

## A Contrarian View of the Wisdom of the Body as It Relates to Dietary Self-Selection

Bennett G. Galef, Jr.  
McMaster University  
Hamilton, Ontario, Canada

The history of studies of dietary self-selection in cafeteria-feeding situations is reviewed briefly. The evidence is not consistent with the view that replete animals can reliably compose a nutritionally adequate diet from an array of food in a cafeteria situation. Similarly, the evidence is not consistent with the view that when deficient in a nutrient (excepting the case of sodium and, perhaps, of phosphorus), animals can reliably select a nutritionally adequate diet when it is present among several deficient diets. General acceptance of the view that omnivores can easily self-select nutritionally adequate diets is attributed both to overreliance on theory and to lack of critical attention to data. The adequacy of functional arguments suggesting that omnivores must be able to self-select nutritionally adequate diets is questioned.

Some 85 years ago, research biochemists and applied nutritionists were locked in “bitter controversy” (Stone, 1942, p. 66). Their disagreement concerned the relative abilities of animals and of scientists to compose adequate diets from a cafeteria of foods of varying nutritional content. Jordan (1906, p. 279) argued the scientific position both with conviction and in language accessible to any layman:

Once in a while someone talks wildly about leaving food valuation to the “old cow.” It is considered sometimes a telling argument against the chemist’s wisdom to declare that he and the old cow do not agree. Certainly the cow knows better than the chemist what she likes to eat, and it is little use to offer her foods she does not relish. Even a chemist knows that. If, however, a dozen commercial feeding stuffs were spread around on a barn floor it would be much safer to trust an agricultural chemist, especially one experienced in stock feeding, to select a ration than any cow ever grown—Holstein, Ayrshire, Jersey, long-horned, dishorned, or what not. The cow would probably get at the corn meal and stay with it until well on the way to a fatal case of indigestibility. Her judgment is just about as good as that of a child with a highly cultivated “sweet tooth.”

Crichton-Browne’s (1910, p. 22) remarks are illustrative of the position of the applied nutritionists:

The lower animals select with unerring precision, as long as they are in a natural environment, from the materials around them those best fitted to their wants, and they do this by instinctive discernment inherited from a long line of naturally selected ancestors, while they are checked in their consumption by a sense of repletion of coeval origin. We unhesitatingly infer that the articles

they choose are, of all the nutrient materials accessible to them, those best adapted to the special needs of their economy, and that their consumption of them is proportioned to their needs for the time being.

This lively debate motivated the free-choice experiments with pigs (Evvard, 1915), cattle (Nevens, 1927), chickens (Dove, 1935; Pearl & Fairchild, 1921), rats (Harris, Clay, Hargreaves, & Ward, 1933; Kon, 1931; Osborne & Mendell, 1918), and human infants (Davis, 1928, 1939), which were precursors to the definitive cafeteria-feeding studies of total dietary self-selection carried out by Richter and his co-workers in the late 1930s and early 1940s.

The results of Richter’s experiments, completed some 50 years ago, were largely responsible for resolution of the argument between biochemists and practical nutritionists, a resolution that was to prove as durable as it was surprising. The surprise lay in the fact that the scientists lost the debate as to whether they or Jordan’s (1906) “old cow” would be better at composing health-promoting diets by selecting foods from an array of ingredients, each of which provided insufficient nutrient to sustain health.

Richter (Richter, Holt, & Barelare, 1938) provided evidence that the selections made by need-free rats from a cafeteria of relatively purified foodstuffs led to growth as rapid as that seen in control animals maintained on the then-standard McCollum diet (McCollum was an eminent biochemist of his day) despite the fact that cafeteria-fed rats ate 18.7% fewer calories than did control rats.

One could infer from Richter et al.’s (1938) data, as Richter implicitly did, that, in Jordan’s (1906, p. 279) words, “any cow ever grown—Holstein, Ayrshire, Jersey, long-horned, dishorned, or what not” was very accomplished at self-selecting a balanced diet and, consequently, that a biochemist would have to be sharp indeed to match her performance.

