

THE PHYSICS OF FORAGING

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ABSTRACT

We relate findings in physics to biological processes like foraging. As in physics, the critical attribute of any individual (elementary particle or animal) is the fact that the dynamics of its behavior cannot be defined with certainty because the individual is inseparable from its history. An individual animal's behavior reflects its evolutionary history (e.g., morphology and physiology), its cultural history (e.g., social and physical environment where the individual is reared), and its ongoing interactions with the environment. This does not mean that behaviors occur in an arbitrary fashion. It means only that the behavior of any individual is determined by connections to a larger historical whole. Because we do not know all of these connections precisely, and because their interrelationships lead to emergent properties, the classical notion of cause and effect must be supplemented with notions of self-organization. Ultimately, each individual's behavior is unique, and the process of foraging can be understood only in a dynamic context, in terms of movement, interaction, and transformation.

KEYWORDS

Physics, behavior, evolution, culture, individual, self-organization

INTRODUCTION

In the eighteenth century, Descartes declared physics as the basis of all sciences when he wrote "All philosophy is like a tree. The roots are metaphysics, the trunk is physics, and the branches are all the other sciences." In this paper we consider how incomplete understanding and misconceptions about physics affect our views of biological processes like foraging. We first review beliefs that have governed physics from the seventeenth century (following Capra 1975, 1982), and then relate those ideas to foraging. We draw analogies between foraging and three facets of physics (Newtonian mechanics, quantum theory, relativity theory). We submit that some facets of foraging are predictable (Newtonian), whereas others are relative (relativity) and considerably less predictable (quantum). We use physics as the basis for the analogy because Newtonian mechanics has pervasive effects on our conceptions of reality (i.e., nature is linear and predictable, if we can just discover the rules). This view of physics has been shaken during the twentieth century, especially among physicists who deal with quantum and relativistic processes, which illustrate that life is not necessarily linear or predictable, even if we know the rules. Instead life self-organizes and in the process leads to manifold possibilities for creating new structures over evolutionary time, and for modifying existing structures and creating new modes of behavior during the lifetime of the individual. Our objective is to ponder what can be known about behaviors like foraging, not to synthesize general principles.

PHYSICS AND NATURE

Newtonian Mechanics. Our view of nature today originated in the sixteenth and seventeenth centuries, following the medieval period. The medieval outlook, based on understanding the meaning and significance of nature rather than prediction and control, changed radically at that time. Following revolutionary innovations in physics and astronomy, culminating in the achievements of Copernicus (heliocentric theory of the solar system), Galileo (proof of the heliocentric hypothesis), and Newton (laws related to the heliocentric

universe), the notion of an organic, living, and spiritual universe was replaced with that of a machine.

The science of the seventeenth century was based on the mathematical description of nature advocated by Francis Bacon and the analytical method of reasoning conceived by Descartes. Descartes' view of nature as a perfect machine, governed by exact mathematical laws, was completed by Isaac Newton, who synthesized the works of Copernicus, Galileo, and Descartes. Newton's mathematical conception of the world has had a profound influence on scientific thought throughout the twentieth century.

The Newtonian universe involved a three-dimensional space of classical (Euclidian) geometry. In Newton's words, "Absolute space, in its own nature, without regard to anything external, remains always similar and immovable" (quoted in Capra, 1982). All changes in the physical world were described in terms of an absolute dimension, time, which had no connection with the physical world and flowed smoothly from the past through the present to the future. As Newton wrote, "Absolute, true, and mathematical time of itself and by its own nature, flows uniformly, without regard to anything external" (ibid. 1982).

In Newton's view, God created particles (atoms), the forces between them, and the laws of space and time. Once the universe was set in motion, it continued to run, like a machine, governed by immutable laws. According to this view, all that happens has a definite cause, and the future of any part of the system can be predicted if its state at any time is known. Thus, the world was viewed as a perfect machine, as originally conceived by Descartes.

New Theories. During the nineteenth century, Maxwell's theory of electrodynamics and Darwin's theory of evolution through natural selection revealed that the universe was more complex than imagined by Descartes and Newton. Electric and magnetic phenomena could not be described properly by Newton's model, and thus electromagnetism dethroned Newtonian mechanics as the ultimate theory of natural phenomena. The notion of evolution, which arose in geology, led scientists to the idea that the present state of the earth was the result of natural forces acting over extended periods of time. Lamarck first proposed a theory of biological evolution, which postulated that living beings evolved from earlier forms under the pressure of the environment, and several decades later Darwin presented overwhelming evidence of biological evolution, thus establishing the scientific credibility of the phenomenon. The subsequent development of the theory of evolution through natural selection forced biologists to abandon the conception of the world as a machine that emerged fully constructed from the hands of the Creator. Instead, the universe was pictured as ever changing, but still ultimately knowable and predictable. Thus, Newtonian mechanics remained the basis of science until Einstein initiated two radical trends in thought. One was a new way of looking at electromagnetic radiation, which became characteristic of quantum theory. The other changed views of time and space and was the basis of relativity theory. These advances shattered the tenets of the Cartesian world view and Newtonian mechanics. None of the long-held notions (e.g., solid objects, absolute space and time, strictly

causal nature of physical phenomena, objective description of nature) could conform to the new developments in physics.

