Fallback Foods, Eclectic Omnivores, and the Packaging Problem

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ABSTRACT   For omnivorous primates, as for other selective omnivores, the array of potential foods in their home ranges present a twofold problem: not all nutrients are present in any food in the requisite amounts or proportions and not all toxins and other costs are absent. Costs and benefits are inextricably linked. This so-called packaging problem is particularly acute during periods, often seasonal, when the benefit-to-cost ratios of available foods are especially low and animals must subsist on fallback foods. Thus, fallback foods represent the packaging problem in extreme form. The use of fallback foods by omnivorous primates is part of a suite of interconnected adaptations to the packaging problem, the commingling of costs and benefits in accessing food and other vital resources. These adaptations occur at every level of biological organization. This article surveys 16 types of potential adaptations of omnivorous primates to fallback foods and the packaging problem. Behavioral adaptations, in addition to finding and feeding on fallback foods, include minimizing costs and requirements, exploiting food outbreaks, living in social groups and learning from others, and shifting the home range. Adaptive anatomical and physiological traits include unspecialized guts and dentition, binocular color vision, agile bodies and limbs, Meissner's corpuscles in finger tips, enlargement of the neocortex, internal storage of foods and nutrients, and ability internally to synthesize compounds not readily available in the habitat. Finally, during periods requiring prolonged use of fallback foods, life history components may undergo changes, including reduction of parental investment, extended interbirth intervals, seasonal breeding or, in the extreme, aborted fetuses. Am J Phys Anthropol 140:615–629, 2009.   © 2009 Wiley-Liss, Inc.

The goal of this essay is to place the use of fallback foods by primates into the broader biological context of eclectic omnivores' adaptations to the packaging problem. Fallback foods are those eaten by animals at times, typically seasonal, when the arrays of foods available to them would result in diets of appreciably lower quality: much less nutritious and more deleterious to harvest and consume than the foods that the animals eat at other times of the year. These qualities can be evidenced directly by analysis of costs and benefits or as suggested by preferences when foods co-occur. As such, they present, in extreme form, the packaging problem: the fact that an animal cannot get at any of its vital resources, including foods, without exposure to entailed risks. Costs and benefits—*good* and *bad*—always come packaged together (Altmann, 1998). Some of these risks are intrinsic to the foods or food plants, such as toxic secondary compounds, thorns, and siliceous material that wears down the molars. Other hazards are extrinsic, including food- and habitat-associated predators and disease vectors, and time-budget limitations.

Even if we focus solely on nutrients, two characteristics of potential foods aggravate the packaging problem. First, no single food provides an adequate diet, with the right proportions of all nutrients. No perfect food exists. Second, no nutrient occurs in isolation in an animal's environment, and in this, nutrients differ markedly from foods. Although an animal requires specific *nutrients*, it can select and consume only *foods*, none of which can be eaten with impunity, none of which is nutritionally adequate, and for none of which the animal has any requirement whatever. The problem and the available solutions are at different levels of organization. The inexorable commingling of costs and benefits is as true of foods as it is for other vital resources, and for foods this results in the omnivore's dilemma: how to solve the packaging problem, how to find a combination of foods that will satisfy nutritional requirements and that can be searched for, harvested, and consumed without excessive risk (Rozin, 1976; Altmann, 1991, 1998; Pollan, 2006).

Among herbivorous animals, degrees of dietary diversity apparently result primarily from certain relationships between the sizes of animals and the sizes of their food patches (Altmann, 1998). In particular, animals that are very small or very large compared with the size of available food patches tend to have diets that are relatively homogeneous over time compared with the diets of animals of intermediate relative size. Animals that are very small experience the world as fine-grained (Levins, 1968), and they feed close to the level of localized biochemical homogeneity. These are within-patch specialists, and in the extreme, food selection becomes synonymous with patch selection. At the other extreme of scale, animals that are very large relative to their available food sources also have diets of relatively homogeneous composition, but for a very different reason: by feeding relatively unselectively on large quantities of diverse

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food items, they rely on the mean quality of very large statistical ensembles. Baleen whales, for example, are highly unselective in their feeding. They sieve the ocean, apparently swallowing anything caught by their baleen filters. Such whales doubtless hold the record for the taxonomic diversity of their diets, probably consuming organisms of every phylum.

For animals intermediate in size relative to their food patches, food is course-grained. Often no single food patch is both large enough and of adequate composition to sustain them, yet small-sample variations (local habitat differences) preclude their relying on the mean quality of an unselected diet. Such animals can either become multi-patch specialists on a particular type of food and master the art of finding and utilizing patches of it, or else become eclectics and search out local concentrations of nutrients, wherever they are. Most mammals use the first strategy and much of the evolution of the major groups of mammals, as indicated by their Orders and Suborders, represents divergences along specialized dietary lines: insectivores (*Insectivora, Microchiroptera*), carnivores (*Carnivora, Dasyuromorpha*), grass-eaters (*Perissodactyla, Artiodactyla*), and so on (Macdonald, 2001). By contrast, most species of primates are eclectic omnivores, exhibiting, in various degrees, the three hallmarks of eclectic omnivory: dietary selectivity, flexibility, and diversity (Altmann, 1998). In what follows, I suggest a suite of traits—some anatomical, physiological, social, or behavioral, others involving components of life histories—that collectively adapt eclectically omnivorous primates to the exigencies of the packaging problem when at its worst: during times of fallback foods.

BEHAVIORAL ADAPTATIONS TO THE PACKAGING PROBLEM

Each of the adaptations to the packaging problem that I describe below entails costs as well as benefits. "There's no such thing as a free lunch" (Friedman, 1975). Behavioral ecologists use the term "costs," to refer to negative consequences of anything an organism is or does. Reduced biological fitness is the ultimate measure of costs. A cost can be as subtle as an activity that eventually results in delayed onset of first reproduction or increased interbirth intervals. It can be as obvious as foraging in areas that increase the chance of being preyed on or eating foods containing toxic secondary compounds. Among the most common costs of primate foraging are intakes of toxic secondary plant compounds and expenditures of limited time and energy.

Seasonal changes in the habitat probably are the most widespread reason that primates resort to fallback foods, but such dietary shifts may occur for other reasons, such as periods of drought, shifts in home range, and competition from other groups or other species. When the moon sets, nocturnal Lydekker's lorises (*Loris lydekkereanus*) reduce their choice of food items from high-energy mobile prey to mainly ants (Bearder et al., 2006).

Eat fallback foods

Seasonal changes in the habitat probably are the most widespread reason for resorting to fallback foods, but such dietary shifts may occur for other reasons, including temporary displacement from prime feeding areas by other groups, destruction of prime food sources by other animals (such as locusts, caterpillars, elephants or flocks of frugivorous birds) or environmentally induced changes in the local habitat and resulting shifts in home ranges.

Example: Corms of grasses and sedges. Saying that some foods are fallback foods goes beyond saying that available diets vary seasonally in quality, some being of lesser value. Demonstrating that some foods are not preferred, as required by the definition above of fallback foods, requires a choice situation, which might be arranged experimentally but can in many cases be done more readily by taking advantage of times when various foods are concurrently available. This can be illustrated by the corms of perennial grass and sedge plants. A corm is a short, vertical, swollen, underground plant stem. Roots grow from its base, leaves from its top, and, in some species, runners (rhizomes, stolons) or new corms grow from its sides, which are covered with protective leaves modified into skins or tunics. The thin tunic leaves are dry, papery, dead petiole sheaths, formed from the petioles of leaves produced the year before. The tunic acts as a covering that protects the corm from insects and water loss. In Africa, corms are an effective adaptation of perennial grasses and sedges to the adverse conditions of dry seasons and the depredations of that continent's abundance of grazing mammals, which, by the end of each dry season, have grazed many grasses and sedges nearly down to ground level. Meanwhile, the corms remain safely below until the onset of the next rains, when, in just a few days, the new shoots arising from the corms turn the land green again–safely below, that is, unless baboons or warthogs dig them up! (Note: Here and in what follows, unless indicated otherwise, information about baboons is based on our research on yellow baboons, *Papio cynocephalus*, in the Amboseli region of East Africa. See http://www.princeton.edu/~baboon for a complete bibliography.)