To explain the great success of their rats at cafeteria feeding, Richter et al. (1938) proposed that animals had “a special appetite not only for salt and sugar, but also for protein, carbohydrate, sodium, calcium, phosphorus, potassium, and the vita-

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Correspondence concerning this article should be addressed to Bennett G. Galef, Jr., Department of Psychology, McMaster University, Hamilton, Ontario, Canada L8S 4K1.

mins" (p. 744). Over the years, it has become clear that, although as Richter proposed, animals do have some special appetites, these can explain response only to those deficiency states in which animals can both directly detect sensory qualities correlated with a nutrient (e.g., sugars, salt, phosphorus, fat, and sodium) and respond to deficiency with appropriate changes in appetite (e.g., water, phosphorus, and salt). Special appetites do not provide a general solution to the problem of food selection in cafeteria situations (Rozin, 1976).

In the decades since Richter's classic experiments on total dietary self-selection by rats, research has shown that animals can associate the flavors of foods with their postingestional consequences, both negative (Garcia & Hankins, 1977) and positive (Booth, 1985). It has also been demonstrated that rats exhibit potentially adaptive changes in their unconditioned responses to novel foods when they are either poisoned or made vitamin deficient (Rozin, 1967, 1968).

Changes in response to novelty and learning about consequences of ingestion provide alternatives to special appetites that might lead animals to select nutritionally adequate diets in cafeteria situations. Still, there is general agreement in the literature that, as Rozin and Schull (1989, pp. 529–530) stated in a recent review, "We cannot yet explain how rats successfully mix balanced diets in the cafeteria feeding situation."

The apparent ability of animals to self-select nutritionally balanced diets, taken together with scientists' inability to explain how they do so, suggests a failure in understanding how animals choose foods to eat. However, as discussed later, current understanding of the mechanisms of food selection by animals may be more complete than is generally recognized.

The central argument of this discussion is that although sometime during the 1940s members of the scientific community abandoned their initial stand in the debate as to the relative competence of scientists and of cows to compose nutritionally adequate diets, there was no need for them to have done so. It is my contention, first, that animals, whether nutritionally replete or nutrient deprived, are in fact not particularly adept at selecting a balanced diet when offered a number of alternatives of varying nutritive value, and second, the data have never indicated otherwise.

Consider Lát's (1967) review of 17 studies of dietary self-selection by rats in Richter-style cafeteria-feeding situations. Lát concluded that in 8 of these experiments (including Richter et al.'s 1938 classic), rats succeeded in self-selecting diets that produced normal growth but that they failed to do so in the remaining 9 studies (see also Epstein, 1967).<sup>1</sup> Although attention historically has focused on the 8 successes, the results of even a descriptive meta-analysis such as Lát's are not consistent with the view that rats can reliably self-select adequate diets when given opportunity to do so.

If my argument were based on the simple observation of a rough equality in the number of successes and failures of self-selecting rats, it could, perhaps, be ignored, but the matter is more complex. Failures to compose an adequate diet from a cafeteria of foods are informative in themselves. Such failures provide prima facie evidence of an inability of animals to respond adequately to the demands of particular feeding situations. Thus, the nine failures reviewed by Lát provide evidence

of nine situations in which rats could not select a nutritionally adequate diet.

Success at self-selection is more difficult to interpret. Success in a cafeteria-feeding situation does not provide complementary evidence of a meaningful ability of animals to self-select adequate diets. As an anonymous author suggested in *Nutrition Reviews* in 1944:

The fact that an animal selects foods from a series of containers and grows normally is not proof that he selects those foods on the basis of need because under most experimental conditions, if the animal ate only at random, his needs would be well supplied. . . . Statistical tests of significance should be applied to all self-selection data. (p. 203)

As the quotation makes clear, the issue to be resolved is not whether an experimenter can choose foods to offer subjects in a cafeteria that ensure that the subject's flavor preferences directly lead it to ingest a nutritionally adequate mix of foods. Rather, the issue is whether animals have sensory, physiological, or behavioral mechanisms that lead them to select a balanced diet when such selection is *not* assured by the relative palatabilities of the array of foods offered to them.