Quantum Theory. The concepts introduced by Newton and Darwin were fairly easy to fathom, but the new ideas in physics posed a serious challenge to physicists' ability to understand the universe. Every issue raised in an atomic experiment led to a paradox. Atoms were not solid objects, but instead consisted of vast regions of empty space in which subatomic particles (electrons) revolved around a nucleus (composed of protons and neutrons). Even the subatomic particles were nothing like the solid objects of classical physics, sometimes appearing as "particles" and sometimes as "waves." At the subatomic level, solid objects fade into wave-like patterns of potentialities, not of things, but of associations. Neither the electron or any other atomic "object" has inherent attributes independent of its environment. Thus, the basic "building blocks" of nature appear as a dynamic web of interrelations. It took physicists a long time to embrace these ideas, and to realize that the paradoxes they encountered occurred when they attempted to portray atomic phenomena in classical terms. Once physicists realized the problem, they were able to devise a suitable conceptual framework for quantum theory, one which ultimately fostered a world view characterized by interconnectedness. The universe was no longer seen as a machine composed of autonomous objects, but as a dynamic, indivisible whole whose parts could be understood only as patterns in a cosmic process.

Relativity Theory. Einstein's general theory of relativity dramatically changed our concepts of space and time. According to Einstein, space and time are relative, reduced to the subjective guise of rudiments of the language a specific observer uses to portray natural phenomena. In relativistic physics, one cannot talk about space and time independently. Space-time diagrams have no specific direction of time. There is no "before" or "after" and no linear relation of cause and effect. All events are interconnected, but the relationships are not causal in the conventional sense. These relationships can be expressed mathematically, but they are difficult to describe in everyday language because words refer to our experience of the environment, and relativistic notions of time and space transcend experience.

One of the most important realizations of relativity theory is that mass is a form of energy. In modern physics, mass is no longer identified with physical substance. At the macroscopic level, the notion of substance is a useful approximation, but it does not pertain at the atomic level. Hence particles are not viewed as consisting of any elemental material but as packets of energy. Energy is associated with movement, and this implies that subatomic particles are inherently dynamic. Atoms consist of particles, but when these particles are observed, no matter is seen, only dynamic patterns ceaselessly changing one into another.

NEWTONIAN PHYSICS AND FORAGING

Shaken Foundations. Newton's once absolute rule over the physical world has been shaken at both ends of the scale in the last hundred years. Quantum theory prevails at the subatomic level, whereas relativity warps space and time at the cosmic scale. Nevertheless, at intermediate scales Newtonian mechanics is still relevant in physics and biology (e.g., bio-mechanics; Pennycuik, 1992), and this leads to some degree of predictability. Optimality models in foraging are analogous to Newtonian mechanics in physics in that both strive to lend a degree of predictability to life. Optimality models, which theorize that herbivores should maximize nutrient gain, are somewhat consistent with experimental findings (Wilmshurst et al., 1995; van Wieren, 1996). Nonetheless, herbivores spend considerable time

feeding in areas that do not maximize nutrient gain, and the inability to predict use of poorer foods implies current models cannot account for all of the interrelationships affecting foraging.

In what follows, we discuss factors that control foraging behavior, and then try to explain why herbivores deviate from what is presumed to be optimum. We submit that experimental analyses enable us to understand physical (e.g., plant nutrients, toxins, structure) and biological (e.g., social interactions) processes that control foraging behavior and the rules by which they operate, but these processes are ultimately nonlinear and unpredictable. Through carefully controlled experiments, scientists attain a degree of predictability by approximating linear conditions, but life in its essence is unpredictable, defined by periods of instability (bifurcations or "choices" in the face of uncertainty) and interludes of tranquility.