For baboons, the corms of grasses and sedges provide paradigms of fallback foods. They meet two criteria. First, corms are selected against: they are available year round but are much eaten only during the dry season when fruits or flowers are not available (see Fig. 1). Second, corms are costly. Even ignoring the time, predation risks, and energy costs of moving from the woodland out onto the open plains where corm-bearing grasses and sedges are abundant, harvesting corms requires much effort and time for very small return. The grass or sedge plant is first laboriously dug from the ground, then all of the adherent inedible materials (dead leaves from the top, roots from the bottom and the corm's covering tunic of dead petiole sheaths) are removed by the hands and teeth, leaving only a very small packet of meristem corm tissue, which is consumed. Compared with other major food categories (runners, meat, non-grass/sedge leaves, flowers, grass leaves, acacia gum, fruits, and seeds), corms consumed the greatest amount of yearling baboons' harvest time and required digging into hard ground in areas of full sun and remote from water. Yet corms provided them with among the lowest rates of nutrient intakes of every proximate nutrient class (see Fig. 2). Corms are eaten not out of preference but out of necessity.

Example: Time-budget tradeoff limits. In some cases, a seasonal diet that consists largely of fallback foods could require more foraging time (travel time plus harvest/consumption time) than is available just to provide an adequate maintenance diet. For adult female baboons
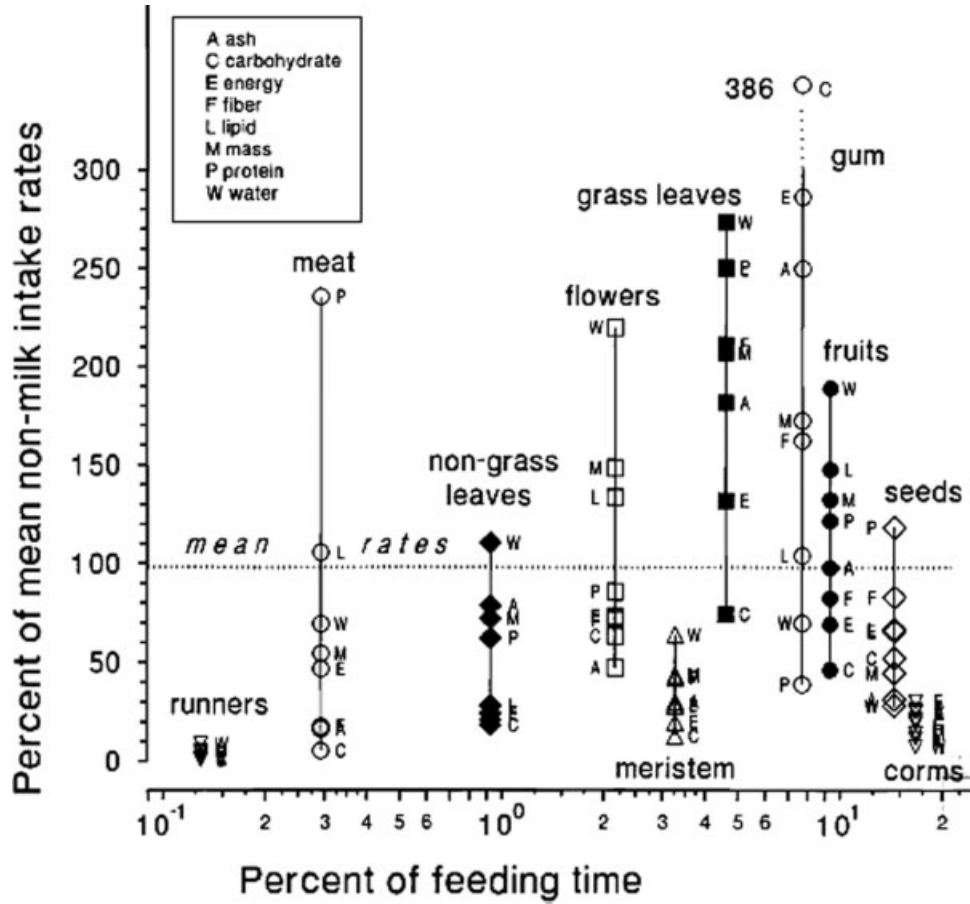
Fig. 1. Costs and benefits of corm feeding. Relative intake rates and feeding time budgets of yearling baboons for corms of grasses and sedges (bottom right) compared with other major food groups. Corms took up more time than any other non-milk food and collectively yielded nutrients at a lower mean rate than any food group other than grass and sedge runners (rhizomes and stolons) (Adapted from Fig. 6.14 in Altmann, 1998).

in the Amboseli basin of Kenya, during a long period of woodland habitat deterioration, foraging ranged from about 66% of daytime during the wetter months of the year to about 73% during the long dry season (mean values, January 1984 to December 1999). During those same months, resting time decreased from 23% to 16%. Socializing remained constant at 4% (Alberts et al., 2005), suggesting that it had reached a critical minimum. This seasonal pattern of spending more time foraging and less time resting in the long dry season than during the wetter months persisted throughout secular changes over years in the amounts of time devoted to these two activities as the habitat continued to deteriorate. "The clear but unsurprising inference is that quality of life is higher during the wetter months and that the dry season represents an ecological challenge for the animals" (Alberts et al., 2005).

Reduce direct costs of consumption

For animals faced seasonally with adverse conditions that lead them to resort to fallback foods, the need for effective diet selection is particularly acute. The obvious optimal strategy would be to find a combination of foods that both maximizes intake of required nutrients and minimizes the various adverse effects of foraging for them. Unfortunately, no general solution exists to the problem of simultaneously maximizing or minimizing more than one function. An alternative is to develop ways of reducing the costs of foraging. However, for grass corms, the baboons apparently cannot further reduce the costs of time, effort, and exposure to direct sun that feeding on these nutritious foods require. When available the green seeds of umbrella trees (*Acacia tortilis*) provide an alternative fallback food, one that can be harvested easily and abundantly in the trees' shade and, like grass corms, provide an abundance of nutrients during the long dry season. Unfortunately, umbrella tree seeds contain a potent toxin, trypsin inhibitor. Without mechanisms for reducing the cost of taking in such toxic secondary compounds (and similarly for other hazards) consumption of nutrient-rich foods would be severely limited.

Example: Trypsin inhibitor in legumes. Trypsin inhibitor is a toxin to which many wild primates are likely to be exposed because it occurs in the seeds of many leguminous plants, including about 80% of the species of peas and beans consumed by humans (Liener, 1962, Table 1). Fortunately for humans, trypsin inhibitor is heat-labile. It is destroyed by the boiling necessary to cook dried beans completely (Baker and Mustakas, 2007) or better, a combination of soaking and boiling (Onwuka, 2006). However, if they are only partially cooked, the effects of trypsin inhibitor on humans can be severe:
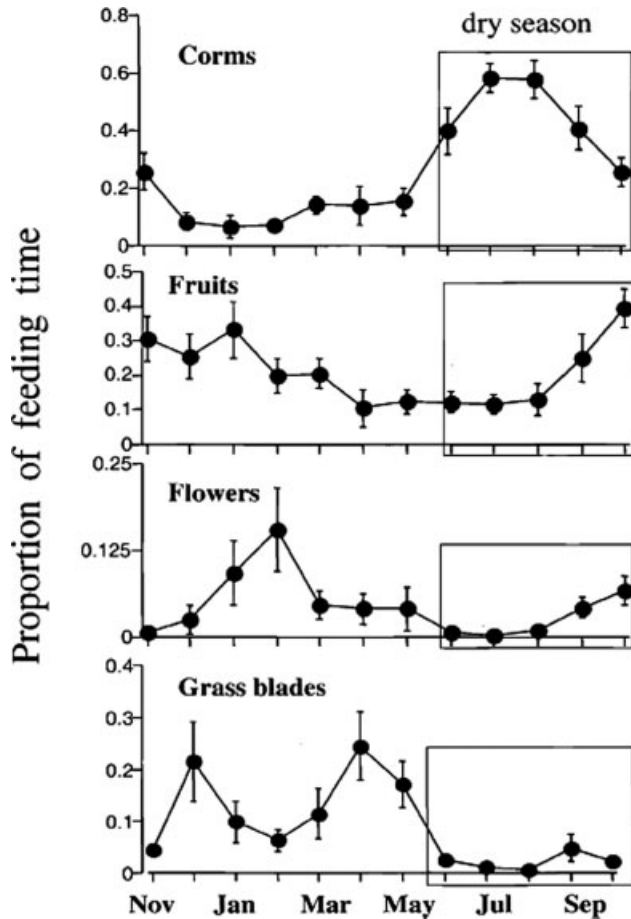
Fig. 2. Seasonal uptakes of sedge and grass corms (paradigm fallback foods) showing feeding time complementarity with fruits, flowers, and green grass blades (Adapted from Figs. 6.10 and 6.11 in Alberts et al., 2005).

simultaneous projectile vomiting and uncontrollable diarrhea (personal experience).

