

Fallback Foods, Optimal Diets, and Nutritional Targets: Primate Responses to Varying Food Availability and Quality

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Abstract

Eating is a risky affair. All animals have to offset risks of feeding such as exposure to plant toxins, increased vulnerability to predation, or conspecific aggression with a food's energetic and nutritional return. What, when, and where an individual eats can impact fitness and, ultimately, species-level adaptations. Here, we explore the variables that influence primate feeding preference: food availability, chemical defense, and nutrient content. We present information demonstrating that consumers manipulate nutrient and energy intake, indicating that what may be a less-than-optimal food for one state of an animal's phenotype may not be for another. This evidence suggests that factors previously assumed to be constraints in Optimal Foraging Theory, Functional Response, and—recently—Fallback Food feeding models would be better categorized as variables. We conclude that “fallback” is not an intrinsic state of the food or the consumer and that this conclusion complicates the application of this concept to morphological features in the fossil record.

INTRODUCTION

Kingdom Animalia is defined on the basis of the requirement to ingest food. This fundamental reality means that considerable attention has been paid to the means by which animals locate, procure, and process foods. Years of cumulative data on wild nonhuman primate diet, as well as advances in field, laboratory, and analytical methods, have revealed two central foraging problems: (a) No single food can offer the full complement of requisite nutrients and energy, and (b) to meet nutritional and energetic needs, a consumer must cope with a tangle of ecological, chemical, and mechanical challenges. From potentially lethal toxins to predation vulnerability and aggression from feeding competitors, all animals have to offset the risks of feeding on a particular food with that food's energetic and nutritional benefits. What, when, and where an individual eats can impact its reproductive success, can affect its interactions with other individuals, can have cascading effects on trophic interactions at the ecosystem level, and may ultimately shape species-level adaptations (Herrel et al. 2008, Ripple & Beschta 2004).

Food resources and an animal's ability to exploit them vary as a function of seasonality; habitat type; predation; competition from other animals; and the nutritional, chemical, and mechanical attributes of the potential food (i.e., the "packaging problem" sensu Altmann 1998). In the case of extreme dietary specialists (e.g., panda bears and their consumption of bamboo), an absence of a certain food can be fatal. However, most primates—including humans—are flexible omnivores and consume multiple food types from more than one trophic level. This means that primates routinely switch among different foods and do so over diverse timescales: within a single feeding bout, between feeding bouts in a day, between days within a season, between seasons, and among years (Karasov & Martinez del Rio 2007). Flexible feeding is indeed a hallmark of being primate (Le Gros Clark 1957, Napier & Napier 1967). This dietary flexibility also poses challenges for biological anthropologists who seek to link feeding traits to dietary specifics (e.g., thick dental enamel and the consumption of hard foods). Moreover, complex patterns of switching foods at multiple scales challenge our ability to explain whether an animal is switching foods because it is optimizing a balance of nutrients or because other, preferred foods are scarce and limited. In the former scenario, we might argue that the diet is "optimal"; in the latter, we might argue that the diet is "fallback."

The food packaging problem has most recently emerged in a discussion regarding the role of fallback foods in human and nonhuman primate feeding biology (Altmann 2009, Constantino & Wright 2009, Lambert 2007, Marshall & Wrangham 2007, Rosenberger 2013). Although authors vary in their use of the term "fallback food," discussion generally centers on the facts that animals exhibit preference for some foods over others and that when preferred foods are not available, others will be exploited. For example, frugivorous primates eat sweet succulent fruit whenever it is available, but when it is not, they consume less easily digestible alternatives such as leaves or bark (Stanford & Nkurunungi 2003). Animal ethologists and ecologists have long appreciated the inconsistency of the world in which animals live and have been evaluating the significance of consuming less-than-optimal foods at a proximate, ecological scale for many years and with little contention (Barboza et al. 2009, Schoener 1971). However, fallback foods have now come to be reified with mechanical and nutritional attributes that are then subsequently used to interpret morphological traits in the fossil record. For example, hard foods have come to mean fallback foods for species with adaptations to consume those hard foods (so-called durophagous feeders) and, as such, has been used to interpret the robust morphology of several taxa [e.g., robust hominins (*Paranthropus*), capuchins (*Cebus*), and mangabeys (*Lophocebus*)] (Lambert et al. 2004, Ungar et al. 2008, Wright et al. 2009). As we discuss, such generalizations are challenged by the facts that

primates adjust behavior and physiology in response to ecological, mechanical, chemical, and nutritional attributes of their foods and that primate feeding biology is too responsive to ecological and nutritional vicissitudes for a food to be classified into a discrete category of fallback foods. Moreover, it is increasingly evident that signals yielded by fossilized anatomical traits related to feeding (e.g., dental morphology, masticatory anatomy) are simply too coarse grained to yield hypotheses regarding preferred versus fallback diets (McGraw & Daegling 2012, Scott et al. 2014, Ungar 2012).

In this review, we explore the pervasive feeding-related risk of procuring enough of the right kinds of food at the right time and the various mechanisms by which primates deal with shifts in food availability and quality. Myriad social, morphological, physiological, and ecological factors influence animal feeding biology; we cannot do this broad topic full justice, and many excellent reviews exist (Brockman & van Schaik 2005, Chapman et al. 2012, Clutton-Brock & Janson 2012, Felton et al. 2009a, Hawes & Peres 2014, Janson & Chapman 1999, McGraw & Daegling 2012, Ross et al. 2012, Strier 2009). Here, we cover the variables that influence feeding preference—namely, food availability in space and time, chemical defense, and nutritional content. We describe classic and more recent conceptual frameworks for evaluating feeding preference and consumption of fallback foods. We present information that indicates that consumers manipulate aspects of nutrient and energy intake—both behaviorally and physiologically—suggesting that what may be a less-than-optimal food for one state of an animal’s phenotype may not be for another. We also discuss recent analytical models on nutrient balancing, demonstrating that omnivores can meet nutritional targets in multiple ways. We argue that “fallback” is not an intrinsic state of the food or of the consumer and that applying this concept to the fossil record is difficult.