Factors that Control Foraging. Plants present a perplexing array of chemical compounds to herbivores, and understanding how herbivores respond to plant chemistry lends an element of predictability to the process of foraging. Animals as diverse as insects (Simpson and Raubenheimer, 1993), rodents (Perez et al., 1996), and ruminants (Provenza, 1995a) respond to nutrients. Elk optimize macro-nutrient gain by selecting appropriate patches of grass, though there is debate over whether energy (Wilmshurst et al., 1995) or protein (Langvatn and Hanley, 1993) is most important. Results of modeling efforts (Wilmshurst and Fryxell, 1995; Fisher, 1997) and behavioral analyses suggest both are important. Lambs acquire preferences even for poorly nutritious foods like straw when consumption of straw is accompanied by intraruminal infusions of energy (Villalba and Provenza, 1996, 1997a) or protein (Villalba and Provenza, 1997b). Lambs maintain a constant ratio of energy to protein in their diet (Egan, 1980; Provenza et al., 1996; Wang and Provenza, 1996ab) by discriminating between feedback signals from energy and protein (Villalba and Provenza, 1997c, 1998). Ruminants also respond to the synchrony of rates of fermentation of energy and protein (Early and Provenza, 1998; Kyriazakis and Oldham, 1997). Lambs typically show stronger preferences for energy than protein (Wang and Provenza, 1996ab; Villalba and Provenza, 1998), in large part because ruminants require five times more energy than protein and because they are so efficient at recycling nitrogen (Orskov, 1982).

Herbivores also respond in predictable ways to toxins (Bryant et al., 1991; reviews in Palo and Robbins, 1991). Animals typically limit intake of nutritious foods that contain toxins in accord with the amount of a particular toxin they can detoxify i.e., the level of toxin satiation (Freeland and Janzen, 1974; McArthur et al., 1991; Launchbaugh et al., 1993), a result that supports the notion that herbivores select for macro-nutrients within the context of plant chemical defense (Wang and Provenza, 1996b, 1997; for exceptions see Provenza et al., 1992; Provenza 1997). The amount of toxin ingested depends on nutritional state, in part because nutrients provide substrate for detoxification (McArthur, et al., 1991; Foley et al., 1995; Illius and Jessop, 1995). Lambs eat more of foods containing the toxin LiCl as the energy content of their diet increases (Wang and Provenza, 1997). Toxins can also encourage animals to eat a variety of foods containing needed nutrients, provided toxins differ in their physiological effects and are detoxified by different mechanisms (Freeland and Janzen, 1974; Provenza, 1996). Interactions between toxins can also affect an herbivore's susceptibility to toxins. Rats eat more of a combination of foods containing tannins and saponins because tannins and saponins interact to reduce the aversive effects of both compounds (Freeland et al., 1985).

Nutrients and toxins occur in a multi-dimensional matrix of plant

physical attributes that include length, width and depth, all of which change temporally and spatially. Research of the past two decades has determined that plant structure affects intake (I) directly through bite size (BS) and bite rate (BR) and indirectly through time spent grazing (GT). Thus, $I = BS \times BR \times GT$. These variables interact as follows (summarized by Hodgson et al., 1997): intake per bite is influenced mainly by the sensitivity of bite depth to changes in sward height; bite size is less sensitive than bite depth to variation in sward conditions; bite rate is inversely correlated with bite mass, reflecting the increasing importance of prehension and mastication as bite mass increases; rate of intake typically increases with increasing bite mass; and as bite size and bite rate decline, time spent grazing increases. Work in this area also suggests differences in macro-nutrient characteristics of foods, along with variations in their vertical and horizontal availabilities, interact with nutritional status to affect foraging (Edwards et al., 1996).

Although there is evidence of the independent effects of chemical and physical attributes of plants on preference, there has been little research to illustrate how these plant properties interact to affect preference. Nutrient intake depends on bite size, bite rate, and nutrient content (i.e., nutrient intake = bite size x bite rate x nutrients/bite), and any combination of plant physical and nutritional characteristics that optimize nutrient assimilation is likely to be preferred. Nonetheless, these factors are confounded under field conditions because foods with high nutrient content are typically easy to harvest (e.g., green grass is highly nutritious and has low tensile strength), whereas those with low nutrient content are usually difficult to harvest (e.g., mature grass is low in nutrients and has high tensile strength). Thus, it remains to be seen how a plant's chemical and physical attributes interact to affect preference.

Deviations from Optimum. Optimality models suggest animals should forage in the most profitable patches, but contrary to predictions, animals spend considerable time foraging elsewhere (Langvatn and Hanley, 1993; Wilmshurst et al., 1995; van Wieren, 1996), and they typically overuse poorer sites and underuse richer sites (reviewed by Kennedy and Gray, 1993). Lambs eat significant amounts of foods of low nutritional quality when foods of higher quality are available, and in complete contradiction to optimality models, some individuals prefer foods of lower quality (Provenza et al., 1996). None of the various nutritional currencies alone can totally account for food preference (Simpson and Raubenheimer, 1993), and even simple interactions between energy and protein are difficult to describe (MacRae and Loble, 1988).