During the season when umbrella trees (*Acacia tortilis*) in the Amboseli region of Kenya have their usual heavy crop of still-soft seeds in fresh green pods, the baboons of the area gorge on them (Altmann, 1998). At that time of year, these seeds provide a preferable and more nutritious alternative to corms. They are harvested in the shade and safety of an umbrella tree canopy, where feeding time may not be as critical, in terms of temperature regulation and predators, as it is in the open.

Baboons' strategies for feeding on these seeds, with their high level of trypsin inhibitor (52.9 TIU/g whole seed), provide a paradigm of a multi-trait adaptive complex (Altmann, 1998). The baboons used five stages of selectivity. First, specific individual umbrella trees were used for at least three successive years during my study of foraging, whereas nearby trees, with abundant pods at comparable stages of ripeness, were bypassed. I therefore suspect that the trees are polymorphic for trypsin inhibitor. Second, some pods were picked, then discarded uneaten or were ignored altogether. Third, immature baboons and adult females removed the seeds from the pods and discarded the pods. At least one juvenile baboon (Dotty at 32 months) moved dry pods of umbrella trees laterally through her lips without using her hands,

stripping the seeds from the pods and into her mouth as she did so. None of the yearlings (30–70 weeks) that I studied did so. (Adult males sometimes crushed the pods, seeds and all, with their teeth, then discarded the fibrous residue.) Fourth, only some of the seeds were removed from any one pod. Finally, the seed coats were removed from the seeds and discarded. This last was accomplished solely by a skillful joint action of the tongue, jaws, teeth, and lips.

What do baboons accomplish by discarding the pod and seed coat (Altmann, 1998)? For every hundred green umbrella tree seeds consumed-which for a yearling baboon represents about thirteen minutes of harvesting-baboons will have discarded 150 mg protein in the seed coat and 664 mg in the empty pods. But in the process they will have enriched the protein content of their food to 160% of the value of whole pods. Similarly for carbohydrates and fiber: by eating the naked seeds baboons get a food that contains 111% of the carbohydrate concentration of whole pods and less than 7% of the fiber that they would have gotten if they had eaten the whole pods, as do the gazelles that sometimes forage below them under the canopy of the tree.

Of particular significance is the effect on trypsin inhibitor intake of eating just the naked seeds: by rejecting both the seed coats and the pods, the baboons reduced their intake of trypsin inhibitor toxin by 91%. Even so, the baboons sometimes vomited after feeding on these seeds, presumably because of the residual trypsin inhibitor in their diet. Yet, even then, they adapted: they kept their lips closed and swallowed their green vomitus. Trypsin inhibitor is a protein, and if they can only keep it down long enough, their digestive enzymes should be able to split the molecule and reap a double benefit: less toxin, more amino acid. That this digestion is not so simple is suggested by the disulfide bridges in the molecule of one component of trypsin inhibitor (Odani and Ikenaka, 1973), which probably make this toxin resistant to enzymatic digestion. This scenario suggests that there has been an evolutionary arms race, played out over time, between these trees and monkeys in successive adaptations and counter-adaptations: eat seeds/evolve toxin/eat from low-toxin trees/selection against low-toxin trees/enzymatic toxin digestion/anti-digestion disulfide bridges/retained vomitus. Perhaps the next step for primates will be the evolution of disulfide-bridge-specific digestive enzymes.

Reduce indirect foraging costs: Save time and energy

Consider primates feeding at places and times when they must rely on fallback foods and when even the best combinations of these would not satisfy their nutritional requirements in the foraging time that suffices during the rest of the year. Under these circumstances, two complementary strategies, increasing nutrient supply and decreasing nutrient demand, can bring them closer to an adequate diet. Ganzhorn (2003, p. 134) describe a variety of ways in which primates can accomplish this: "During the lean season they can change group size, travel longer distances in search of food, switch to low-quality food, change diet composition, use food patches of different sizes, or save energy by simply reducing their activity . . . . "

Example: Efficient routing. Of particular significance for these purposes are the time and energy invested in

foraging. For most mammals, travel probably represents the largest single expenditure of non-basal metabolic energy and a large part of their non-sleeping time budget. Unfortunately, available information on energetics and locomotion appears to underestimate grossly the fraction of metabolic energy that mammals of different sizes devote to locomotion (Altmann, 1987, 1998). However, whatever the actual values, a reduction in energy demand and thus in food intake will accrue if shorter safe routings are used. The same is true for greater efficiency in other tasks.

From the time of our first study of Amboseli baboons (Altmann and Altmann, 1970), we were very impressed with their apparent ability to navigate from any place in their large home range to any other, even when the goal was out of sight (cf. Noser and Byrne, 2007). In doing so, they gave the impression of using the shortest available safe routes. It is as if they have a mental map and could solve a version of the so-called traveling salesman's problem, such as finding the shortest driving route for leaving the home office in the morning, traveling during the day to assigned companies in various cities, then returning to the home office at the end of the day (or, in another version, going home at the end of the day). However, as the number of cities increases, finding the shortest route rapidly becomes much more difficult and various versions of the traveling salesman's problem are mathematically intractable (see Anderson, 1983), and so expecting wild animals to solve them seems unreasonable.

On a smaller scale, consider a foraging primate–say, a baboon digging up and eating grass corms–as it moves from one food source to another, selecting at each food source among those in sight. In doing so, the animal may have simple strategies that, while not always resulting in the shortest overall routing, may result in reasonable efficiency. One of the simplest foraging strategies, a one-step look-ahead strategy, is always to move next to the nearest resource site that has not been eaten. This requires no skill more complex than looking around and estimating distances to food sites from the observer's current site. Somewhat more complex is to evaluate the shortest total path length to the two closest food sites, proceed to the first of these, then repeat this evaluation at each site. Beyond that, one can imagine a corresponding three-step or higher evaluation (Altmann, 1974). Anderson (*supra*) modeled a different multi-step look-ahead strategy. Its evaluation by computer modeling lead to the surprising result that a one-step look-ahead strategy did as well as or better than 2-, 3-, and 5-step look-ahead strategies. For a recent survey of other approaches to route selection, see Janson (2000).

Examples: Three neotropical primates. A study of neotropical tamarin monkeys (*Saguinus mystax* and *S. fusciocollis*) by Garber and Hannon (1993) suggests that these animals have a remarkable ability to remember the locations of several hundred sleeping and feeding trees and to navigate efficiently among them. In revisiting fruiting trees that still contained ripe fruit, the tamarins took the shortest possible overall travel route (sleeping trees plus feeding trees) on at least half the days and only once (out of 29 days) took a route that was neither the shortest nor second-shortest. This they did despite the fact that their sleeping tree changed from night to night (ten trees altogether), and thus starting and ending points were highly variable.

In a study of route integration by wild capuchin monkeys (*Cebus apella nigritus*), Janson (2007) used feeding platforms arranged such that once the monkey group had chosen one site to feed, they had a choice between two remaining sites, a close one with less food and another that was up to 2.3 times as far away but with more food. The capuchins generally first chose the close feeding site, even when the more distant site offered up to 12 times as much food. The results suggest that the monkeys were integrating information on spatial location, reward, and perhaps potential food competition. Their behavior is consistent with a simple rule: do not use the detour unless the energy gain from extra food outweighs the energy cost of extra travel. Several other studies of primates (Janson, 2007, references therein), indicate a common tendency for monkey groups to travel to the closest available unused or not recently used resources.

If, even with an increase in foraging time during the season of fallback foods, the animals' diets are not adequate for maintenance, they might be able to offset the shortfall by mobilizing previously stored resources, such as oil-soluble vitamins and glycogen in the liver and metabolizable lipids stored in fat deposits. The extent to which such mobilization of stored nutrients occurs has not yet been studied in any wild nonhuman primate but developments in remote monitoring of physiological processes should soon make such a study practicable. Total body fat can be determined by the use of doubly-labeled water (Altmann et al., 1993).