FOODS VARY IN AVAILABILITY, CHEMICAL DEFENSE, AND NUTRITIONAL CONTENT

Availability

Among the most fundamental factors influencing a consumer’s feeding choices and preference is food availability, which varies in both time and space (van Schaik et al. 1993). Much of this variation is driven by patterns of plant phenology. Phenology refers to the timing of life history events and is derived from the Greek root “phaino,” which means “to show or to appear”; thus, literally, from the perspective of the consumer, phenology refers to the appearance of food (Rathcke & Lacey 1985). Primates, as a broadly omnivorous Order, are both primary and secondary consumers and tailor feeding according to the phenology of both plants (e.g., leafing, flowering, fruiting) and insects (e.g., eggs, larvae, pupae, and nymphs). This tailored feeding has cascading impacts on other secondary consumers (Ripple & Beschta 2004, Saunders 2002, Schowalter 2006, van Schaik et al. 1993).

At higher latitudes, the timing of plant phenophases is constrained by climate and other abiotic variables. In the tropics—where most primates are found—phenophases are much less tightly constrained by climate, resulting in a diversity of phenological patterns among plant individuals, species, and communities (Boyle & Bronstein 2012). Tropical tree species exhibit every phenological pattern possible for each phenophase (Boyle & Bronstein 2012, Fenner 1998). For example, a tree may produce fruit at the same time as other individuals in a population (synchronous fruiting) or at different times. A tree may also yield fruit piecemeal or as synchronous, mass productions of large fruit crops (“mast”). Generally, young leaf and flower production typically follows maximum insolation (i.e., total amount of solar radiation at a given surface area) (van

Schaik et al. 1993). Fruiting phenology, however, varies widely; some species in a forest produce fruit in some seasons, but not in others, and some species produce fruit in adjacent sites of similar forests (Chapman et al. 1999, Hemingway & Bynum 2005). The timing of plant life history events can vary manyfold interannually, and even forests in the same region that have similar edaphic and climate conditions can differ widely in plant species composition, tree distribution, and phenology. This variability can impact primate feeding dramatically. For example, orangutans have significantly reduced calorie intake and substantial weight loss during fruit-scarce seasons, and gibbons (*Hylobates albibarbis*) preferentially feed on asynchronously fruiting tree species, likely because they are more consistently available (Dillis et al. 2013, Knott 2005).

Chemical Defense

Flowering plants have not been passive victims of herbivory over the past 65 million years; indeed, natural selection for thwarting herbivory has resulted in the evolution of an extraordinary diversity of defensive plant chemicals—so-called “secondary metabolites” (Harborne 2001, Iason et al. 2013). The gamut of compounds—including nitrogen-containing and sulfur-containing terpenoids and phenolics—have been classified into two broad categories in terms of effect on consumers: (a) digestion inhibitors, which interfere with the efficiency with which nutrients are obtained by the animal, and (b) true toxins, which are harmful to the animal in that they interfere with normal physiology and may result in death (Feeny 1976, Freeland & Janzen 1974, Waterman & Kool 1994). As with plant food availability, plant chemical defense varies among species, populations, and individuals (Koricheva & Barton 2013). The total diversity of plant chemical defenses is unknown, although hundreds of thousands have been identified (Harborne 2001, Iason et al. 2013). In chemical defense, organic substances are accumulated in plant tissues in such a way that if they are consumed or tasted by an animal, feeding is deterred (Harborne 2001). Such substances may be bitter, have an unappealing odor, be poisonous to the extent of being lethal, or have an antinutritional impact (Feeny 1976, Freeland & Janzen 1974, Waterman & Kool 1994).

Primates have thus evolved in a chemically inhospitable environment and cannot simply consume any plant that they encounter. However, the ways in which plant chemical defense impacts primate feeding decisions, health, and fitness are poorly known, because of both the staggering diversity of compounds primates may ingest and the methodological challenges associated with measuring the compounds’ biological and chemical activity (Rothman et al. 2012). Primate species respond differently to plant secondary metabolites in relation to the other foods in their diet, their ability to detoxify or tolerate the toxic metabolites, and food availability. In general, primates probably avoid condensed and hydrolysable tannins, which bind dietary protein, reduce digestibility, and can be toxic, although results are inconsistent (Waterman & Kool 1994). In a classic study conducted by Wrangham & Waterman (1981), vervet monkeys (*Cercopithecus aethiops*) preferred *Acacia* trees with lower levels of phenolics and tannin content; however, in other studies, some primates—for example, chimpanzees in Uganda—did not avoid tannins in fruits they consumed (Reynolds et al. 1998, Wrangham et al. 1998). In comparative work on marsupials, food avoidance and decreased population densities were strongly associated with increased chemical defenses (DeGabriel et al. 2014, Stalenberg et al. 2014). That there are interspecific differences in tolerance is evident. For example, the golden bamboo lemur (*Haploplemur aureus*) specializes on bamboo that has approximately 10 times the amount of cyanide that would be lethal to a human (Ballhorn et al. 2009, Glander et al. 1989). Other lemurs are not as resilient to toxins. Ring-tail lemurs (*Lemur catta*) that ate diets including a tree (*Leucaena leucocephala*) containing the pyrrolizidine alkaloid mimosine lost hair on their coats and tails (Jolly 2009).