Herbivores forage at rates considerably lower than their potential, evidently because constraints like time are more elastic than predicted by optimality models (Owen-Smith, 1993). Chewing is considered a constraint on intake rate, but steers compensate for less grazing time by increasing intake rate without reducing bite weight (Greenwood, 1989, cited in Laca and Demment, 1996). As Illius and Hodgson (1996) point out, "Although intake rate maximization is assumed to apply in teleonomic models of mammalian herbivore foraging there is little direct evidence that herbivores select diets which do actually maximize intake rate....Amongst the few reports of animals selecting diets which maximized intake rate are those of Black and Kenney (1984) and Demment et al. (1993), and in neither case is the evidence particularly striking. More often, herbivore diets are characterized by the diversity of constituents - that is, they contain a mixture of food items with apparent disregard for the intake rate each offers."

These findings highlight the inability of current models of foraging (verbal or mathematical) to predict the behavior of *individuals*. Some

suggest the lack of predictability occurs because individuals vary in perceptual ability (Spencer et al., 1996). Others contend unexplained behaviors occur because animals must eat a variety of plants to track changes in nutritional quality, they make discrimination errors in assessing nutritional quality, or individuals differ in nutritional optima (Wilmshurst et al., 1995; van Wieren, 1996). Sampling and inability to discriminate are unlikely given the relatively simple conditions under which most experiments are conducted (Edwards et al., 1997), conditions which are apt to preclude "mistakes" in foraging by animals and result in the high degree of predictability observed in some optimality studies. On the other hand, variation among individuals warrants careful consideration, and it is our primary concern for the remainder of the paper.

We submit that the evolution of an individual's behavior in life can be understood, but it cannot necessarily be predicted, because of the complexity and uncertainty of life. As Prigogine and Stengers (1984, p. 207) point out, "In view of the complexity of the questions...the way in which biological and social evolution has traditionally been interpreted represents a particularly unfortunate use of the concepts and methods borrowed from physics -unfortunate because the area of physics where these concepts and methods are valid was very restricted...The foremost example of this is the paradigm of optimization. It is obvious that the management of human society as well as the action of selective pressures tends to optimize some aspects of behaviors or modes of connection, but to consider optimization as the key to understanding how populations and individuals survive is to risk confusing causes with effects. Optimization models...ignore both the possibility of radical transformations...and the inertial constraints that may eventually force a system into a disastrous way of functioning...this gives a reassuring representation of nature as an all-powerful and rational calculator, and of a coherent history categorized by global progress. To restore both inertia and the possibility of unanticipated events...we must accept (nature's) fundamental uncertainty."

QUANTUM THEORY AND FORAGING

In quantum reality, specific events do not always have a clearly-defined cause. The movement of an electron from one orbit to another, or the decay of a subatomic particle, may occur spontaneously without any apparent cause. Thus, we cannot predict subatomic phenomena; we can only predict their probabilities. This does not mean that atomic events arise in an arbitrary manner; it means only that the behavior of any part is determined by "nonlocal" connections to the whole, and because these connections are unknown, the classical notion of cause and effect must be replaced with the statistical concept of probability.

The notion of "nonlocality" is embodied in Bell's theorem (see Capra (1982) p. 83-85 for a discussion of Bell's theorem), which is supported by experiments that pair two electrons in a system such that the total spin of the electrons is zero (e.g., if one electron's spin is "up" then the other's spin "down"). When the electrons are subsequently separated by vast distances, and the direction of spin of one of the electrons is changed, the direction of spin of the other electron changes instantly in the opposite direction, such that the total spin of the two-electron system remains zero. According to Einstein, it is impossible for a measurement on one electron to instantly determine the direction of the other electron's spin because no signal can travel faster than the speed of light (310,000 km/sec). According to Bohr, the two-electron system is an indivisible whole that cannot be analyzed in terms of independent parts. Bell's theorem supports Bohr's position and proves that Einstein's view of reality as consisting of independent parts is incompatible with the laws of

quantum theory.

