Phil taught for many years. *Te desidero*.

Acknowledgments

The empirical research from my laboratory described in this article was supported by NIH grant 1RO1 DK064712. I thank Deniz Atalayer and Kimberly Robertson for their helpful comments and suggestions during the preparation of this manuscript.

References

1. Stellar E. The physiology of motivation. *Psychol Rev.* 1954; 61:5–22. [PubMed: 13134413]
2. Kennedy GC. The role of depot fat on the hypothalamic control of food intake in the rat. *Proc R Soc Lond B: Biol Sci.* 1953; 140:578–96. [PubMed: 13027283]
3. Mayer J. Glucostatic mechanism of regulation of food intake. *New Engl J Med.* 1953; 249:13–6. [PubMed: 13063674]
4. Speliotes EK, Willer CJ, Berndt SI, Monda KL, Thorleifsson G, Jackson AU, et al. Association analyses of 249,796 individuals reveals 18 new loci associated with body mass index. *Nat Genet.* 2011; 42:937–48. [PubMed: 20935630]
5. Brown PJ, Konner M. An anthropological perspective on obesity. *Ann N Y Acad Sci.* 1987; 499:29–46. [PubMed: 3300488]
6. Pennington, R. Hunter-gatherer demography. In: Panter-Brick, C.; Layton, RH.; Rowley-Conwy, P., editors. *Hunter-gatherers: an interdisciplinary perspective.* Cambridge: University of Cambridge Press; 2001. p. 170-204.
7. Gaulin, SJC.; Konner, M. On the natural diet of primates, including humans. In: Wurtman, RJ.; Wurtman, JJ., editors. *Nutrition and the brain.* Vol. 1. New York: Raven Press; 1977.
8. Gearhardt AN, Grilo CM, Dileone RJ, Brownell KD, Potenza MN. Can food be addictive? Public health and policy implications. *Addiction.* 2011; 106:1208–12. [PubMed: 21635588]
9. Power, ML.; Schulkin, J. *The evolution of obesity.* Johns Hopkins University Press; 2009.
10. Sterling P. Allostasis: a model of predictive regulation. *Physiol Behav.* 2011 [Epub June].
11. Le Magnen J, Devos M. Parameters of the meal pattern in rats: their assessment and physiological significance. *Neurosci Biobehav Rev.* 1980; 4(Suppl 1):1–11. [PubMed: 6927706]
12. Smith GP. The controls of eating: a shift from nutritional homeostasis to behavioral neuroscience. *Nutrition.* 2000; 16:814–20. [PubMed: 11054585]
13. Fischler, C.; Masson, E. *Manger: Français, Européens et Américains face à l'alimentation.* Paris: Odile Jacob; 2008.
14. Foerster S, Cords M, Montfort SL. Social behavior, foraging strategies, and fecal glucocorticoids in female blue monkeys (*Cercopithecus mitis*): potential fitness benefits of high rank in a forest guenon. *Am J Primatol.* 2011; 73:870–82. [PubMed: 21495049]
15. Hohmann, G. The diets of non-human primates: frugivory, food processing, and food sharing. In: Hublin, J-J.; Richards, MP., editors. *The evolution of hominin diets: integrating approaches to the study of palaeolithic subsistence.* Springer; 2009. p. 1-14.
16. Altmann, SA. *Foraging for survival.* Chicago IL: University of Chicago Press; 1998.
17. Foltin RW. Tasting and wasting behavior in non-human primates: aberrant behavior or normal behavior in times of plenty. *Physiol Behav.* 2006; 89:587–97. [PubMed: 16942783]
18. Collier G. A functional analysis of feeding. *Adv Stud Behav.* 2005; 35:63–103.
19. Ungar PS, Grine FW, Teaford MF. Diet of early homo: evidence and a new model of adaptive versatility. *Ann Rev Anthropol.* 2006; 35:209–28.
20. Lucas, PW.; Sui, Z.; Ang, KY.; Tan, HTW.; King, SH.; Sadler, B., et al. Meals versus snacks and the human dentition and diet during the Paleolithic. In: Hublin, J-J.; Richards, MP., editors. *The evolution of hominin diets: integrating approaches to the study of palaeolithic subsistence.* Springer; 2009. p. 31-41.
21. Lee, RB.; Daly, R. Foragers and others. In: Lee, RN.; Daly, R., editors. *The Cambridge encyclopedia of hunters and gatherers.* Cambridge: Cambridge University Press; 1999. p. 1-19.
22. Winterhalder, B. The behavioural ecology of hunter-gatherers. In: Panter-Brick, C.; Layton, RH.; Rowley-Conwy, P., editors. *Hunter-gatherers: an interdisciplinary perspective.* Cambridge: University of Cambridge Press; 2001. p. 12-38.