Potential ambiguity in the interpretation of positive results of self-selection studies is a real problem. Consider Rozin's (1969) innovative investigation of food-sampling patterns by thiamine-deficient rats. Rozin made 10 rats thiamine deficient, feeding them a diet lacking thiamine, and then tested each rat with a choice (for 8 hr/day for 10 days) of four diets, one of which contained thiamine. During testing, 4 of the 10 deficient rats developed preferences for the thiamine-rich food available to them; another 2 of the 10 developed preferences for two of the four diets (one of the two being the thiamine-enriched diet), and 4 rats did not develop preferences for the food containing thiamine.

Optimality theorists will focus on the fact that the glass is almost half filled, that is, that 4 thiamine-deprived subjects solved the problem; skeptics will focus on the 4 subjects that failed to exhibit a preference for the nutritionally adequate diet available to them; others, like the anonymous reviewer of 1944, might ask for statistical comparison of the behavior of thiamine-deprived and control subjects in the choice situation in order to determine whether deficient rats were behaving adaptively or simply selecting foods in accord with their respective palatabilities.

Two examples serve to further illustrate the difficulty in accepting reports of success in self-selection tasks at face value. Secondary sources often cite Wilkins and Richter's (1940, p. 866) summary of Davis's (1928) classic report of "a child [fed in

<sup>1</sup> Richter, Holt, and Barelare (1938) provided their rats with access to a cafeteria containing both multiple sources of protein and a relatively unpalatable carbohydrate (Epstein, 1967). As both Scott (1946) and Lát (1967) have indicated, protein intake is the major determinant of survival and growth of rats in cafeteria-feeding situations. Richter et al.'s choice of foodstuffs was such as to lead to relatively high protein intakes by rats choosing foods on the basis of palatability alone (see Galef & Beck, 1990, for further discussion). Thus, Richter's cafeteria of foods, unlike many others (Kon, 1931; Pilgrim & Patton, 1947; Scott, 1946), was one in which rats were likely to thrive (see Galef & Beck, 1990, for further discussion).

a cafeteria situation] with Vitamin A deficiency [(rickets) who] took large amounts of cod liver oil and *thereby* [emphasis added] caused the deficiency symptoms to disappear." Secondary sources never mentioned in the same connection Davis's (1939, p. 258) later remarks concerning 4 other children in her 1928 study who also had rickets but were not given access to cod liver oil.

No other of the 15 children [in the study] had any cod liver oil . . . or other dietary adjunct at any time during the study and all four of the other cases of rickets were healed in approximately the same length of time as was the first [who had access to cod liver oil].

Nor do secondary sources discuss Richter's finding (Richter, 1942–1943) that more than 95% of young children with no known disease liked the taste of cod liver oil and spontaneously drank substantial amounts of it. Indeed, with few exceptions (Rozin, 1976), and only relatively recently (Galef & Beck, 1990; Story & Brown, 1987), have secondary sources indicated, as Davis herself was well aware, that human infants could self-select an adequate diet only when nutritious, unsweetened foods were offered as choices. As Davis (1939, p. 261) stated, "Self-selection can have no, or but doubtful value, if the diet must be selected from inferior foods." In humans, as in rats (Galef & Beck, 1990), the ability to self-select adequate diets depends on which foods are offered for choice. Provision of an assortment of nutritious, roughly equally palatable foods, rather than an ability to select needed foods, was probably responsible for much of the success of Davis's subjects.

Overmann (1976, p. 221) summarized the famous anecdotal report of Green (1925) concerning bone eating by cows as follows:

In the phosphorus-poor grazing land of South Africa, cattle frequently become osteophagic, or bone eaters, presumably to satisfy their phosphorus requirements . . . when bony materials were not available, the normally herbivorous cattle were even observed to consume live turtles. . . .

The same article (Green, 1925) was summarized (Anonymous, 1944, p. 200) as follows:

[These cattle] had developed the habit of chewing bones. In severe cases, the cattle would chew tin cans and sticks of wood. Thus, no specific appetite for phosphate was evident, but probably only a generalized hunger.