The crucial connection between quantum theory and foraging is the realization that the behavior of any individual cannot be understood independently of its “nonlocal” connections to a larger whole, which in the case of foraging includes an animal’s evolutionary history (i.e., morphology and physiology, Williams, 1978), its cultural history (i.e., social and physical environment where the individual is reared, Provenza, 1995b), and its ongoing experiences of the environment (Provenza, 1996; Howery et al., 1998). We do not know these “nonlocal” connections precisely for each animal, just as nonlocal historical connections among electrons are concealed, and thus these factors may appear to function independently of one another. They may also appear to be of little importance because they seem detached temporally and spatially from the foraging behavior of the moment. Yet “nonlocal” connections ultimately interact to determine the kinds and likelihoods of behavioral responses and to give behavior emergent properties that may be difficult to predict. As with quantum theory, the process of foraging is best understood in terms of interconnectedness and transformation, both of which are manifestations of the process of self-organization.

SELF-ORGANIZATION, COMPLEXITY AND FORAGING

Foraging is a self-organizing process (Provenza and Cincotta, 1993). Self-organizing systems create new structures and forms of behavior without external intervention and they display several properties (Prigogine, 1980; Prigogine and Stengers, 1984; Figure 1). A self-organizing system is greater than the sum of its parts, and hence the behavior of the system cannot be deduced fully from its parts or the rules by which they interact. Thus, the behavior of the system does not follow any ubiquitous predictive law but is unique, and its functioning can be determined only by operating the system. Self-organizing systems evolve from the interaction of feedback loops, such that the system’s structure and behavior change irreversibly over time. Self-organizing systems operate far from equilibrium and consequently they require continuous inputs of resources (i.e., energy and matter). Near equilibrium, repetitive phenomena and universal laws exist, but as a system moves away from equilibrium, it shifts from the universal to the unique. In the case of food and habitat selection, this leads to the richness and variety of behaviors that are the hallmarks of life (Skinner, 1981).

Self-organizing systems are characterized by feedback loops, or circular arrangements of causality (Figure 1), which control the behavior of the system on the basis of actual performance rather than on the basis of expected performance (Capra, 1996). The behavior of a self-organizing system emerges from interactions at different scales, described by the term holon. A holon is an independent, autonomous entity when viewed from the perspective of its constituent subsystems, such as an animal from the viewpoint of various organs. However, when viewed from a larger scale, the same holon appears merely as a component of the larger system, for example, an organ in an animal in a social system within an ecosystem. Thus, self-organizing systems are composed of holons that range in scale from subatomic particles to the cosmos. Within any system, the behavior of smaller-scale holons is affected by the larger scales (e.g., an individual may not be able to eat the foods it prefers if it is a member of a social group that does not forage in areas where those foods occur; Scott et al., 1995). Larger-scale holons, in turn, are not independent of the actions of smaller-scale holons (e.g., the nutritional requirements of the cells that compose the body dictate which nutrients an animal must ingest). Thus, holons interact via feedback loops at all levels of resolution.

Self-organizing systems may be stable and deterministic for a time, but internal (e.g., within an animal) and external (e.g., in the social or physical environment) oscillations inevitably cause the system to change. Evolutionary change is marked by bifurcation points at which the system may take several paths. The path taken depends on the system’s history and current environmental conditions, and it is sensitive to perturbations. Slight fluctuations at bifurcations can favor one path over a number of other equally possible paths at microscopic (e.g., biochemical and cellular processes) and macroscopic (e.g., individual and social processes) levels. In biological and ecological systems, the variables that control these interactions with the environment are not constants; rather, physical (e.g., climate, soils, plant nutrients and toxins) and social (e.g., interactions with mother and peers) environments are dynamic and that inevitably leads to bifurcations and fluctuations which create instability in a system. As Prigogine and Stengers (1984, p. 176) point out, “Self-organization processes in far-from-equilibrium conditions correspond to a delicate interplay between chance and necessity, between fluctuations and deterministic laws. We expect that near a bifurcation, fluctuations or random elements would play an important role, while between bifurcations the deterministic aspects would become dominant.” Appreciation of indeterminacy as a fundamental attribute of natural phenomena is a profound reconceptualization in science.

During the 1960s, Ilya Prigogine came to realize that systems far from equilibrium must be described mathematically by nonlinear equations that produce an array of possible solutions (Prigogine and Stengers, 1984). During the past three decades, the mathematics of complexity has helped to illustrate the dynamics of self-organizing systems. The new mathematics is one that emphasizes qualitative relationships and patterns, rather than quantitative solutions and predictions (Capra, 1996). Nonlinear models can be used to portray the dynamics of behavioral processes like food and habitat selection, and they can illustrate how perturbations lead to the richness and variety of behaviors manifest by herbivores (Provenza and Cincotta, 1993). Nonetheless, while nonlinear models can portray patterns of self-organization in the short-term, the process is unpredictable in the long-run because of perturbations at bifurcation points and the nonlinear nature of the equations, i.e., mathematical iterations lead to slight errors in calculations which inevitably make predictions impossible (Capra, 1996). The behaviors that emerge are unique, and as in Einstein’s theory, relative to each individual’s frame of reference.