Locomote efficiently

Grand (1984, p. 64) provides an illuminating descriptions of the unique compromises made by members of each of four genera, macaques (*Macaca*), howler monkeys (*Alouatta*), spider monkeys (*Ateles*), and gibbons (*Hylobates*) during arboreal locomotion. The brachiations of the latter two are particularly efficient, first because "in pendular motion, more than 70% of body weight (truncal mass and the free limbs) progresses by a series of arcs …. This weight constitutes an energy reservoir since the swing is induced by gravity; forward motion *does not require* constant energy input … (italics in original). Second, brachiation enables gibbons and spider monkeys to cross forest gaps that animals of the other two species would have to go around. "In sum, greater control of space by spider monkey and gibbon permits more direct movements, greater choice of travel route and increased access to food" (Grand, 1984, p. 67).

The graceful pendulations of brachiating spider monkeys and gibbons may be very efficient but surely are not energy free. They just make it look easy! In addition to overcoming air resistance, energy must be expended in the animals' limb–joint torsions, in grasping and releasing branches, in lowering and raising the center of mass by extension and flexion of the hind limbs, in the torque of $180°$ rotation of the entire body on its vertical axis, etc., all repeated during each pendulation cycle (Chang et al., 2000). Brachiation by a spider monkey (*Ateles geoffroyi*) used 1.4 times the energy that it used to move upright on a treadmill (Parsons and Taylor, 1977).

Exploit outbreaks of valuable foods

The example above, of reducing uptake of a toxin by discarding the most toxic components of umbrella tree pods and eating only the naked seeds, illustrates an

advantage of eclectic primates' dietary selectivity. Their dietary flexibility is shown dramatically in their ability to shift their diet on those rare occasions when there is a sudden increase in availability of a highly palatable and highly profitable food. The most extreme example that I observed in my studies on foraging in Amboseli baboons was a rare, massive outbreak of a single species of caterpillars that were quickly denuding the grass plants of their green leaves. For about two weeks, the baboons ate hardly anything else, each day feeding voraciously on these soft-bodied creatures, pulling them off the grass with both hands, rapidly alternating. Caterpillars are highly nutritious (Leung, 1968).

Live in social groups: Forage safely, learn from others, try new foods

The food-related rationale for social learning has been eloquently stated by Galef and Laland (2005, p. 489): "Many of the things that young animals have to learn must be learned rapidly. A fledging bird or weaning mammal ... sustained by adults of its species, has to learn to avoid predators before it is eaten by one. It has to learn to select a nutritionally balanced diet before it exhausts its internal reserves of any critical nutrient, and without ingesting harmful quantities of toxins. A naive young animal ... faced with such challenges, would be well advised to take advantage of opportunities provided by interaction with adults of its species."

Almost by definition, adults are individuals that have acquired patterns of behavior allowing them to avoid predators and the ingestion of toxins, to select an adequate diet, and to find water and safe refuges. Most important, adults are doing all of these things in the environment where the juveniles with which they interact are struggling to achieve independence. Consequently, to the extent that ignorant juveniles can use the behavior of adults to guide development of their own behavioral repertoires, juveniles should often be able to acquire necessary responses to the demands of the particular locales in which they are living without incurring many of the costs associated with individual trial-and-error learning."

All anthropoid primates spend their entire pre-adult life in association with at least one adult, in a few cases such as orangutans, with just their mother. Anthropoids of many other species live in permanent social groups that extend well beyond parents and their dependent offspring and that continue throughout the year even in species in which breeding is highly seasonal. When foraging, the members of these permanent groups move as a unit or in some cases break up into temporary subgroups. Such group foraging provides anthropoid primates not only with greater safety from predators but also with lifetime opportunities to learn from others and thereby benefit from what others have learned. However, in foraging together, competition over food can be expected, depending on the animal's dietary shortfall, the number of co-feeding individuals, and the spatial distribution of food (Janson and van Schaik, 1988). In the long run, individuals must gain more from improved nutrition and greater safety than they loose from traveling and feeding with their most potent food competitors, the members of their own species.

Several aspects of primate group life may make possible this advantage of group foraging. First, group foraging provides safety while traveling to remote sites of food, then harvesting and consuming it. It can appreciably reduce the risk of predation because a group of individuals, with its many eyes, is difficult for a predator to approach undetected (Hamilton, 1971), because of the protection provided to each individual by its close proximity to other potential prey individuals (Altmann, 1974), and because groups of some primate species are capable of driving off a predator. Second, food competition may be reduced in groups consisting of reciprocating kin. Lastly, group living facilitates learning what is edible, what is currently in flower or ripe, learning the locations of perennial sources of food concentrations and the safe routes for getting to them, then how to extract the edible from the inedible portion of the food item—the "what, where, when, and how" of foraging (Galef and Giraldeau, 2001). It also provides a mechanism whereby new foods that an individual finds can become known by all of the other members of the group.

In their development, starting at conception, primates, like other mammals, can acquire information from others about how and what to eat from several sources. First, from the history of the species, information is encoded in the genome about traits that subserve foraging and diet selection. Such genetic effects can be expected at every level of biological organization. Second, in mammals, social learning begins before birth. The ability of the mammalian fetus to learn olfactory cues that affect its postpartum behavior has now been demonstrated in a variety of mammals, including rats, rabbits, sheep, and humans. The introduction of odorants into the amnion, either as a result of maternal ingestion or by direct infusion, affects later infantile responses to the same stimuli (Schaal et al., 2000). Chemosensory information continues to affect behavior in the orientation of the neonate to the odor of its mother's breast (Porter and Winberg, 1999) and in compounds in milk that reflect her diet and that provide the infant with cues that influence its subsequent dietary preferences (Galef and Henderson, 1972; Galef and Sherry, 1973; Wuensch, 1978).

Next, infant baboons and, I assume, other infant primates, while clinging to their mother's ventrum as she feeds, will sometimes pick up and place into their mouth shreds of her food that fall onto her ventrum. They also watch as their mother feeds. As they get older, attention to what others are eating extends to other members of the group, particularly those eating something unfamiliar. This learning from the feeding behavior of others continues for the rest of their lives. No specialized food signals are required, only the feeding activities themselves—what Darwin (1896) referred to as serviceable associated habits. Baboons (Altmann, 1998), like many other primates (Chauvin and Thierry, 2005; Laidre, 2009) and rodents (Galef and Stein, 1985) also sniff each other's muzzles, almost always when the sniffed individual is chewing. King (1991), in a study of infant baboons not more than 32 weeks old found that they preferentially sniffed the muzzles of baboons that were both older and that were feeding or chewing. The infants were more likely to feed when their mothers, rather than other relatives or nonkin fed, and they fed on the same of seven food types as the mother. Such co-feeding by infants occurred when the type of food being eaten was apparently difficult for the infants to process.

Finally, some young baboons begin to explore new foods on their own, first passing them very rapidly back and forth from the tip of their tongue to their nares,

alternately tasting and smelling, sometimes holding it in their mouth for a while. In these various ways, information is transmitted from one individual to another and from one generation to the next. The social group provides a repository of the collected food knowledge of its members, past and present, a repository to which all can contribute and from which all can benefit.

Whitehead (1986) found that infant mantled howler monkeys (*Alouatta palliata*) learn which leaves to include in their diet by observing their mother, but chose fruits apparently by trial-and-error learning, independent of social learning. Leaves typically have higher levels of toxic secondary compounds than fruits. One of the yearling baboons whose feeding behavior I studied, Ozzie, was unusually curious. As an infant, he attended closely to many things that other members of his group ignored, including potential foods. Between the ages of 30 and 70 weeks, Ozzie discovered and ate three new foods: the fruit caps of a white mushroom (*Agaricus* prob. bukavuensis), the underground tuber of a cucumber-related plant (*Cucumis prophetarium*), and an unidentified small, red berry. As Ozzie harvested and ate these, he was intently watched at close range by at least one other individual in the group: his older sister in the case of the mushroom, a subadult male in the case of the red berry, and by essentially the whole group as he busily dug up and then ate the *Cucumis* tuber. From Ozzie's unhesitating procedure as he went about harvesting and eating these three foods, I surmise that he had eaten them before I first saw him do so. From the quiet, close attention of the others, I surmise that they were not familiar with these foods but probably learned about them by watching Ozzie. I have no subsequent records of Ozzie or others eating these foods, but these foods were sufficiently rare in the habitat that I can not rule out the possibility that the baboons did. Ozzie's case suggests the possibility that a few particularly talented individuals can make inordinate contributions to the collective knowledge of the group.