Both reports are factually accurate, yet each leads readers to quite different conclusions concerning the ability of animals to self-select adequate diets.<sup>2</sup>

Contradictory outcomes both within and between studies of self-selection of foods are consistent with the view that the particular foods offered to subjects and individual differences in both food preference and patterns of food sampling are significant influences on success. One should not ask whether rats (or humans) can self-select adequate diets but instead inquire as to the characteristics of choice situations affecting the probability that individuals with differing food preferences will come to eat an adequate diet. In permissive ingestive environments, like those provided by Richter et al. (1938) or Davis (1928), the spontaneous sampling patterns and food preferences of subjects often produce relatively immediate solutions. In less permissive environments, spontaneous sampling and sensitivity to the con-

sequences of ingestion can sometimes lead to solutions (Booth, 1985; Rozin, 1976). In harsh environments, it is very unlikely that animals will ingest needed nutrients (e.g., see Kon, 1931).

Focus on positive outcomes and spectacular possible implications of data (and the complementary ignoring of failures and of prosaic explanations of phenomena) by members of an academic community often characterized by outsiders as overly negative and suspicious is surprising. Its causes are, of course, impossible to know, but I would suggest that the source of the uncritical approach to analyses of studies of cafeteria feeding may lie in too much emphasis on theory and too little scrutiny of data in discussions of dietary self-selection.

As indicated in the introduction to this article, Crichton-Browne (1910, p. 22) was one of many who proposed a process that could produce perfection in diet selection by animals: "Animals select with unerring precision . . . by instinctive discernment inherited from a long line of naturally selected ancestors." Richter et al. (1938, p. 734) provided informal evidence of animals' expertise in dietary self-selection:

The survival of animals and humans in the wild state in which the diet had to be selected from a variety of beneficial, useless, and even harmful substances is *proof* [emphasis added] of this ability . . . to make dietary selections which are conducive to normal growth and development.

Or, as Osborne and Mendel (1918, p. 20) had asserted some years earlier, "The biological evidence of the survival and well-being of innumerable species testifies to the success of their *instinctive* dietary habits."

On such views, laboratory demonstrations of self-selection of superior diets serve only to confirm the existence of abilities that could be logically deduced either from evolutionary theory or from the observation that, in nature, animals secure adequate nutrients for growth and reproduction. There was no perceived need to examine critically laboratory evidence of the ability of animals to self-select nutritive diets; such evidence demonstrated only what theory dictated must be true.

Consequently, when rats failed to self-select an adequate diet in some experimental situation, the failure was often interpreted after the fact, for example by Richter (1942–1943), as resulting from a laboratory artifact of some kind: the use of domesticated animals (although evidence from domesticated animals was acceptable if that evidence conformed to expectation), age-related exhaustion of regulatory functions (although age of subjects was not correlated with success in self-selection; Lát, 1967), or the use of complex natural foods in choice situations (Richter et al., 1938). This last laboratory artifact put Richter and his colleagues in the logically awkward position of arguing that choice among purified dietary components provided a better laboratory analogue of food choice in nature than did choice among natural foods.

On occasion, such theoretically induced bias seems to have

<sup>2</sup> It is irrelevant to the preceding discussion whether cows actually have a specific appetite for phosphorus. Recent evidence (Blair-West et al., 1989) suggests that phosphorus-depleted cows have an appetite for bones but not for inorganic phosphate salts. The point is that the evidence in Green (1925) is ambiguous and could be interpreted as consistent with various theoretical positions.

made it impossible for researchers even to accurately describe their own findings. For example, in a pioneering study, Osborne and Mendel (1918) compared weight gains of pairs of growing, young rats matched for sex and age that were given either a single, complete diet to eat or a choice between two diets: one the complete diet, the other a similar diet either lacking all protein or lacking a specific amino acid. Osborne and Mendel (1918, p. 27) concluded that

although . . . growth was not the maximum that might have been expected, nevertheless nine out of ten rats ate such proportions of the two foods offered in each case to enable them to grow at a nearly normal rate.