RELATIVITY, SELF-ORGANIZATION AND FORAGING

In Newton’s world, time and space are absolute because there are no universal constants. Thus, when light is sent from one place to another, different observers would agree on the time the trip took because time and space are absolute. Conversely, in Einstein’s world, time and space are relative because the speed of light is a universal constant. Thus, all observers must agree on how fast light travels, but they would disagree on the distance light has traveled because space is not absolute, and as a result, they must also disagree over the time it has taken for light to make the journey. Thus, relativity puts an end to absolute time.

Just as in relativity there is no “absolute” description of time and space, so in life there is no “absolute” characterization of behaviors like foraging. In relativistic physics it is impossible to define the absolute simultaneity of two events so “one man’s now is another man’s then.” Likewise in foraging it is impossible to assign any absolute values to foods so “one man’s meat is another man’s poison.” That is not to say that physics and foraging are “subjective” sciences.

Rather, relativistic physics and foraging are subject to intrinsic constraints that identify individuals as a part of the physical world we attempt to describe.

In foraging, these constraints mean that the consequences of behavior depend on an animal's evolutionary and cultural history and its ongoing interactions with the environment (Skinner, 1981). As with relativity, these processes can be understood only in terms of a given frame of reference, which in the case of behavior is relative to the individual (Maturana and Varela, 1980). The uniqueness of the individual is a result of the process of self-organization, which creates novel structures over evolutionary time and modifies existing structures and creates new modes of behavior during the life of the individual.

Evolutionary History. An animal's evolutionary history represents eons of self-organization contained in the genotype. Genes in turn play an important role in the development of each individual morphologically and physiologically. The critical point is that every individual is unique, as Williams (1978) points out: "Stomachs, for example, vary in size, shape and contour...They also vary in operation...A Mayo Foundation study of about 5000 people who had no known stomach ailment showed that the gastric juices varied at least a thousand fold in pepsin content...Such differences are partly responsible for the fact that we tend not to eat with equal frequency or in equal amounts, nor to choose the same foods...In fact, marked variations in normal anatomy are found wherever we look for them...Some of the most far-reaching internal differences involve the endocrine glands—thyroids, parathyroids, adrenals, sex glands, pituitaries—which release different hormones into the blood. These, in turn, affect our metabolic health, our appetites for food, drink, amusement and sex, our emotions, instincts and psychological well-being...Our nervous systems also show distinctiveness...Since our nerve endings are our only source of information from the outside world, this means that the world is different for each of us."

Like people, herbivores differ in morphology and physiology. Variations in dental arcade cause individual sheep and goats to forage with different efficiencies (Gordon et al., 1996). Differences in organ mass and how animals metabolize macro-nutrients also affect foraging (Konarzewski and Diamond, 1994). Lambs of uniform age, sex, and breed vary in their preferences for foods. Some lambs prefer foods high in energy, whereas others prefer foods of medium or even low energy (Provenza et al., 1996). Doses of sodium propionate that condition preferences in some lambs condition aversions in others (Villalba and Provenza, 1996). The same variation occurs in response to toxins (Provenza et al., 1992). Some sheep fed a high level of *Galega officinalis* failed to show any symptoms of toxicosis, whereas others were killed by a low dose (Keeler et al., 1988). Sheep show similar variation in susceptibility to *Verbesina encelioides* (Keeler et al., 1992), as do goats to condensed tannins in *Coleogyne ramosissima* (Provenza et al., 1990). Thus, different preferences for foods and habitats occur in part because individuals differ morphologically and physiologically.

Cultural History. An individual's evolutionary history influences its interactions with the environment, which in turn alter each individual's morphological and physiological makeup (so-called phenotypic plasticity). Thus, the behavior of an adult is influenced by where the animal was born and reared, and by patterns of behavior that emerged from interactions with the social (mother and peers) and physical (different foods) environment (Provenza, 1995b). These processes are self-organizing (Provenza and Cincotta, 1993), and they are typified by the development of the central nervous system.

While gestating *in utero*, billions of neurons are produced. Those that are used form elaborate networks one with another (reflecting the unique experiences of each individual), whereas those that are not used simply wither and die (Aoki and Siekevitz, 1988; Kalil, 1989; Shatz, 1992). In that sense, one can argue that the brain determines the structure of experience, but it is equally true that experience determines the structure of the brain. Experiences thus lead to the development of behaviors (e.g., food and habitat preferences), which in turn cause neurological, morphological, and physiological changes that help to make each individual unique (e.g., rats, Coppersmith and Leon, 1984; goats, Distel and Provenza, 1991; sheep, Distel et al., 1994, 1996).