Table 1 A comparison of the general nutritional characteristics of broad categories of foods consumed by primates

	Insoluble fiber	Soluble fiber	Fat	Protein	Sugars	Plant secondary metabolites
Mature leaves	High	Moderate	Low	Moderate	Low	High
Young leaves	Moderate	Moderate	Low	High	Moderate	Moderate
Ripe fruit pulp	Low	Moderate	Variable; can be very high	Low	High	Low
Unripe fruit pulp	Moderate	Moderate	Variable; can be very high	Low	Moderate	Moderate
Flowers	Moderate	Low	Low	Moderate to high	Moderate	Low
Gums	Low	High	Low	Low	High	Variable
Stems/pith	Moderate	High	Low	Low	Moderate	Low
Bark/wood	Very high	Low	Low	Low	Low	Low
Insects	Moderate (chitin)	Low	Moderate	High	Low	Low/variable
Vertebrates	None	None	Moderate	High	None	None

Note: These represent generalizations and that foods vary widely in their nutritional composition both within and between species.

Nutritional Content

In addition to contending with the vagaries of food availability and defensive chemistry, primates must cope with the reality that foods are not equivalent in nutritional content and that, moreover, nutrients (carbohydrates, protein, and lipids) vary not only between plant parts but also with the stage of the plant part. Whereas animal prey generally provides high concentrations of protein and lipids, it contains few or no carbohydrates (Rothman et al. 2014). Fruits usually have high levels of easily digestible sugars and moderate amounts of fibrous material, whereas young leaves are typically moderate in their sugar contents but high in protein and moderate in fiber content. Mature leaves are typically the hardest to digest, with high levels of fiber compared with those of young leaves and fruit. Aside from animal matter and some fatty fruits, little fat can typically be found in primate diets. Fruits that are ripe are typically higher in sugar and lower in fiber and secondary metabolites than those that are unripe (Houle et al. 2014). Other less commonly eaten items include gums, flowers, and bark, each of which provides different sources of nutrients. For example, gums are an excellent source of soluble fiber that can be used as energy (Isbell et al. 2013), and bark/wood can be high in sodium (Reynolds et al. 2009, Rothman et al. 2006). Flowers apparently have higher protein than do fruits and may be closer in protein content to leaves (Oftedal 1991) (**Table 1**).

However, although generalizations can be made to a certain degree, we would like to emphasize that plants exhibit high intraspecific variability in nutrient content over different spatial scales and timescales. For example, depending on location, young leaves of the same species eaten by monkeys in Kibale National Park, Uganda, varied in protein content from 22% to 47% (Chapman et al. 2003), and the fat content of a single species of ripe fruit in this forest varied seasonally from 0.3% to 30% (Worman & Chapman 2005). Fruits in Kibale also varied in dry weight according to the layer of the tree crown where they were found (Houle et al. 2014). In Madagascar, sun-exposed leaves had more protein than did shaded leaves (Ganzhorn 1995), and ring-tail lemurs (*Lemur catta*) ate tamarind (*Tamarindus indica*) leaves and fruits that varied in nutritional composition according to forest type (Mertl-Millhollen et al. 2003).

CONCEPTUAL FRAMEWORKS FOR UNDERSTANDING FEEDING CHOICES

Given the tangle of ecological, chemical, and nutritional challenges presented to consumers, predicting an animal's feeding decisions is concomitantly challenging and is of considerable interest to researchers seeking to explain feeding behavior and morphology. Indeed, when and why animals switch foods have been important discussions in animal ecology since the 1960s (Charnov 1976, MacArthur & Pianka 1966, Stephens & Krebs 1986), with particular reference to primates since the 1970s (Clutton-Brock & Harvey 1977, Hladik 1973). Researchers have developed many nutrition and feeding models, such as the Classic Insect Nutritional Ecology (CINE) model and the Ecological Stoichiometry model (see Raubenheimer et al. 2009). However, most discussion of fallback foods either implicitly or explicitly rests on early classic work that evaluated foraging in terms of the energetic costs and benefits of feeding on a particular food (Optimization and Optimal Foraging Theory models) and in terms of how feeding responds to food abundance (Functional Response models). Although discussion of fallback foods per se is unique to the primate literature (Fallback Food models), nutritionally explicit models recently have been utilized with high success across multiple taxa outside primates (Geometric Framework models).

Optimization and Optimal Foraging Theory

The earliest models for evaluating feeding decisions, Optimal Foraging Theory (OFT) models, stem from optimization theory—a mathematical approach to selecting the best available element from some set of available alternatives given a defined domain (or a set of constraints). In their landmark paper, MacArthur & Pianka (1966) applied optimization to animals making decisions about which patch or prey item to feed on given a set of constraints. This framework provided animal ecologists with a means to model the effects of costs and benefits of feeding behavior on animal fitness. Building an OFT model requires defining three critical components: currency, constraints, and decision rules. Currency is the unit that is hypothesized to be optimized by animals as they forage. In classical animal foraging models, this currency has been energy gain per unit time, and factors such as search time and handling time have been costs (constraints) of currency optimization. Models have also incorporated digestive turnover as a constraint (Verlinden & Wiley 1989). After the currency is determined, the next step is to decide which factors should be considered either constraints (fixed elements) or variables. As we discuss, some features that have classically been considered constraints (e.g., digestive biology) may be somewhat under the control of the consumer. Decision rules define the set of behaviors that form the animal's strategy to optimize currency given a set of constraints. In discussion of fallback foods, currency is often defined in terms of energy (or, less commonly, in terms of nutrient density); constraints as searching, handling, and processing as costs to energy or nutrient yield/unit time; and decision rules as when the animal should switch foods altogether (e.g., when to stop searching for preferred food and switch to fallback food).

