

Introduction to the Symposium Issue

The Importance of Fallback Foods in Primate Ecology and Evolution

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ABSTRACT The role of fallback foods in shaping primate ranging, socioecology, and morphology has recently become a topic of particular interest to biological anthropologists. Although the use of fallback resources has been noted in the ecological and primatological literature for a number of decades, few attempts have been made to define fallback foods or to explore the utility of this con-

cept for primate evolutionary biologists and ecologists. As a preface to this special issue of the *American Journal of Physical Anthropology* devoted to the topic of fallback foods in primate ecology and evolution, we discuss the development and use of the fallback concept and highlight its importance in primatology and paleoanthropology. *Am J Phys Anthropol* 140:599–602, 2009. ©2009 Wiley-Liss, Inc.

“Fallback foods” are foods which people and other animals utilize when preferred foods are unavailable (Marshall and Wrangham, 2007). They have been discussed in studies of modern humans (e.g., Ellis, 1982; Cutler, 1986; Bardhan, 1996), and have received particular attention in the fields of primatology and paleoanthropology. This is due to the recognition that fallback foods may have played a major role in shaping human ecology and evolution as well as the ecology and evolution of our primate relatives (Lambert et al., 2004; Rogers et al., 2004; Laden and Wrangham, 2005; Cuzzo and Sautner, 2006; Grine et al., 2006; Hanya et al., 2006; Hernandez-Aguilar et al., 2007; Marshall and Wrangham, 2007; Xiang et al., 2007; Ungar et al., 2008; Vogel et al., 2008).

Despite the recent introduction of fallback foods into the primatological lexicon, there has been little consensus as to how they should be defined and how inquiry into their importance in primate evolution should be operationalized. This was the primary reason behind a symposium organized for the 77th meeting of the American Association of Physical Anthropologists held in Columbus, Ohio in April of 2008. The symposium had three objectives: define fallback foods, discuss methods for identifying and measuring fallback foods and fallback dietary strategies, and explore the role of fallback foods in the ecology and evolution of primates through the presentation of recent field studies. With these objectives in mind, the symposium was divided into three sections: theoretical context, methods for evaluating the role of fallback foods in the evolution of living and fossil taxa, and case studies in extant primates. This special edition of the *American Journal of Physical Anthropology* (*AJPA*) maintains this organizational structure in presenting the resulting papers from the 2008 symposium. As with more traditional submissions to *AJPA*, all papers appearing here have been peer-reviewed. In this brief preface, we introduce the fallback concept, explore

its history including its introduction to primatology and paleoanthropology, and discuss current areas of research within these fields. We do not review or discuss the articles that follow. This is expertly done by Joanna Lambert at the conclusion of this issue.

THE ECOLOGICAL AND EVOLUTIONARY IMPORTANCE OF FALLBACK FOODS

The ecological and evolutionary importance of fallback foods was made clear in studies of Darwin's finches conducted by Peter Grant and his team on the Galapagos Islands. In 1977, a drought on the island of Daphne Major resulted in a significant decline in the abundance of small seeds, the most frequently utilized food of Darwin's medium-sized ground finch, *Geospiza fortis*. During the drought, large seeds such as those of *Tribulus cistoides* declined in abundance less rapidly than did small seeds, but the large seeds could only be opened by the larger-beaked members of *G. fortis*. This resulted in the preferential survival of large-beaked individuals, and because beak size is largely heritable, this translated into a rapid evolutionary increase in the average beak size of *G. fortis* (Boag and Grant, 1981).

For *G. fortis*, the seeds of *T. cistoides* could be labeled as a fallback food. They were virtually ignored in years

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before the drought but became a critical resource when smaller seeds disappeared. Because only individuals with large beaks could take advantage of this fallback food, it had a major impact on the morphology of the species in subsequent generations. Interestingly, a drought in 2003 and 2004 had the opposite effect on the beak morphology of *G. fortis*. By 2003, the giant-beaked ground finch, *G. magnirostris*, had established itself on the island and regularly consumed the large seeds of *T. cistoides*, thus excluding them as a fallback food for *G. fortis*. The result was increased survivability within *G. fortis* of smaller-beaked individuals. It is believed that these smaller-beaked members of *G. fortis* were able to survive by taking advantage of the very small seeds of *Sesuvium edmonstonei* and *Tiquilia fusca*, although there are no feeding observations to demonstrate conclusively that this was the case (Grant and Grant, 2006). Therefore, while *G. fortis* was able to utilize large *T. cistoides* seeds as a fallback food in 1977, competitive exclusion appears to have led to their exploitation of alternative, and possibly less preferred, fallback foods in 2003 and 2004.