As a result of experiences early in life, offspring come to prefer the foods and environments where they are reared (Key and MacIver, 1980; Biquand and Biquand-Guyot, 1992; Howery et al., 1998). When resources are abundant, animals prefer familiar to novel environments, and they prefer to eat a variety of familiar foods. Conversely, a lack of resources can cause animals to sample novel foods and move to unfamiliar environments (Wallis de Vries, 1994; Howery et al., 1998). As discussed below, over-familiarity (i.e., satiety from eating foods too frequently or in excess) can also encourage animals to sample novel foods and to forage in new locations. The interface between the familiar (known, safe) and the unfamiliar (unknown, potentially dangerous) represents bifurcation points that lead to the dynamics of self-organization; by "making a choice" to venture into the unknown an individual literally creates its own world (Figure 1; Maturana and Varela, 1980; Skinner, 1981).

Individual Experience. Self-organizing systems are characterized by feedback loops that involve causally connected components or links (Capra, 1996). The initial input circulates around the links of the loop such that each link affects the next, until the last link "feeds back" to the first link in the cycle. Feedback loops can be self-balancing or self-reinforcing. Self-balancing loops add stability to a system; they are characteristic of homeostatic controls that in the case of foraging regulate intake of nutrients and toxins. Self-reinforcing feedback loops, commonly referred to as vicious cycles, create instability in a system; they occur when animals ingest certain kinds of poisonous plants (Provenza et al., 1992; Provenza 1997).

Food preference results from the interaction of various feedback loops that integrate taste with postingestive feedback from nutrients and toxins (Provenza, 1995a, 1996). Taste (as well as smell and sight) allows animals to discriminate among foods and is a source of hedonic sensations, whereas postingestive feedback calibrates a food's taste (hedonic value) with its homeostatic utility such that the taste-feedback loop is self-balancing. Various morphological structures and physiological mechanisms are involved in the process (Provenza, 1995b). Collectively, they identify foods with needed nutrients, thereby increasing an animal's preference. These mechanisms also decrease preference for foods deficient in nutrients or foods containing excess toxins (Provenza, 1995a, 1996).

Food ingestion causes a temporary decrease in preference for food just eaten, which encourages animals to eat a variety of foods (Provenza, 1996). A key feature of this process is aversion, the decrease in preference for food just eaten as a result of sensory input (taste, odor, texture) and postingestive feedback (from nutrients and toxins) unique to each food. Aversions are pronounced when foods contain toxins or when they are deficient in specific nutrients. Aversions are less pronounced, but they still occur when animals eat nutritionally adequate foods because satiety and surfeit are points along a continuum. Thus, eating any food is likely to cause a mild

aversion, and eating a food too frequently or in excess is likely to cause a strong aversion. Such taste-feedback interactions cause non-equilibrium conditions that encourage animals to ingest a variety of foods (Early and Provenza, 1998). They also affect choice of foraging location. Cattle prefer to feed in areas that contain a variety of nutritious plants, as opposed to more homogeneous areas; cattle also alternate feeding among the more nutritious plants, and they avoid homogeneous sites with plants of low nutritional quality for as long as three weeks after foraging in those locations (Bailey, 1995). These observations are consistent with the hypothesis that aversions cause animals to eat varied diets and that aversions are more pronounced when animals ingest foods inadequate in nutrients.

State-Dependency. Taste-feedback interactions depend on an animal's physiological condition and a food's chemical characteristics (Scott, 1991; Provenza, 1995a, 1996), and herbivores from insects (Chambers et al., 1995) to rodents (Perez et al., 1996) to ruminants (Provenza et al., 1996; Wang and Provenza, 1996a) select among foods to meet needs for macro-nutrients. When protein demands are high during pregnancy (Cooper et al., 1994) or a nematode infection (Kyriazakis et al., 1994), sheep increase their preference for foods high in protein; otherwise, they show greater preference for foods high in energy (Wang and Provenza, 1996b; Villalba and Provenza, 1998). Lambs deprived of 20% of their daily energy or nitrogen requirements prefer flavored non-nutritive foods previously associated with intraruminal infusions of energy (starch, glucose, propionate, acetate) or nitrogen (urea, casein, gluten), respectively (Villalba and Provenza, 1996, 1997abc). Lambs that receive a preload of energy or nitrogen before a meal increase preference for flavors previously conditioned with nitrogen or energy, respectively, during the ensuing meal (Villalba and Provenza, 1998). The role of nutritional needs is also apparent when lambs are fed flavored straw with intraruminal infusions of NaCl; when lambs' need for NaCl are met, they reject the flavored straw (Villalba and Provenza, 1996). Salty tastes approach the bitter domain when animals are sodium replete, and they approach the sweet domain when animals are sodium deficient (Scott, 1990).