Functional Response Models

Because of their reliance on feeding as a function of availability, definitions of fallback foods (Table 2) also implicitly reference Functional Response models. Holling (1959, 1965) first described functional responses in terms of how the number of food items eaten by a consumer changes as a function of the food's density and handling time (Holling 1959, 1965). For example, at high prey food densities, a predator's attack rate is the limiting variable of how much food that

Table 2 Examples of fallback food definitions

Constraint	Example definition	Reference(s)
Availability	Foods consumed during severe seasonal or supra-annual episodes of food shortage	Vogel et al. (2009)
	Foods consumed during periods of low fruit availability	Hladik (1977)
Food attributes (e.g., nutrient density, energy return, mechanical features)	Foods that have lower energy return per unit foraging time	van Schaik & Brockman (2005)
Availability + preference	Foods consumed during seasons when preferred foods are unavailable	Grueter et al. (2009)
	Foods that are relied on when preferred items are unavailable	Altmann (1998)
	Foods that are eaten when more preferred foods are not available	Marlowe & Berbesque (2009)
Availability + preference + food attributes	Foods that have relatively poor nutritional quality and high abundance and that are eaten particularly during the period when preferred foods are scarce	Yamagiwa & Basabose (2009)
	Foods consumed during periods of scarcity of preferred foods, with less-preferred foods tending to be stiffer, tougher, or harder than preferred foods	Constantino et al. (2009) Lucas et al. (2009)
	Foods that are of limiting importance during periods when other, more nutrient dense, more abundant, or less-protected foods are scarce	Lambert (2007)
	Foods that are less preferred, mechanically challenging, and eaten during times of resource stress when preferred foods are unavailable	Ungar et al. (2008)

animal will consume (Barboza et al. 2009, Holling 1965, Karasov & Martinez del Rio 2007, Krebs & McCleery 1984). More generally, the rate at which an animal can assimilate a currency (e.g., nutrient x or total energy) is constrained by the relationship between food intake and food abundance (the functional response). As the abundance of a particular food increases, the likelihood of encountering that food also increases. Functional responses are thus curvilinear from zero intake to maximum rates of food intake as a function of availability. How the abundance of a food item impacts a consumer varies both by the animal's energetic and nutritional requirements and by the qualities of the food. "Giving-up density" is the threshold abundance of a food below which animals stop feeding. Because giving-up densities are lower for foods with lower energetic yield or nutritional density, dietary breadth tends to increase overall as higher-ranked foods become scarcer.

Fallback Foods

Definitions of fallback foods vary, and the term has historically been used interchangeably with other terms such as dietary switching and keystone resources (Constantino & Wright 2009, Hemingway & Bynum 2005, Lambert 2007, Marshall et al. 2009, Sauter & Cuzzo 2009). All definitions, however, center on the key features discussed here (availability, chemical/mechanical defense, and nutrient density) and thereby rest on an assumption of preference—i.e., foods that are selected disproportionately relative to their abundance in a habitat (Leighton 1993)—as well as on aspects of either OFT or Functional Response models. In theory, an animal should exhibit preference for the most profitable foods—that is, foods that are nutrient dense, easy to find, and easy to access. Foods that are less nutrient dense, harder to find, or more difficult to process are presumably less profitable and not preferred. As such, "fallback" has been used to indicate food

preference, availability (absolute abundance or abundance relative to preferred foods), or the inherent nutrient density and energy return (Conklin & Wrangham 1994, Fox et al. 2004, Furuichi et al. 2001, Gautier-Hion & Michaloud 1989, Gursky 2000, Laden & Wrangham 2005, Lambert et al. 2004, Tutin et al. 1997, Ungar 2004, Yamakoshi 1998) (**Table 2**).

Marshall & Wrangham (2007) provided an operational definition of fallback foods: foods whose use is negatively correlated with the availability of preferred foods. This operationalized definition is by far the most commonly used one in the primate literature and has been cited 191 times as of July 2015 (according to Google Scholar). Beyond providing an operational definition, Marshall & Wrangham (2007) also consider the evolutionary and ecological implications of consuming fallback foods, suggesting that they be classified into two subsets: “staple” and “filler.” Staple fallback foods are food resources that are annually available and thus can be accessed throughout the year; during seasonal shortages of other foods, staple foods may comprise the majority of a primate species’ diet. In contrast, filler fallback foods can be either seasonally or annually available, but they never comprise a majority of the diet.

Recent discussion of fallback foods has also centered on linking feeding to anatomical form and function, although these scenarios are often “fuzzy” on the details (McGraw & Daegling 2012, p. 204). Laden & Wrangham (2005) and Wrangham et al. (2009) have suggested that derived features of early hominin mandibular and dental morphology can be explained by the exploitation of critical fallback foods such as underground storage organs. Along these lines, Lambert (2007) classified fallback foods into two broad categories: (*a*) those of lower nutritional density and energy return that are abundantly distributed but that inherently require more handling time and anatomical adaptation (e.g., thicker dental enamel, longer molar shearing crests, long digestive retention times), and (*b*) foods of higher nutritional density and energy return that are rare, are heavily protected, and select for cognitive ability and tool use.