The ecological and evolutionary importance of fallback foods was further emphasized in a mathematical model developed by Robinson and Wilson (1998) as a solution to Liem's paradox. Liem's paradox is the observation that species with seemingly specialized phenotypes can sometimes behave as ecological generalists. For instance, numerous cichlid fish species with elaborate morphological feeding specializations frequently feed on prey items for which their specializations are seemingly not adapted. In one specific example, African cichlids specialized for eating the scales of other fish are often found feeding on algae, zooplankton, or aquatic insects. This discovery initially led researchers to doubt the role of feeding competition as a key diversifying force in ecology and evolution. Karel Liem, a prominent ichthyologist and evolutionary biologist, argued that the morphological specializations of these cichlids are not likely to be adaptive but instead the product of phylogenetic or developmental constraints that are able to persist because they are adaptively neutral (Liem, 1990). The Robinson and Wilson (1998) model presents an alternative solution to this paradox by revealing that morphological specializations for fallback foods may be niche broadening characters that also maintain and encourage community diversity if they do not inhibit the ability to feed on more abundant, nonfallback foods. This model is based on optimal foraging theory, which states that organisms forage in such a way as to maximize their energy intake per unit time (MacArthur and Pianka, 1966). Under this theory, foods that are abundant, high in calories, and/or easily accessed and processed should be preferred by all members of the community. When these preferred foods become scarce, the community can continue to live in sympatry and remain diverse if the species partition the available resource base by turning to less desirable, fallback resources. These resources are often difficult to acquire or process and may therefore require "specialized" morphological features for their exploitation. At the same time, the less challenging and seasonally abundant resources can continue to be exploited by an array of morphological complexes. Robinson and Wilson's (1998) study emphasized the often mechanically-demanding nature of fallback foods while also providing a theoretical basis for the potentially influential role of fallback foods on morphology.

FALLBACK FOODS VERSUS KEYSTONE RESOURCES

Some researchers, intentionally or not, often use the terms "fallback" and "keystone" resources interchangeably (Tutin et al., 1997; White, 1998; Yamakoshi 1998; Ungar, 2004). A point of clarification must be made because, as Marshall and Wrangham (2007) pointed out, these terms do not mean precisely the same thing. A keystone resource is one that plays a critical role in an ecological community. The concept was first introduced by Robert Paine in 1969 to describe the importance of certain predator species in intertidal and coral reef communities. He described the importance of these species in maintaining ecological stability, calling them the "keystone of the community's structure" (Paine, 1969, p. 92). Following Paine's publication, the term was widely adopted, particularly by conservation biologists, and became applied to species in many different taxonomic groups and at many different trophic levels (Mills et al., 1993). Ultimately, the term was extended to resources that are critical to the survival of many species in a community, even though the resource may be rare or narrowly distributed (Primack, 1993).

Even with the broadening of the keystone concept, the central tenant of its definition has always been the disproportionately large effect that the keystone species or resource has on maintaining the community (Terborgh, 1986; Power et al., 1996; Peres, 2000). Removing the keystone causes the community to collapse. Fallback foods need not have such broad importance. It is possible that a fallback food is only exploited by a single species, and the absence of this food in the environment may or may not be detrimental to the consumer, depending in part on whether other fallback foods can be exploited in its place.

FALLBACK FOODS IN PRIMATOLOGY AND PALEOANTHROPOLOGY

The fallback food concept appeared relatively early in primatology. It seems to have been introduced by Hladik (1973) who was commenting on chimpanzees' increased consumption of leaves and stems during periods of low fruit abundance (Tutin et al., 1985). Although the term "fallback food" does not seem to have been widely used at this time, seasonal variation in primate diets quickly became a regular part of primate feeding studies (e.g., Waser, 1975; Chivers, 1977; Fossey and Harcourt, 1977; Hladik, 1977; Wrangham, 1977). These studies made it clear that most primate diets shifted seasonally, even in species living in "stable" tropical forests (Hladik, 1988). In light of optimal foraging theory (MacArthur and Pianka, 1966), researchers also recognized that certain primate foods should be more "preferred" than others. For example, in a study of the feeding behavior of Bornean orangutans, Rodman (1977) discussed the difference between "preferred" and "less preferred" foods and argued that bark was less preferred than fruit because it has a lower energy yield and greater cost of procurement. The combination of these two concepts, dietary seasonality and the prioritization of food resources, led to the understanding that many primates experience a particular time of the year when preferred foods are in short supply and that certain fallback foods can be critical for the survival of these populations (Leighton and Leighton, 1983).