An animal's physiological state also dictates the degree to which it will discriminate among foods. Even when we measure specific nutrients in plants we cannot predict how an animal will respond to a particular nutrient, or mix of nutrients, unless we know the animal's physiological state. Animals deprived of energy or protein prefer foods that provide those nutrients, and they respond to subtle differences in food quality, whereas animals that ingest an adequate diet are less discriminating (Villalba and Provenza, 1998). Within some contexts (e.g., abundance of nutritious foods) and nutritional states (e.g., nutrient inputs indistinguishable from the physiological background), food selection may appear to be random because the need to discriminate among different foods is largely irrelevant. This apparent lack of discrimination has led some to conclude that ruminants cannot select diets that meet their nutritional needs. These conclusions ignore the fact that food preference is state-dependent.

Taste-feedback interactions are not linearly integrated (by metabolites, hormones, neurotransmitters) to change food preference. Intraruminal infusions of energy (i.e., volatile fatty acids, VFA) depress intake in a way that is not explained by the addition of osmolalities from each VFA (Mbanya et al., 1993). Intraruminal infusions of propionate and acetate condition the strongest preference in lambs as the proportion of propionate increases (Villalba and Provenza, 1997c). Sodium propionate and cholecystokinin do not affect intake when administered separately, but they depress intake by 44% when infused together (Farningham et al., 1993). The

complexity of these interactions, and the large number of interacting feedback loops, suggests that taste-feedback signals are integrated in a nonlinear way that is relative to the current physiological state and past experiences of the individual.

THE IDEAL DIET

One goal of scientists studying foraging behavior is to predict the optimal diet and foraging behavior of a given species. By the same token, people in agriculture (e.g., ranches, dairies, feedlots) want to provide their animals with an ideal diet. Yet, as a result of each animal's unique evolutionary and cultural history, and its current physiological state, it is impossible to predict diet selection at the level of the individual. As in quantum mechanics, it is only feasible to predict the likelihood of particular foraging behaviors.

The large degree of variation among individuals means each animal "possesses" its own ideal food. Thus, when we attempt to predict the optimal diet, to devise a nutritionally balanced ration (i.e., the ideal food), to create the ideal pasture, or to describe the ideal habitat the results are likely to apply only to a limited number of animals. The existence of sensory-, nutrient-, and toxin-specific satieties and state-dependent foraging decisions also means the ideal food changes because the ingestion of any food modifies preference in subsequent meals (Provenza, 1996). This does not mean the effort to find the ideal diet is futile, only that it will be more productive if it is done with an appreciation for the uniqueness of the individual. For free-ranging animals, this implies that different individuals within a species are likely to be suited to use different parts of the environment. For animals on pasture and in confinement, this view presupposes that animals be provided with a variety of foods (Provenza, 1996). From the standpoint of research, it suggests we begin to consider multiple solutions to nonlinear questions, and to emphasize qualitative patterns over quantitative predictions. From a philosophical viewpoint, it implies we begin to embrace the dynamics of behavior.

Just as physicists have been forced to change their views of the world, people in the life sciences must eventually abandon their Newtonian perspective for one which reflects the dynamics of life. Twentieth-century physics has shown that there is no absolute truth in science, that all concepts and theories are limited and approximate. Science is a quest for understanding, for truth, an attempt to account for observable phenomena in the physical and biological worlds, but science cannot be perceived as "true" or "final" in any absolute sense (Campbell, 1972). It is merely a tentative organization of "working hypotheses" that, for the moment, best account for the facts concerning physical and biological processes, whose interconnections provide the fabric of a web characterized by change. The dynamism of the web of life arises because foraging maintains nonequilibrium conditions, and the very act of food ingestion leads to the realization that from death comes life and endless transformation.

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Figure 1

Manifold possibilities of reality collapse, as a result of each individual's evolutionary and cultural history, through the process of self-organization. Self-organization occurs in open systems far from equilibrium, and thus it requires a continual flow of energy and nutrients. Self-organization is a recurrent process that leads anew to manifold possibilities (1) for creating new structures over evolutionary time, and (2) for modifying existing structures and creating new modes of behavior during the lifetime of the individual.