Geometric Framework Models

The fact that foods are termed “fallback” suggests that they have been evaluated as being deficient in some way, further suggesting an ideal or optimal balance of nutrients. However, knowing whether an animal is or is not meeting an optimal diet is challenging in flexible feeders. More recently, the Geometric Framework (GF) has been used as an analytical tool for evaluating “nutritional targets,” or the state-dependent nutrient need. The GF considers the nutritional decisions of animals on the basis of interactions among nutrients and toxins (Felton et al. 2009a; Raubenheimer & Simpson 1997; Simpson & Raubenheimer 1995, 2012; Villalba & Provenza 1999). For example, grasshoppers balance their diet to a particular concentration of carbohydrate and protein if foods are tannin free. Tannins bind with protein, and if the tannins are present in the high-carbohydrate component of the diet, high-protein foods are eaten in greater quantities (Behmer et al. 2002). In contrast, if tannins are present in the high-protein portion of the diet, tannin intake is not reduced, indicating not an effect of tannins on the decision to consume protein but instead a trade-off of an imbalanced diet. If both foods contain equivalent tannin levels, carbohydrates and proteins are balanced similarly to the way they are balanced in tannin-free foods (Behmer et al. 2002).

Within the context of the GF, primates are represented as living in a nutritional landscape, whereby they move across the environment in search of the nutrients that meet their nutritional needs from multiple possible food sources (Simpson & Raubenheimer 2012). Within this space lies the nutritional target that a primate must meet to survive and successfully reproduce. Reaching this dynamic nutritional need requires that primates select, locate, ingest, and digest particular foods. The GF allows us to assess how animals balance multiple nutrients simultaneously (Simpson & Raubenheimer 2012), and specific models have been developed for conditions in which measuring

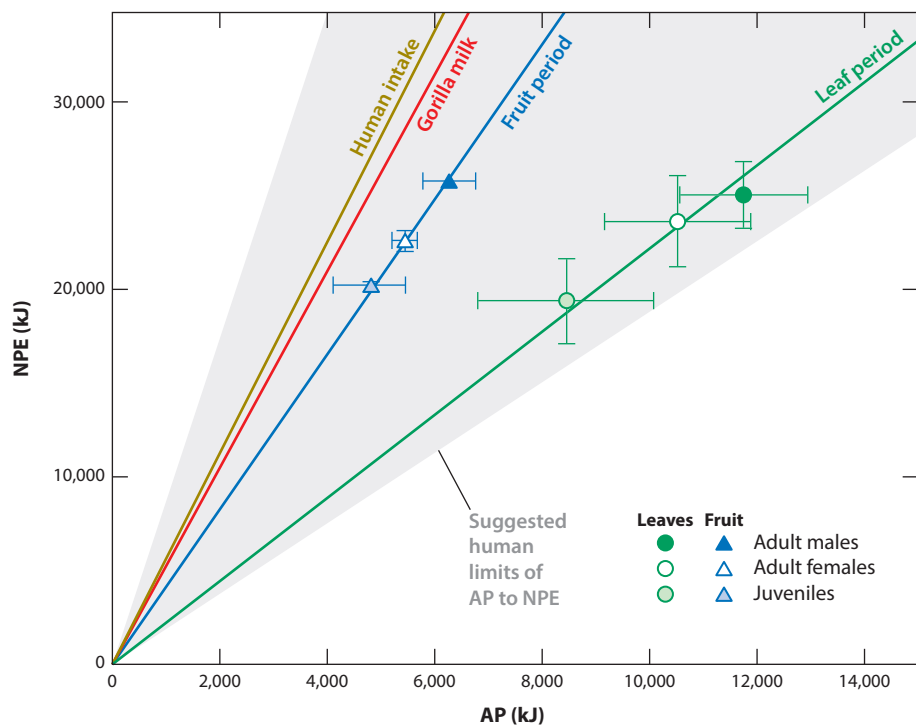


Figure 1

A geometric plot of the mean daily intakes (\pm SD) of available protein (AP) and nonprotein energy (NPE) by mountain gorillas (*Gorilla beringei*) during fruit periods (triangles) and leaf periods (circles). Nutritional rails (straight colored lines) indicate AP-to-NPE balance in fruit periods (blue), in leaf periods (green), and in midlactation gorilla milk (red), as well as the recommended AP-to-NPE balance for humans to maintain healthy diets (brown). The gray area represents the upper and lower limits of the AP-to-NPE balance suggested for humans. Whereas leaves were available year round, fruits were available only in some seasons. The gorillas ate similar amounts of NPE in the fruit and leaf periods across all age-sex classes, allowing AP to vary widely, indicating an energy prioritization strategy. The AP-to-NPE balance in gorilla diets in the fruiting season is close to the balance in gorilla milk and the recommended concentration for humans. Figure adapted from Rothman et al. (2011) with permission.

amounts is not possible (Raubenheimer et al. 2015) (**Figure 1**). For example, in a 30-day study of a single female chacma baboon (*Papio ursinus*) in which every food consumed was recorded, the baboon consumed a combination of native and exotic vegetation, as well as human food from garbage pits (Johnson et al. 2013). The baboon chose foods that were very different in nutrient composition—for example, small herbs and cooked chicken—and daily ate varying amounts of protein and nonprotein energy (sugar, fat, and digestible fiber). Throughout the 30 days, however, she maintained a remarkably tight balance of the two (**Figure 2**).