Shift home range

Outer bounds on the home range of any animal and on its species' range is established by the areas lying within cruising range of that essential resource with the most restricted spatial distribution relative to the needs of the animal (Altmann, 1974). Thus shifts in the locations of resources can lead to shifts in home range and in extreme cases, to migration into completely separate areas.

For many water-dependent mammals that live in arid regions, such as Amboseli baboons, the most spatially restricted essential resource is drinking water. During the long dry season (June through October), Amboseli baboons drank from permanent water sources (spring-fed water holes and swamps) nearly every day. But once the rains began, they could obtain water from puddles and rain pools as well, and they frequently made sorties into and fed in areas that were inaccessible during the dry season (Altmann and Altmann, 1970). At the beginning of the rains, most of the large, water-dependent grazing mammals move completely out of the Amboseli basin's area of permanent water sources, by which time the supply of graze there is severely depleted, then return months later, when the temporary water sources dry up.

Seasonal flowering, fruiting, or leaf-flushing of certain species near the periphery of a group's home range can provide a stimulus for temporary range extensions. A revealing example occurred in Amboseli in the mid 1970s, a time when the baboons of a study group rarely moved west of Kitirua Hill, at the western boundary of Amboseli National Park, except to drink from the water holes at the base of the hill. One day, while foraging in the central core of their range, well to the east of Kitirua, they came upon a few isolated *Lycium* "europaeum" bushes that had ripe fruit, which they ate. That night, they slept in that area but early the next morning, they made a long, steady progression westward that terminated beyond Kitirua to the next hill west of that, Naarbala, at the base of which was the only large concentration in their home range of *Lycium* bushes. The fruit on these was ripe, and the baboons gorged on them. *Lycium* berries are a good source of provitamin A (Altmann, 1998).

Migrate

When habitat conditions become bad enough, animals may completely abandon their home range and settle elsewhere. During the second half of the twentieth century, the water table in the Amboseli region of Kenya moved progressively upward by several meters (Western, 1973). A rise in the water table was first noted by Smith (1986) in 1957, in the middle of the dry season! As the water table continued to rise, the fever trees that made up most of the woodland of the Amboseli basin deteriorated, then died out completely, except for one well-watered and enclosed research area. The extremely high mortality rates of the fever trees in the central basin during 1950–1967 were documented by Western (1973) from trees identifiable on aerial photos and by me during 1969–1975 using tagged trees. One explanation for the demise of the fever trees is that the elevated water table brought salts in the soil up to the tree roots and damaged their ability to pump water (Western and Van Praet, 1973). This is consistent with the way in which most of the trees died: from the top down. Other explanations have been proposed (references in Alberts et al., 2005).

The demise of the fever tree woodland and its associated understory meant the loss of many of the baboon's primary non-fallback food sources, shade trees, and night roosts. The woodland was replaced by a treeless halophytic community.

Whatever the cause of this transformation of the habitat in the central basin, it gradually resulted in a precipitous decline in the baboon population from 1964 to 1969. Over a period of years, surviving groups gradually migrated out of the central basin, in each case settling about 8 km west, in an area of the Amboseli basin, the "western basin," with a relatively high density of well-foliated fever trees. However, during the 1990s, the fever trees of the western basin also began to decline. Time spent foraging increased slightly in the late '90s and time spent resting decreased, during both the long dry season and the wetter months (Alberts et al., 2005, Fig. 6.8).

The long-term effects on Amboseli baboons remain to be seen. What is clear from such events is that the loss of access to prime food sources that leads to reliance on fallback foods can occur not only over time (typically seasonally, as prime food sources wax and wane) but also across space, for animals that are excluded from prime

foraging areas by competitors or other hazards, and by combinations of temporal and spatial effects during long-term changes in habitat compositions.

MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS

An extensive literature is now available on the physical and physiological traits of primates that are relevant to their abilities at obtaining at least an adequate diet, even under the severe conditions that lead to the use of fallback foods. A brief sample of morpho-physiological adaptations of particular salience to fallback foods and the packaging problem is presented below. Fortunately, Fleagle (1999) has provided a masterful survey of primate structural adaptations, including their ecological and evolutionary consequences.

Body size

"Among the morphological traits that influence animal foraging capacities, body size has the most pervasive effects" (Temerin et al., 1984, p. 217). "An animal's size is associated with both opportunities and restrictions on its ecological options, and many of the differences between species in structure, behavior, and ecology are correlated with absolute body size" (Fleagle, 1999, p. 283).

Example: Cebine monkeys. In a trenchant review of numerous field studies, Janson and Boinski (1992, q.v. for references) provide a revealing perspective on the interplay of morphological and behavioral adaptations for foraging in neotropical cebine monkeys, *Saimiri* (squirrel monkeys) and the much larger *Cebus* (capuchin monkeys). Unlike other neotropical primates of their body size, cebines obtain virtually all their protein from insects, rarely ingesting substantial quantities of leaves or other vegetation. Many differences in insect feeding between squirrel monkeys and capuchins probably are entailed by differences in body mass and thus in strength and agility. For example, snatching of potentially mobile prey is much less common in the larger *Cebus* than in *Saimiri*. Conversely, exploitation of tough substrates such as palm frond bases, cane, bamboo, dead branches and termite nests is barely present in the foraging behavior of *Saimiri* (0.7% of substrates searched), while comprising 32.4% of substrates searched by the gracile *Cebus albifrons* and 44.3% of substrates use by the robust *C. apella*. However, it takes *Cebus* many minutes to search a single palm crown, while *Saimiri* require only several seconds to open a leaf or grab an insect off an exposed surface. As a result, capuchins spend about half of their day manipulating substrates and ingesting prey, while *Saimiri* spends barely one-half as much in these activities. Furthermore, when foraging for insects, the smaller *Saimiri* forage faster than *Cebus* (more attempts per hour) and are markedly more successful per attempt. Thus, only the smaller *Saimiri* can survive purely on invertebrate foraging for extended periods.

Cebines succeed in obtaining most of their proteins from insects despite a lack of clear morphological specializations for insectivory. While body size is extremely important in explaining differences in cebine diets, their overall emphasis on faunivory is facilitated more by behavioral than by morphological specialization. Whatever morphological specializations are present probably are favored at the most food-depauperate time of the year, that is, when the animals must resort to fallback foods. In particular, the extremely thick molar enamel and robust jaw morphology of *C. apella* are likely related to its extensive use of vegetative plant tissues and hard palm seeds during the period of fruit scarcity. The seeds of *Astrocaryum* palm are an important alternative resource for capuchins when fruit is scarce and they show a complex set of behaviors in choosing and opening them.

Example: Big baboons vs. little vervets. Baboons (here taken to mean members of the genera *Mandrillus* and *Papio*) are among the largest nonhuman primates, exceeded in body mass only by the great apes. As a result of a complex of traits, many of which are correlated with body size, they are eclectic omnivores *par excellence*, obtaining diets of high-quality and relatively low-bulk. By being able to do so, they have spread into virtually every non-alpine terrestrial habitat on the African continent, ranging from rain forest to desert.

Large body size is not without its costs. Age at maturity, gestation length, weaning age, and interbirth interval all increase with body size; litter size, where variable, decreases (Clutton-Brock and Harvey, 1983). As a result, age at first reproduction and mean generation time have major impact on the intrinsic rate of natural increase (Cole, 1954), which declines with body size in mammals (Bonner, 1965; Fenchel, 1974). These reproductive costs associated with major size increases suggest that there are compensating advantages to large size in mammals, which may vary from group to group. For example, the thermal inertia of larger mass partially buffers large mammals against changes in body temperature. Larger mammals may better withstand periods of acute food shortage, produce larger and stronger offspring, reduce predation, travel farther in search of food and water, utilize a greater diversity of habitats, have the strength needed to extract otherwise inaccessible foods, subsist on food of lower nutritional value, and compete successfully for food resources (Clutton-Brock and Harvey, 1983; Altmann, 1998).