The modern investigator would almost surely reach a different conclusion after examining Osborne and Mendel's (1918) data. Both 20 days into the experiment and at its conclusion at 50 days, 9 of the 10 subjects choosing between diets weighed less than did their paired controls, and at 20 days, those 9 subjects weighed on average 80.9% as much as control subjects. Two of 10 subjects offered a choice of foods gained no weight at all for 20 days and trailed their respective controls by more than 30% in weight. Furthermore, 9 of the 10 experimental subjects ate a greater amount of deficient diet in the last 10-day block of the experiment than in the first.

The generally poor weight gains of subjects choosing between one adequate and one deficient diet, their failure to learn to avoid eating deficient diet, and their extreme variability in weight gain would not, today, be seen as "testify[ing] to the success of their instinctive dietary habits" (Osborne & Mendel, 1918, p. 21). Indeed, the data appear to demonstrate the opposite of Osborne and Mendel's (1918, p. 21) conclusion of a "somewhat surprising ability of rats to make selections between two food mixtures of somewhat similar physical character, one of which may be characterized as nutritively inferior. . . ." The basic problem here is, I think, acceptance of special pleading in favor of data supporting a theoretical position and the ignoring, as irrelevant, of data that appear to contradict that theoretical position.

It is, in fact, almost embarrassingly easy to create situations in the laboratory in which rats are unable to develop adaptive food choices. As the number of nutrient-poor foods offered together with a nutrient-rich food increases beyond two, the probability of adaptive food selection falls off rapidly (Harris et al., 1933). As delay to onset of reinforcement contingent on eating nutrient-rich food increases, probability of learning to choose a nutrient-rich food declines (Harriman, 1955; Westoby, 1974; Young & Wittenborn, 1940), and as relative palatability of nutrient-rich foods decreases, probability of learning to eat those foods falls dramatically (Kon, 1931; Scott & Quint, 1946). As noted earlier, only 40% of thiamine-deficient rats choosing among four diets, one of which contained thiamine, managed to clearly identify the thiamine-rich food (Rozin, 1969). Similarly, when Beck and Galef (1989) offered young rats a week-long choice among four different-flavored diets, three of which were both relatively palatable (5% sugar and 5% casein) and protein-poor and one of which was both relatively unpalatable (0% sugar and 20% casein) and protein-rich, 14 of their 18 subjects failed to develop a preference for the protein-rich food and lost weight during the week-long test. Rats deprived of protein

for a week before introduction into the same situation did no better than their protein-replete counterparts at learning to focus their intake on the protein-rich diet (Beck, 1990; Galef, Beck, & Whiskin, in press).

Yet, the argument that natural selection should have produced animals able to redress nutrient deficiencies seems sound. As Crichton-Browne (1910) suggested, members of extant species are indeed descended from a long line of ancestors that should have been selected for their ability to avoid or redress nutritional imbalance. Furthermore, as Richter et al. (1938) pointed out, animals do survive in nature while selecting their own foods. Why, then, is it not safe to assume that animals will exhibit a suite of adaptations evolved to produce avoidance or redress of nutritional imbalance when animals select among foods in the laboratory?

First, consider two arguments relevant to Richter et al.'s (1938) assertion that the survival of animals in nature is evidence of their ability to self-select nutritionally adequate diets.

Members of any species, even those as cosmopolitan in distribution as Norway rats, are not found everywhere within their respective species' ranges. By definition, individuals can survive only in those portions of the environment that provide all resources necessary for life. An area would be devoid of rats if it contained a necessary nutrient only in a form that rats could not learn to eat.

Existence of an omnivorous species in nature tells little about the range of environments in which its members have the ability to self-select nutritionally adequate diets. Persistence of omnivores outside the laboratory shows only that there exist relatively permissive portions of the environment where the behavioral capacities of species members are sufficient to permit development of a dietary repertoire conducive to self-maintenance, growth, and reproduction. In particular, existence of an omnivorous species in nature does not suggest that omnivores in the laboratory should be able to select nutritionally adequate diets from among a cafeteria of purified dietary components.