As discussed, there is considerable intraspecific variability in the nutritional content of particular plant species; however, at any given time, each item eaten contains a static amount of nutrient mixtures (such as protein, energy, and minerals) and secondary metabolites (such as condensed tannins). Because primates switch their foods continuously throughout the day, many balances of nutrients (e.g., protein-to-carbohydrate, sugar-to-fat, and toxin-to-macronutrient balances) are represented in this nutrient space (Felton et al. 2009b). Foods that are optimal overlap the intake target such that ingesting that food in adequate levels provides the animal with its exact nutrient

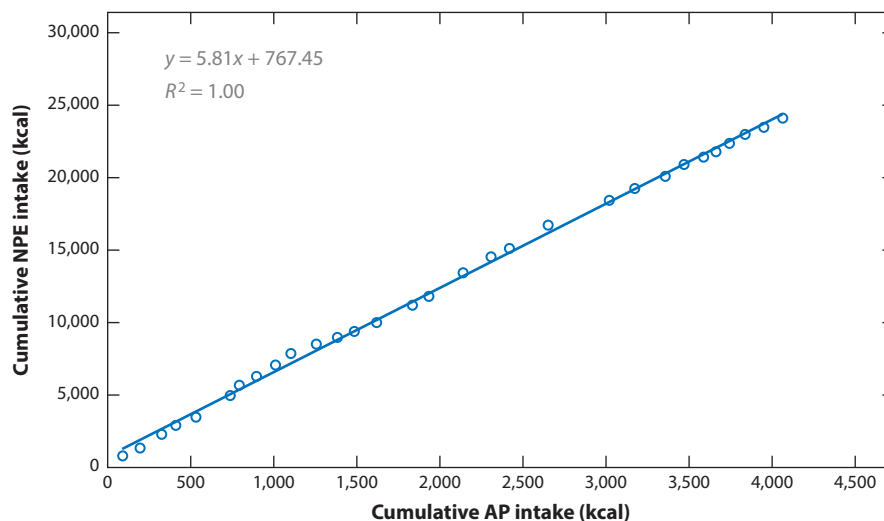


Figure 2

A geometric plot of the cumulative daily intake of available protein (AP) and nonprotein energy (NPE) consumed by a chacma baboon in South Africa. The baboon ate different amounts of food daily but maintained a tight AP-to-NPE balance, given the cumulative intake over a month. This result indicates a nutrient-balancing prioritization strategy. Figure modified from Johnson et al. (2013) with permission.

needs. In most cases, a single food that is nutritionally balanced does not occur in the wild, so animals must consume a mixture of foods to meet their nutritional needs (Kohler et al. 2012). How animals achieve this balance is based on a regulatory system whereby selection has acted to allow primates to detect nutrients and food attributes through sensory mechanisms (Dominy et al. 2001, Laska et al. 1999, Lucas et al. 2012). The ability of primates to regulate their nutrient intake allows them to make food choices that best achieve fitness gains. Prioritizing nutrients is a way of regulating intake such that when prioritized, a particular nutrient is more tightly regulated, or less variable, in the diet than other nutrients. When one nutrient is prioritized, another nutrient might be consumed in excess or in deficit.

Whereas the GF has provided new insights into the nutritional ecology of many species—including slime molds (Dussutour et al. 2010), insects (Lee et al. 2008, Mayntz et al. 2005), birds (Kohler et al. 2012), domestic mammals (Hewson-Hughes et al. 2011), and even humans (Simpson & Raubenheimer 2005)—it has only more recently been applied to wild, nonhuman primates (Felton et al. 2009b, Johnson et al. 2013, Rothman et al. 2011). Recent applications of the GF to primate diet have demonstrated that nutrient prioritization can differ by species. For example, mountain gorillas have long been thought to prioritize protein intake because they select high-protein leaves (Ganas et al. 2008; Watts 1984, 1988), but this idea presents a paradox because primates generally require low-protein diets, and the amounts of protein in leafy diets are quite high (Rothman et al. 2011). Using the GF, researchers demonstrated that folivorous gorillas prioritize energy rather than protein and consume an excess of protein (Rothman et al. 2011).

BEHAVIORAL RESPONSES TO SHIFTS IN FOOD AVAILABILITY

Although a few cases of famine have been reported (e.g., Barro Colorado Island, Panama; see Foster 1993, van Schaik et al. 1993), they are rare, and with few exceptions (Altmann 1998),

explicit links between the presence/absence of particular nutrients/secondary metabolites or of overall food abundance and individual fitness or population abundance are virtually nonexistent. However, no one doubts that “periodic and, especially, prolonged resource scarcity has presumably led to the evolution of a wide range of morphological, behavioral, and physiological adaptations in primary and even secondary consumers” (van Schaik et al. 1993, p. 368). As a consequence, a rich history of research measures indirect indicators of the impact of shifting food availability. In primate research, these indirect measures have included observations of changing habitat use and day range, shifting group size and—of particular interest here—dietary switching.

Habitat Use, Day Range, and Group Size

In response to shifting food availability, primates may increase their total day range, alter where they forage, increase their time spent traveling, increase the size of their home range or, rarely, change their home range altogether. Responses can also be influenced by social neighborhoods. Crofoot (2013), for example, demonstrated that capuchins (*Cebus capucinus*) undergo energetic shortfalls during food-scarce seasons as they alter their ranging to avoid competing social groups. In his classic exploration into the socioecology of a monkey community, Terborgh (1984) detailed the different ways that three sympatric monkeys—*Cebus albifrons*, *C. apella*, and *Saimiri sciureus*—cope with shifting food availability in Manu National Park, Peru. Although these three species have generally similar diets, day ranges, and home ranges, differences among the three species become striking during food-scarce dry seasons. *C. apella* groups visit central parts of the range frequently and the periphery only occasionally, conforming most closely to a central-place foraging model. Conversely, *C. albifrons* habitat usage is concentrated in widely scattered foci in which groups exploit food to exhaustion and then move to another food source, corresponding to a shifting-patch model. Terborgh (1984) described *Saimiri sciureus* as nomadic during dry seasons in which groups may have long day ranges in search of food resources; treks may last several days and cover many kilometers.