In this regard, a comparison of Amboseli baboons with Amboseli vervet monkeys (*Cercopithecus aethiops*) is particularly revealing (Hall, 1965; Struhsaker, 1967; Altmann and Altmann, 1970; Klein, 1978; Altmann, 1998; Alberts et al., 2005). The two species are members of the same subfamily, Cercopithecinae. They are very similar in gross morphology, sexual dimorphism (including long, sharp, upper canines in males), social systems, and behavior patterns. The ranges of baboons and vervets overlap extensively, both in their distributions in Africa and at the level of social groups. In Amboseli, they sleep in the same species of trees, sometimes in the same grove, and react to each other's alarm calls to the same mammalian predators. Both species are omnivores. They eat many of the same foods and drink from the same waterholes. Yet, the diets of Amboseli baboons include about 2.5 times as many foods as the area's vervets. The list of foods eaten by baboons but not vervets (Altmann, 1998) is long: about two hundred foods!

The critical differences in their diets involve two types of foods. The first consists of subterranean foods. During the dry season, the corms of grasses and sedges and also the bulbs of lilies are major fallback foods of baboons (Altmann, 1998; Alberts et al., 2005), but vervets do not eat them, apparently because vervets, with their much smaller bodies, lack the size and strength to excavate

subterranean foods. (Adult baboons weigh about 2.5 times more than vervets.) Other foods eaten by baboons but not vervets occur in open, treeless areas, where vervets rarely go and do not linger, or in remote areas beyond their reach. Mean day-journey length increases with body size in mammals (Garland, 1983). Amboseli baboons walked eight to ten kilometers per day (Altmann, 1998, note 15). By contrast, the smaller vervets of the area averaged 1.2 km (Struhsaker, 1967). In the open, vervet monkeys probably are much more susceptible to attack by avian and mammalian predators. In Amboseli, these size-related dietary differences probably contributed to two costs for vervets: the lost-opportunity cost of strong seasonality in breeding and local extinction from the central basin of Amboseli when the fever tree woodland degenerated there. By contrast, baboons mate and conceive during every month with only small seasonal variation (Alberts et al., 2005), and as the fever tree woodland of the central Amboseli basin died out, the baboons there gradually migrated to another area. In sum, the smaller size of vervets means both that their diets are less diverse and more specialized than those of baboons and that they are less flexible, less adaptable than baboons to seasonal and long-term changes in habitat.

However, baboon reproduction is not completely immune to changes in seasonal environmental conditions (see section on Reproductive adjustments, below).

Collect and integrate information

The ways in which animals integrate information from their numerous sense organs provide superb illustrations of coadapted traits that subserve foraging and that probably undergo particularly intense selection during the location and selection of fallback foods. Suppose that we are in a tropical forest watching a monkey as she picks and eats a piece of fruit. What perceptions, what information has led her to select this particular piece of fruit? Why not another from the same tree, especially why not one that she previously picked, investigated, then dropped? Indeed, why this tree rather than another of this species in the same grove? Why this grove? As she picks each piece of fruit, she has already rejected others within reach on the basis of their appearance (Color? Size? Shape? Breaks in the skin?). Then after picking one, she quickly sniffs and palpates it. She drops it and reaches for another. After inspecting that one, she takes a bite, holds it briefly in her mouth, then spits it out and reaches for yet another. Why were these fruits rejected? Too few of the aromatic compounds of really ripe fruit? Wrong mouth feel? Bitterness? Astringency? Too much like fruits of this species that on previously occasions have eventually nauseated her? What about those that she consumes? Better smell, flavor and texture? Combined with fewer disqualifications?

On what basis did she and the other members of her group select this tree? Was it in response to the sight of the ripening fruits as they got near the grove? Or the blend of aromatic compounds from ripening fruits and the ethanol of fermentation? Did the monkeys cue on the calls of the fruit-eating birds in the trees? And how, from the beginning of this morning's journey to this area, did her group navigate to this grove from their sleeping trees, from which the grove is invisible? Perhaps they relied on a detailed collective knowledge of their home range that comes from years of walking this area, learn-

ing how the various features of their home range are laid out and knowing how remote each is from each other, thanks to their proprioceptors and other internal sensors that give them information about efforts expended in moving from place to place, which might be more important for them than the geometers' distances. Dominy et al. (2001) provide an excellent review of the sensory ecology of primate food perception. Recent studies of primate sensory ecology include those by Bolen and Green (1997), Visalberghi and Neel (2003), Laska et al. (2007), and Siemers et al. (2007).

Example: Color vision. The ecological interpretation of color vision is a persistent puzzle, despite a large body of information on its genetic and molecular basis, on taxon and individual differences in spectral sensitivity, and its likely association with food selection (Lambert, 1999a; Dominy and Lucas, 2004, and references therein). Color vision depends on specifically tuned photoreceptor pigments (opsins), in the cone cells of the retina, each tuned to particular wavelengths of the light spectrum. Extant diurnal mammals are almost all dichromatic: the cone cells of their retina possess two opsins. Trichromacy is apparently uniform in catarrhines (Old World monkeys and apes). However, in platyrrhines (New World monkeys), a variety of genetic variations has lead to a variety of types. Nocturnal owl monkeys (*Aotus*) have but one opsin and so are color blind. Howlers (*Alouatta*) are trichromatic. In other platyrrhines, di- and triallelic variation on the X-chromosome yields as many as three dichromatic and three trichromatic phenotypes. Thus six forms of color vision may characterize a foraging group! Allelic trichromacy appears to be maintained by an adaptive advantage, usually thought to be related to food selection. Proposed advantages of color vision include detection of proteinaceous red-green leaves and ripe fruits. "Young leaves are an abundant source of protein and they almost certainly represented fallback resources for the earliest catarrhines, particularly as leafing generally occurs when insect abundance is lowest" (Wright and van Schaik, 1994). "We suggest that the abundance of cryptically colored keystone resources in the Neotropics and Madagascar never favored the evolution of routine trichromacy because young leaves never became critical fallback foods" (Dominy and Lucas, 2004, p. 31).

Example: Sense of smell. Janzen (1977) suggested that the primary reason why yeasts manufacture alcohol is to render ripe fruits distasteful or unacceptable to wild vertebrates. On the other hand, Dudley (2000) suggested that low levels of ethanol in fruits might attract seed dispersers because of associated caloric and physiological benefits. Thus ethanol could be a foraging cue to anthropoid primates, used in detecting and navigating toward edible fruits (Dudley, 2000) and thereby selected for anthropoid primates' keen sense of smell. Laska et al. (2003 and references therein) have demonstrated exquisite sensitivity (low thresholds) of monkeys to fruit-associated odors, such as aliphatic esters, aldehydes, and alcohols. Unfortunately, few studies have focused directly on the use these compounds as foraging cues (Dominy, 2004).

Example: Sound and mass. In an experiment, Visalberghi and Neel (2003) showed that two capuchins (*Cebus paella*) could both tell the difference between nut shells containing food and those without food by cueing

on differences in mass and sound or only on mass. However, only the subject who spontaneously finger-tapped on the nut shells could distinguish nuts that differed only in sound. (Full nuts are heavier and produce low-pitched sound when tapped). The aye-aye (*Daubentonia madagascarensis*) uses its long middle finger to tap on branches and then, apparently using acoustical effects of the tapping, excavates and eats wood-boring insects (Erickson et al., 1998).

Synthesize environmentally sparse essential metabolites

From an evolutionary standpoint, a metabolic pathway for synthesizing a physiologically required compound is likely to evolve and be maintained only if the cost of synthesizing it is less than the cost of obtaining it from the diet (Charnov, 1984). During long periods of reliance on fallback foods, the cost of obtaining adequate dietary supplies of some vital compounds may favor selection for the ability to produce them internally from available substrates. Two groups of compounds have characteristics that suggest an evolutionary history of such selection. The first are amino acids, the building blocks of proteins.

Example: Non-essential amino acids. Mammals have dietary requirements for only some amino acids. All others that are needed can be synthesized internally from the essential amino acids, each with its own dietary requirement, plus a general amine pool. There seems to be no intrinsic reason why some amino acids can be internally synthesized, yet others cannot. Perhaps the reason is external, that some amino acids are so sparse in available foods relative to their internal needs that during times of fallback foods, selection is intense for development of their internal synthesis. If so, taxon differences in which amino acids are synthesized internally should correspond to long-term habitat differences in which amino acids are in short supply in the habitat, relative to the needs of the animals, during prolonged bottleneck periods when the animals must rely heavily on fallback foods. Conversely, an amino acid should be essential in the diet only for taxa that have, for long periods, lived in habitats in which that amino acid was reliably available at all times of the year. The data needed to test these predictions are not available.