Second, the fact that many individuals can be observed self-selecting adequate diets in natural circumstances gives no indication of the probability that any given individual will be able to learn to do so. In many species, failure to reach reproductive age is far more frequent than success. Death at weaning, when the pressure to learn to select adequate diets may be greatest (Beck & Galef, 1989), is a common cause of failure to survive. For example, yellow-eyed juncos (*Junco phaeotus*), locally common in southern Arizona, are, obviously, able to find adequate food in natural habitat. However, mortality among juveniles during the 14 days after their parents stop feeding them is 3.9% *per day*, and fewer than 43% of recently independent juveniles survive the first 2 weeks of independent foraging even in years when food is relatively abundant. Recently independent juveniles both select smaller prey with lower energy content than do experienced juveniles and die of starvation because they cannot forage efficiently (Sullivan, 1988, 1989). The existence of juncos in nature provides no evidence that they can learn to select an adequate diet with particular ease.

Last, I consider whether, as Crichton-Browne (1910) suggested, natural selection will necessarily result in animals adaptively specialized to avoid or redress nutrient deficiencies. In a classic, though zealous, critique of the adaptationist program,

Gould and Lewontin (1978) questioned the validity of the strategy of breaking an organism up into constituent traits and then proposing an adaptive story to explain the function of each trait considered separately. Such a strategy may be informative if the traits selected for discussion are, in fact, structures shaped by natural selection for some function. However, the strategy has the potential to mislead if purported traits are not meaningful structures acted upon as functional units by natural selection.

Within such a framework, it is reasonable to ask whether either the ability to avoid or to redress nutritional imbalance is a functional unit upon which natural selection has acted and which selection may have optimized. It may not be.

If introspection is any guide, when an organism becomes ill, it cannot discriminate illness resulting from dietary deficiency from illness resulting from ingestion of a toxin (Rozin, 1968); from ulceration or other organic malfunction; or from viral, bacterial, or parasitic infection. Without deficiency-state detectors, a general strategy for coping with deficiency-induced illness would be of relatively little use; there would be no indication of when to use it.

Illness caused by ingesting a toxin can be redressed only by reducing dietary breadth. Illness caused by nutrient deficiency can be corrected only by increasing dietary breadth. Obviously, a strategy optimizing response to deficiency cannot evolve without a means for differentiating deficiency-induced illness from toxicosis-induced illness, a discrimination that Rozin's (1968) data suggest may be difficult for rats to make.

As the history of the discovery of vitamin-deficiency diseases and their cures by human scientists makes clear (Carpenter, 1986; Guggenheim, 1981), humans lack the ability to distinguish deficiency states from illness having other causes. For example, during the 17th century, scurvy and syphilis were often confused by doctors (Carpenter, 1986), although one is a deficiency disease and the other is not.

Hence, it may not be possible to discover strategies that have evolved in response to nutrient deficiency because such strategies may not exist. Animals may have behavioral strategies evolved for response to perceived illness (malaise is a detectable state), and strategies for responding to malaise may reflect the relative frequencies with which members of a species have experienced illness due to various causes over evolutionary time. There is, however, no way to know a priori which illness-causing agents have predominated in shaping response to malaise. Consequently, there is no way to predict to which types of illness (if any) natural selection has optimized response.

The notion that the processes resulting in avoidance or redress of nutrient deficiency are units optimized by natural selection is a hypothesis worthy of empirical test. Unbiased examination of relevant data suggests that rejection of that hypothesis, rather than its acceptance, may be in order.

In conclusion, it is perhaps relevant to note that the study of dietary self-selection by rats in cafeteria-feeding situations is not the only area of behavioral investigation where one might argue that expectations based on compelling theory may have led to systematic bias in interpretation of data. In this age of optimality models and adaptationist argument, it is easy to forget that, although theory is of great use in guiding the direction of research, data must be examined critically to determine

whether they are, in fact, consistent with the theories that instigated their collection.

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