Group size is an important indicator of how primates respond to the vagaries of food availability (Janson & van Schaik 1988). Species such as chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles* spp.) that live in social groups characterized by fission-fusion have been particularly useful models for interpreting shifts in group size as a consequence of fruit availability. Chapman et al. (1995) evaluated the relationship between average feeding party size of common chimpanzees and availability of fruit resources in Kibale National Park, Uganda, and the same relationships in *Ateles geoffroyi* in Santa Rosa National Park, Costa Rica. More than 50% of the variance in feeding party size was explained by the density and distribution of fruiting resources generally. Availability of some fruit species had particularly strong effects on feeding party size. Availability of *Mimusops bagshawei*, for example, explained 77% of the variance in chimpanzee subgroup feeding size. Even primate species with access to abundantly distributed leaves exhibit response in group size as a function of food availability. For example, in response to limiting food, groups of eastern red colobus monkeys (*Procolobus rufomitratus*) in Kibale National Park, Uganda, compared with smaller groups, travel longer distances, spend more time feeding, and spend more time feeding in widely ranging patch sizes (Snaith & Chapman 2007).

Diet Switching

All primates, even the most specialized folivores and frugivores, are flexible feeders in response to the shifting availability of foods. For example, chimpanzees are described as ripe-fruit specialists by all researchers who have studied wild populations, with behavioral (fission-fusion), morphological

(bunodonty, thin dental enamel), and physiological adaptations for feeding on ripe fruit. However, during fruit-scarce periods, chimpanzees switch foods and consume high levels of the pith of terrestrial herbaceous vegetation. In the Neotropics, squirrel monkeys can become almost pure insectivores in the absence of fruit resources (Terborgh 1984), frugivorous tamarins and owl monkeys shift to consuming nectar (Terborgh & Stern 1987), and capuchins use tools to open hard palm nuts (Moura & Lee 2004).

Dietary switching almost always accompanies a shift in dietary breadth. Consumers may either increase the total number of foods consumed or decrease the number of food types consumed during food scarcity (Hemingway & Bynum 2005, Oates 1987). Animals may switch among food types (e.g., leaves to fruit, fruit to insects, fruit to bark) or switch within a food category (e.g., from one fruit species to another). Examples of dietary switching are found throughout the primate literature. Lambert et al. (2004) found that during an extreme drought of an El Niño year, gray-cheeked mangabeys (*Lophocebus albigena*) switched from a diet emphasizing fruit to one that focused on bark. In Japan, *Macaca fuscata* focuses on a particular food type—fruit, seeds, leaves, or invertebrates—depending on the time of year (Hill 1999).

PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSE TO DIET

Phenotypic adjustment is an a priori expectation in omnivores in response to varying food availability and quality (Karasov & Martinez del Rio 2007, West-Eberhard 2003). Physiological and morphological accommodation to dietary switching and food attributes can take place over many timescales, including between feeding bouts (intestinal nutrient transporters, digestive retention times), between seasons (ratio and composition of body tissue), or over the course of an individual's lifetime (mandibular form).

Enzymes, digestive retention times, and gut microbe communities are particularly responsive to diet and can be either up- or downmodulated depending on the nutrient in question and its abundance (Lambert et al. 2014). For example, the transport of nutrients across small intestine cell membranes is upmodulated in the presence of increasing sugars, amino acids, or peptides. Conversely, in the case of vitamins and minerals, nutrient transport is upmodulated in deficiency but downmodulated with increasing levels to avoid toxicity (e.g., iron) (Karasov & Martinez del Rio 2007). Afik & Karasov (1995) found that when warblers and American robins consume fruit, they have the shortest digestive retention times; when consuming seeds, they have the longest digestive retention times; and when ingesting insects, they have intermediate digestive retention times. These shifts took place not as a function of the food type they were consuming (e.g., banana, mealworms, sunflower seeds) but instead as a result of the nutritional content of those foods; the shifts were prompted by carbohydrates, lipids, and protein, along with the biochemical pathways involved in the breakdown and absorption for each of the major macronutrients. Primates, too, shift their retention times as a function of diet. Milton & Demment (1988) fed chimpanzees two experimental diets differing in total fiber (structural carbohydrates): a high-fiber diet (34% neutral detergent fiber, or NDF) and a low-fiber diet (14% NDF). Chimpanzees modulated their digestive retention times according to diet type and increased digesta passage of the higher-fiber diet. More recently, scholars have demonstrated how the gut microbiome (i.e., the community of microorganisms—bacteria, protozoa, archaea, and fungi—occupying the gastrointestinal tract) shifts as a function of the host consumer's diet (Amato 2013, Benson et al. 2010, David et al. 2014, Turnbaugh et al. 2009). This shift has been demonstrated in a diversity of mammalian taxa, although much of this information stems from experimental investigation and medical studies. For example, dramatic shifts in the composition of the gut microbial community in mice take place when the consumer shifts from a high-fiber diet to one that contains more simple sugars, digestible

carbohydrates, and high lipids (Turnbaugh et al. 2009). Although primate microbiome research is in its infancy, researchers have detected species-specific patterns of gut microbes, which probably respond to diet (Amato et al. 2015, McCord et al. 2014).