Example: Ascorbic acid. Ascorbic acid is another particularly interesting compound from an ecological and evolutionary perspective. Because ascorbic acid, unlike oil-soluble vitamins, is not stored internally by primates, any primates that cannot synthesize it internally must, to avoid getting scurvy, find sources of ascorbic acid (vitamin C) among their fallback foods and indeed in their diets during every extended part of the year.

With one possible exception among primates (see below), currently available data are consistent with the generalization that all prosimians (strepsirrhines) are synthesizers, all monkeys and apes (haplorhines) are non-synthesizers. [Several studies of ascorbate production included samples on trees shrews, *Tupia glis*. However, on the basis of recent evidence, all species of tree shrews have been removed from the primate taxon and placed in an Order of their own, Scandentia (Groves, in Wilson and Reeder, 2005).] "Evidence thus far suggests then that ability for L-ascorbate synthesis was eliminated somewhere between the prosimian and simian stage of development …." However, "it is premature to conclude that the prosimians are *generally* able to synthesize L-ascorbate and that *all* higher primates lack the ability" (Nakajima et al., 1969).

Ascorbic acid has among the simplest molecular structure among vitamins. This suggests that it would not be a metabolically expensive compound to synthesize internally, as many mammals do, and that metabolic pathways for its internal synthesis would more readily evolve than would those for more complex metabolites. All studied non-synthesizers are deficient in L-gulonolactone oxidase, the last in the sequence of four enzymes in the synthesis of ascorbic acid. This implies that there is no alternate synthetic pathway for its synthesis (Pollock and Mullin, 1987). Consequently, a mutation in even one of the genes that is required for production of L-gulono-lactone could be enough to block the synthesis of ascorbic acid. As a result, once such a mutation occurred, the ability to produce ascorbic acid could quickly disappear in any lineage of synthesizers that, even in the seasons of fallback foods, consistently and readily were able to obtain more than adequate dietary supplies of ascorbic acid. The fact that all tested strepsirrhine primates can synthesize ascorbic acid—possibly excepting Horshfield's tarsiers, *Tarsius baneanus* (Pollock and Mullin, 1987)—but that none of the haplorrhines can suggests that such a mutation occurred in the stem haplorrhines after it split off from the strepsirrhines and that, judging by the small sample of tested species, no appropriate back-mutation has occurred in this suborder.

The above taxon differences in the ability to synthesize ascorbates leads to several predictions about extant primate species. Those that can not synthesize ascorbic acid will not be able to withstand prolonged fallback periods in which available dietary supplies of ascorbic acid are inadequate without suffering from subclinical symptoms of ascorbic acid deficiency (in rhesus: weakness, lethargy, anorexia, weight loss, and muscle and joint pain) or scurvy. Strong selection will favor mutations that enable ascorbate synthesis.

Conversely, those species that can synthesize ascorbic acid may or may not have extended fallback periods in which dietary sources alone would be adequate, but in either case they will not get scurvy or have subclinical symptoms. Among the members of such species that live in long-term stable habitats with reliable and adequate supplies of ascorbic-acid-rich foods, there may be mutant non-synthesizers of ascorbic acid. Selection against any such mutation should be relatively weak. Finally, because ascorbic acid intake has an unusually wide safety margin (Stone, 1972), both synthesizers and non-synthesizers can live on ascorbic-acid-rich diets without ascorbic hypervitaminosis. Thus, from this standpoint, highly frugivorous prosimians are not a paradox. In an unusual study of the habitat, Milton and Jenness (2005) analyzed the ascorbic acid concentrations available in Panamanian neotropical vegetation. During the transition from wet to dry seasons, they were higher in leaves than in most fruits and vegetables.

Store nutrients internally

Some compounds can be stored in the body. For example, lipids are stored in adipose tissues. Glycogen (which can be converted into glucose), oil-soluble vitamins, and iron (Finch et al., 1950) are stored in the liver. "Vitamin B12 is required in very small amounts, is stored in the

tissue, and is passed on from dam to offspring" (Coates, 1968). Thus, for such compounds, excess dietary supplies during some seasons and shortages during others can be converted into adequate availability in all. However, other compounds, those for which no body storage is known, such as water-soluble vitamins and essential amino acids, require frequent access to dietary sources, even during the seasons of fallback foods. Thus, they may exert strong constraints on animals' selection of suitable fallback foods. For essential amino acids, that constraint may be particularly acute: in order to be utilized, essential amino acids must be consumed within a short time of each other, measured in hours, not days (Block and Mitchell, 1946; Albanese and Orto, 1973).

Japanese macaques (*Macaca fuscata*) living in the northern regions of Japan, present an extreme case of adaptation to non-tropical climates. They survive the severe winters by a combination of reliance on winter fallback foods: (buds and bark in deciduous forest, leaves in evergreen forest, which can supply only 60% of their energy requirements and leaves in evergreen forest, which can satisfy 90% of their diet) and fat deposits stored when feeding on high quality foods during the warmer months (young leaves in spring, fruits, insects or mature leaves in summer, and fruit and seeds in autumn). They are heaviest in autumn and lightest at the end of winter (Hanya et al., 2006).

Disperse seeds

A growing body of evidence indicates that many fruit-eating primates disperse seeds from the fruits that they eat, by spitting, dropping, or defecating them (Lambert and Garber, 1998; Lambert, 1999b; and references therein). This is a scenario that at once combines behavior, ecology, anatomy, physiology, and coevolution. Some seeds are of an unusual size (very small) or shape (lenticular) that may favor their passage intact through an animal's dentition and gut. The survival of consumed seeds and the distance from the parent tree at which they are deposited depend on a variety of factors, including the oral processing of the fruit, digestive processes, and gut passage time. While some primates, including Colobinae and Pitheciinae, have evolved dental and gastrointestinal traits that overcome the challenges of a seed diet, for others, such as red-tailed guenons (see below), the pulp surrounding the seeds is the primary source of nutrients that the fruits provide. In the latter species of primates, seeds may account for a considerable portion of the mass of fruits consumed. The naked seeds of fruits are thereby an unwanted mass, and the adhesive pulp must be removed and naked seeds discarded one way or the other (i.e., by mouth or anus). The fruit-producing plants thereby have their seeds dispersed and the primates get fruit pulp that is rich in polysaccharides.

Lambert (2001) discovered an interesting relationship other than seed dispersal in the relationship between red-tailed guenons (*Cercopithecus ascanius*) and the seeds of *Strychnos mitis* trees. Either biting into or swallowing the seeds might be lethal: they contain strychnine. But the seeds are coated with a sweet pulp. In their mouths, the guenons remove the pulp, then spit out the seeds. Lambert found a distinct advantage to the tree in having the guenons remove the pulp. Germination and establishment of seedlings occurred in 60% of the cleaned seeds that the guenons spat out, whereas only 5% of unprocessed seeds did so. The difference apparently resulted from fungal pathogens that attack unprocessed seeds. By facilitating the propogation of *Strychnos* trees, these guenons may thereby increase the fitness of their descendants generations in the future, when today's seedlings become mature *Strychnos* trees. Similarly, my children and my grandchildren will inherit the apple orchard that I planted, even though that was not my motivation for doing so.

ADJUST LIFE HISTORY TRAITS
Life history traits that facilitate learning

Compilations of the literature on species values for life history and other traits, such as those by Kappeler and Pereira (2003), Calder (1983), DeRousseau (1990), Harvey et al. (1987), Peters (1983), document correlations of many traits with body size. However, if other traits are each highly correlated with body size, then correlations among these others are not surprising but should not be assumed. For example, age at weaning is positively correlated with gestation length for extant primates and other Orders of mammals of the same body size (Harvey and Pagel, 1991), contrary to predictions based on an assumed evolutionary trade-off between the two components (e.g., Eisenberg, 1981). The argument runs that, for their adult body size, precocial mammals have long gestation lengths (which is true), produce large and well-developed young (true), which rapidly become independent of their mothers (false).