23. Rowley-Conwy, P. Time, change and the archaeology of hunter-gatherers: how original is the 'Original Affluent Society'? In: Panter-Brick, C.; Layton, RH.; Rowley-Conwy, P., editors. *Hunter-gatherers: an interdisciplinary perspective*. Cambridge: University of Cambridge Press; 2001. p. 39-72.
24. Jenike, MR. Nutritional ecology: diet, physical activity and body size. In: Panter-Brick, C.; Layton, RH.; Rowley-Conwy, P., editors. *Hunter-gatherers: an interdisciplinary perspective*. Cambridge: University of Cambridge Press; 2001. p. 205-38.
25. Bartness TJ, Keen-Rhinehart E, Dailey MJ, Teubner BJ. Neural and hormonal control of food hoarding. *Am J Physiol Regul Integr Comp Physiol*. 2011; 301:R641–55. [PubMed: 21653877]
26. de Castro J. The control of food intake in free-living humans: putting the pieces back together. *Physiol Behav*. 2010; 100:446–53. [PubMed: 20450867]
27. Wansink B. From mindless eating to mindlessly eating better. *Physiol Behav*. 2010; 100:454–63. [PubMed: 20470810]
28. Wansink B, Payne C, Shimizu M. Is this a meal or a snack? Situational cues that drive perceptions. *Appetite*. 2010; 54:214–6. [PubMed: 19808071]
29. Tolkamp BJ, Allcroft DJ, Barrio JP, Bley TAG, Howie JA, Jacobsen TB, et al. The temporal structure of feeding behavior. *Am J Physiol Regul Integr Comp Physiol*. 2011; 301:R378–93. [PubMed: 21525177]
30. Collier G, Hirsch E, Hamlin P. The ecological determinants of reinforcement in the rat. *Physiol Behav*. 1972; 9:705–16. [PubMed: 4655163]
31. Atalayer D, Rowland NE. Meal patterns of mice under systematically varying approach and unit costs for food in a closed economy. *Physiol Behav*. 2009; 98:85–93. [PubMed: 19394352]
32. Chaney MA, Rowland NE. Food demand functions in mice. *Appetite*. 2008; 51:669–75. [PubMed: 18590781]
33. Vaughan CH, Rowland NE. Meal patterns of lean and leptin-deficient obese mice in a simulated foraging environment. *Physiol Behav*. 2003; 79:75–9.
34. Goulding EH, Schenk AK, Juneja P, MacKay AW, Wade JM, Tecott LH. A robust automated system elucidates mouse home cage behavioral structure. *Proc Natl Acad Sci USA*. 2008; 105:20575–82. [PubMed: 19106295]
35. Rowland NE, Robertson KL. Effect of two types of environmental enrichment for singly housed mice on food intake and weight gain. *Lab Anim*. 2005; 34:29–32.
36. Smith GP. The evolution of an operant psychologist. *Appetite*. 2002; 38:166–72. [PubMed: 12027379]
37. Raslear TG, Bauman RA, Hirsch SR, Shurtleff D, Simmons L. Rapid demand curves for behavioral economics. *Anim Learn Behav*. 1998; 16:330–9.

Fig. 1.
The nutritional ecology of feeding (adapted from [24]).

Fig. 2.

The reciprocal relationship between meal size and number in rats as the foraging (procurement) cost is varied. Derived from data in [30].

Fig. 3.

Numbers of 20-mg nutritionally complete food pellets taken by a single mouse in each 15 min interval through a representative 23-h test session (night period indicated by black bar at top of panel). The mouse was housed in a standard behavior test chamber, and 10 nose poke responses were the fixed cost for each pellet. From other studies, each nose poke takes 0.5–1.0 s to perform and each pellet takes ~10 s to handle, chew and swallow.

Fig. 4.

Feeding in mice constrained to eat discrete meals. The overall design of the protocol is shown in the top panel, with mice given 4, 8, or 16 opportunities per day (last 4 h of day and the night period), 160 min total. The bottom panel shows group means in each 5 min bin within every other meal opportunity for the 8 opportunity group at a pellet price FUP = 2. Note that the first meal has a high initial feeding rate that is not sustained, and that the last meal is very small.