Phenotypic adjustment to differing food availability is not limited to behavior and physiology. Indeed, shifts in morphology have been found in both gut and masticatory apparatuses of various taxa. For example, Lake Victoria cichlids (e.g., *Haplochromis squamipinnus*, *Cichlasoma minckleyi*) produce different phenotypes of teeth, jaws, and muscles depending on food availability and food hardness (Witte 1984). Shifts in mandibular and craniofacial features as a function of in vivo mechanical loading from hard or soft diets have been demonstrated in several mammalian models, particularly white rabbits (*Oryctolagus cuniculus*) and domestic mice (*Mus musculus*) (Ravosa et al. 2008, Scott et al. 2014). Lee & Houston (1993) have found that microtine rodents (*Clethrionomys glareolus*, *Microtus agrestis*, and *Arvicola terrestris*) increase surface area of the small intestine and cecum in response to varying levels of fiber between seasons. Martin et al. (1985) found that captive primates have, on average, lower intestinal surface area than do their wild counterparts. This phenomenon likely relates to differences in fiber load between a captive diet and a wild diet. Zoo diets, on average, tend to have much lower fiber fractions than diets of wild primates (Lambert & Fellner 2012, Milton 1999).

“FALLBACK” IS NOT AN INTRINSIC STATE

Primates evolved in dynamic landscapes in which vicissitudes in food availability, chemical and mechanical defense, and nutritional content are a reality. In the case of some extremely successful taxa (e.g., *Papio*, *Macaca*, *Homo*), adaptation may have been to the change itself and not to an intrinsic state of a particular resource (Potts 1999). That primates can modulate phenotype (behavioral, physiological, and nutritional) as a consequence of high intraspecific variation in foods suggests that those foods cannot necessarily be placed into discrete categories—they are neither inherently fallback nor optimal—and models that make a priori assumptions about such foods are not nutritionally explicit (Raubenheimer et al. 2009).

Important lessons on primate feeding ecology have emerged from years of field study. In short, a food defined as fallback over the course of a year may emerge as just one of many foods that a primate consumes over the course of a much longer period of time (greater than 10 years); this is true not only of highly flexible omnivores but also of more specialized folivores and frugivores (Chapman et al. 1995, Struhsaker 2010). For example, although *Bursera simaruba* fruit were available every year of a six-year study of *Ateles geoffroyi* in Costa Rica, it was only in the sixth year that the spider monkeys fed on this fruit (Chapman et al. 1995). As succinctly stated by Altmann (1998), “[n]either nutrients nor toxins occur with the same abundance or even have the same abundance rank in all foods, nor do all nutrients rank inversely with all hazards. Consequently, the ‘value’ of a food is neither an independent property nor a scalable one. Its value depends on what other foods in the diet provide and fail to provide. As a result no one-dimensional scaling of foods combined with a top-down rule will lead systematically to the set of adequate and optimal diets” (p. 20). The following scenario is an illustration of this point: Canned beans and packaged rice are in the kitchen cupboards of most American households. They are well balanced in protein and carbohydrates for human nutrient needs, but most of us do not eat them daily unless our refrigerators and cabinets are otherwise bare. Thus, although beans and rice could be considered fallback foods by definition, they could easily be more nutrient dense than preferred foods.

These observations suggest some rethinking of how we categorize and model diet. For example, the first step in designing any optimality model (on which most Fallback Food discussion is premised) is deciding which aspects of the system constitute a true constraint and which are actually

variables (Krebs & McCleery 1984). What may have originally been identified as a constraint (e.g., a food's handling time or nutrient density) may in fact be under a consumer's control. This is true not only of more labile behavioral and physiological features (e.g., diet switching, nutrient mixing, and gut physiology) but also of traits that have historically been viewed as less flexible, such as gut and masticatory anatomy. For example, Scott et al. (2014) recently demonstrated that adult phenotypes of mammal jaw robusticity differed as a function of how much mechanical loading (from foods that are tougher to process) took place either seasonally or continuously throughout the year.

For these reasons, application of a fallback concept to a single phenotype as preserved in the fossil record is difficult (Lambert 2009). Demonstrating that diet switching during critical periods (as a function of food availability) impacts adaptations in fossil species rests on assumptions that attributes of foods and animal phenotype are constraints (Herrel et al. 2008, Lambert 2007, McGraw & Daegling 2012). The reality is that for flexible feeders, limiting components (nutrients, energy, and availability) may change daily, hourly, or within a single feeding bout, and signals yielded by fossilized anatomical traits related to feeding (e.g., dental morphology, masticatory anatomy) are simply too coarse grained to yield hypotheses regarding preferred versus fallback diets (Ungar 2012). This fact suggests that the Fallback Food concept should be used in conceptual scenarios of heuristic value and not as an explicit, operationalized model for predicting consumer behavior and feeding decisions.

SUMMARY POINTS

1. Animals exhibit a diversity of phenotypic adjustments (behavioral and physiological) to variation in food availability, chemical defense, and nutritional content.
2. Primates are flexible foragers and can arrive at nutritional targets in multiple ways.
3. "Fallback" is not an intrinsic, static state of either the food or the consumer, suggesting that factors previously assumed [in Optimal Foraging Theory (OFT), Functional Response, and Fallback Food models] to be constraints would be better categorized as variables. We suggest that Geometric Framework (GF) models best capture these complex interactions.
4. Application of a fallback scenario to a fossilized phenotype is challenged by the diverse means by which primates and our hominin ancestors cope(d) with temporal and spatial availability of foods, chemical defense, and nutritional content.

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