Statistical techniques have been developed for analyzing, across species, the correlations among traits independent of their correlation with body size or their taxonomic proximity. Lucid expositions of these methods are provided by Purvis et al. (2003) and by Harvey and Purvis (1991). As a result, the growing literature on life history processes and traits closely related to them is not just limited to documenting size-independent correlations of traits across species but uses those correlations to test causal hypotheses about why the revealed correlations evolved and what the directions of causality were. A recent volume edited by Kappeler and Pereira (2003) provides an excellent overview of research on primate life histories and their relationships to socioecology. I limit my discussion to three examples.

Example: Extended length of juvenile period. In the introduction to Anita Stone's study of risk aversion and foraging behavior in juvenile squirrel monkeys, she wrote (Stone, 2005, p. 105, q.v. for references): "Primates are characterized by the longest juvenile period (time between weaning and first reproduction) relative to body size of all mammals (Pereira and Fairbanks, 1993). One explanation for an extended juvenile period is that much time is needed to master complex behaviors needed for adulthood, such as social skills (Poirier and Smith, 1974; Joffe, 1997) and appropriate foraging behaviors (King, 1994; Kaplan et al., 2000). Ross and Jones (1999) and Deaner et al. (2003) classify these explanations as the 'need-to-learn' (NTL) hypothesis for prolonged juvenility in primates." The juvenile period is defined by Stone and others as beginning at the age when nursing terminated, eight months of age in the case of squirrel monkeys. Janson and van Schaik (2002) review evidence from various primate species that juvenile foraging success is less than that of adults.

As a test of possible effects of complex foraging, Stone (2005) studied age-related differences in foraging behavior and efficiency in infant, juvenile, and adult squirrel monkeys (*Saimiri sciureus*) in Brazil. The data revealed no appreciable differences between the foraging behaviors of juveniles, as defined, and adults, and so were considered to be inconsistent with the hypothesis that the need to develop foraging skills accounts for the primate pattern of extended juvenility. Through the first of Stone's three juvenile classes (J1, months 8–12) and then onward through adulthood, only minor differences occurred in the proportions of fruit vs. live prey and in the arthropod capture rate, primarily a peak in arthropod feeding during that first juvenile period.

However, for data relevant to learning to feed, one must look at Stone's data on the transition over the three stages of the squirrel monkeys' *infancy*. The percent of foraging and feeding time that was devoted to fruit (mostly small berries) and to nursing declined steadily as the percent of time devoted to arthropod prey rapidly increased until, during the sixth and seventh months of infancy, both the percent of time devoted to catching and eating Arthropods and the capture rate were essentially indistinguishable from the value for mid- and late juvenile stages and adulthood! That is, for this species and perhaps others, the apparent lack of (or minimizing of) difference between juvenile and adult foraging and thus of any indication of juveniles' learning how to forage can be an artifact of how the juvenile period is being defined. That fact is not surprising when one considers the ability of young primates to learn at very young ages (section 'Live in social groups,' above). In order to evaluate the impact of learning about food on the length of preadulthood, consideration should be given to including in the juvenile stage the period that Langer (2003) refers to as the mixed-feeding period, that is, extending from the time of first intake of solid food until weaning from milk.

Example: Relating brain size and life histories. Deaner et al. (2003), in an analysis of possible linkages between brain size and life history, provide a fine example of the method of multiple working hypotheses (Chamberlin, 1890, reprinted 1965). Across primate species, several studies have shown correlations of brain size with various intercorrelated life history variables that indicate that large-brained primates generally have slow, prolonged growth periods, late sexual maturation, and long lives. For each of seven hypotheses that have been proposed to account for why this "slow lane" cluster of traits has coevolved, Deaner et al. examine implications and evidence that might support or falsify it.

Within-species analysis of life-history socioecology

As revealed by the volume edited by Kappeler and Pereira (2003), almost all attempts at relating primate life histories to social and ecological processes have been based on interspecific comparisons. A complementary approach is to make use of the considerable power of intraspecies analyses of life histories: schedules of survival and reproduction across the life span and of the traits that affect them and that thereby affect fitness. Two approaches have been developed for systematically carrying out such analyses. One is to use demographic matrix models, and in their chapter in that volume, Alberts and Altmann (2003) provide a lucid exposition of

this topic and illustrate it with an example based on data from baboons (*Papio cynocephalus*). Such models provide two results of particular interest in life history analysis. The first is λ, an estimate of the population growth rate, which is analytically equivalent to the relative fitness of the mean phenotype in the population. Second, the strength of selection on life history parameters can be estimated. For example, McDonald (1993), using elasticity analysis, demonstrated that, for long-tailed manakins, selection on survival is an order of magnitude stronger than selection on fertility, that selection on prereproductive survival is much stronger for male manakins than for females, and that male generation times are more than double those of females. Matrix methods can also be used to compare patterns across populations and even between species (e.g., Pfister, 1998).

For analyzing fitness differences among individuals and for identifying selection pressures, the use of matrix models overlaps those of multivariate methods developed by Lande and Arnold (1983), Arnold (1983, 1988), Arnold and Wade (1984a,b). For an illustration of how the method of Arnold (1983) can be applied to measuring contributions to fitness of correlated traits in primates, see Altmann (2006).

Reproductive adjustments to unpredictably severe conditions

Although a majority of cercopithecine primates exhibit seasonal breeding, baboons (spp.) are among the few exceptions (Berkovitz and Harding, 1993), breeding continuously throughout the year. However, when adverse environmental conditions, such as those that lead baboons to resort to fallback foods, are particularly severe or unusually prolonged, females may not be able to maintain physiological status adequate to reproduce.

In an analysis of long-term data on reproductive cycles in adult female yellow baboons, Beehner et al. (2006) studied the effects of two adverse conditions that preceding some cycles, namely, drought or extreme heat. The data that they used are from 2483 reproductive cycles in 166 fully mature females obtained during 1976–2004 as part of the Amboseli Baboon Research Project. A drought was defined as a dry period—that is, months with less than 50 mm of rain—lasting longer than the usual five months of the long dry season, June–October. By this definition, 75% of droughts were a result of failure of the yearly 'short rains,' which normally begin during October–December, thereby producing an extension of the long dry season. Thus droughts are extended periods during which the baboons subsist on a diet consisting largely of fallback foods, such as the underground corms of dry grass plants. Periods of extreme heat (heat waves) were defined as two-month periods in which the mean of maximum daily air temperatures was at least 35°C.

The results demonstrate "that the success of each reproductive event (cycling, conception, and live births) depends primarily on optimal temperature and rainfall conditions preceding each stage. Specifically, after periods of both drought and heat, females were significantly less likely to cycle than expected. Furthermore, if females did cycle after these conditions, they were significantly less likely to conceive. If they did conceive after conditions of drought (conditions of heat were not significant), they were less likely to have a successful pregnancy" (Beehner et al., 2006, p. 746). That is, "baboon

females have a facultative reproduction strategy that 'aborts' at any of the several stages if conditions deteriorate" (Beehner et al., 2006, p. 748). These results combined with the remarkably low levels of total body fat in the one female Amboseli baboon that has been tested (Altmann et al., 1993) suggest that prolonged dry periods are times of strong selection for adaptations to fallback foods.

SUMMARY

Fallback foods are those eaten by animals at times, typically seasonal, when the arrays of foods available to them would result in diets of appreciably lower quality: much less nutritious and more deleterious to harvest and consume than the foods that the animals eat at other times of the year. Fallback foods are foods eaten not by choice but out of necessity. Conversely, high quality diets are not then available because, during fallback food times, no combination of available foods would provide an abundance of each required nutrient at little risk.

The inextricable combination of costs and benefits in all potential foods at all times of the year is the so-called packaging problem and presents primates with the omnivore's dilemma: how to find a combination of foods that will satisfy nutritional requirements and that can be searched for, harvested, and consumed without excessive risk. Times of fallback foods represent the packaging problem at its worst and probably are times when selection for adaptations to the packaging problem is particularly strong.

A sample of primate adaptations to these extreme conditions are described. They occur at every level of biological organization, including group processes, individual behavior, and traits at anatomical, physiological, and subcellular levels, and include components of life histories. That these traits are each discussed in turn does not imply that natural selection acts independently on the traits of organisms. Organisms are integrated, coadapted systems and the extent to which any one trait can develop without jeopardizing the organism's fitness is constrained by the effects of such development on other traits (Futuyma, 1979, p. 49). The sample of adaptations presented herein suggests that food ultimately ramifies into everything that we and other creatures are and everything we do (Altmann, 1989, 1991, 1998).

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