Despite the recognized importance of these seasonally critical resources, the use of the term “fallback food” still did not become widespread until it made numerous appearances in a series of publications on great ape feeding behavior in the 1990s by Wrangham and colleagues (Wrangham et al., 1991, 1996, 1998; Malenky and Wrangham, 1994; Conklin-Brittain et al., 1998). These papers stressed the chemical and nutritional significance of fallback foods and did much to highlight their vital role in primate diets as well as their possible effect on primate social systems. The value of fallback foods was further investigated by Altmann (1998) in a dietary analysis of yearling baboons. Building again on optimal foraging theory, Altmann (1998) argued that food preference is a trade-off between the mean energy density of a food and the rate at which that food can be harvested, and he demonstrated that the low harvest or intake rate of grass corms resulted in them only being eaten by baboons during periods when more preferred foods were scarce.

Another influential study involving fallback foods was that of Lambert et al. (2004) who proposed that the thick tooth enamel of grey-cheeked mangabeys was the result of their fallback diet of hard bark and seeds. This notion that some foods, due to their physical, mechanical, or chemical properties, can play a major selective role in shaping morphological features had been previously explored by Rosenberger and Kinzey (1976) in their discussion of Neotropical primate masticatory adaptations. They noted that the morphology of many species reflected a “critical function,” such as the processing of mechanically-demanding foods. However, Lambert et al.’s (2004) study implicated fallback foods as the agents of morphological change and led both primatologists and paleoanthropologists to think more critically about the selective agents leading to particular trophic adaptations.

The idea of fallback foods influencing morphology has recently been adopted by many paleoanthropologists seeking to understand the dietary adaptations of early hominins. For instance, Laden and Wrangham (2005), building on the earlier work of Hatley and Kappelman (1980), suggested that many of the derived masticatory traits of early hominins could have been the adaptations for the exploitation of plant underground storage organs (USOs). USOs (bulbs, corms, roots, rhizomes, and tubers) are geographically and temporally widespread resources that can pose both ingestive and digestive challenges (Dominy et al., 2008). Fallback foods have also been proposed as a possible solution to unexpected dental microwear patterns in early hominins. Although certain hominin taxa appear to have been morphologically adapted to eating fracture-resistant foods such as hard nuts or seeds, there is little or no sign of these foods in the dental microwear signal of these hominins. For example, Grine et al. (2006) found little evidence of hard foods in the microwear of *Australopithecus (Praeanthropus) afarensis*, and perhaps even more surprisingly, Ungar et al. (2008) found no evidence of hard object feeding in the microwear of *Paranthropus boisei*, a species with large jaws and teeth, thick tooth enamel, and anteriorly-positioned (and presumably large) chewing muscles. In each case, the authors suggested that the consumption of fracture-resistant fallback foods could have been the selective pressure that led to the “robust” masticatory morphology of these hominins. The reasoning is that if the consumption of these foods was a rare but critically important event, then the dental microwear signal would not necessarily show evidence of these foods because

dental microwear only reveals evidence of items that contacted the individual’s teeth in the last few days or even hours before its death (Grine, 1986; Teaford and Oyen, 1989). On the other hand, one could argue that many individuals die during periods of food scarcity, and because it is during these periods that fallback foods are consumed, it is surprising that they would not be represented in the microwear profile of several individuals from a species. Interestingly, if the authors of these microwear studies are correct, then the case of *P. boisei* fits the model proposed by Robinson and Wilson (1998) to solve Liem’s paradox since their “specialized” masticatory morphology would reflect adaptation to the use of an infrequently selected and mechanically-challenging food (Ungar et al., 2008).

As will become evident after reading the contributions to this volume, fallback foods are an important topic of study within both primatology and paleoanthropology. They appear to play a role in the ecology and possibly the evolution of all the major groups of primates. In addition to their influence on morphology, they have been implicated as possibly affecting group size and density (Matsumoto-Oda et al., 1998; Hanya et al., 2006), home range (Hanya et al., 2006), habitat type (Laden and Wrangham, 2005; Dominy et al., 2008), life history (Cuozzo and Sauter, 2006), and even tool use (Yamakoshi, 1998; Fox et al., 1999). Hopefully this volume will serve as a good introduction to the importance of fallback foods, and will set the stage for much further research into this topic.

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LITERATURE CITED

- Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press.
- Bardhan P. 1996. Efficiency, equity and poverty alleviation: policy issues in less developed countries. *Econ J* 106:1344–1356.
- Boag PT, Grant PR. 1981. Intense natural selection in a population of Darwin’s finches (Geospizinae) in the Galapagos. *Science* 214:82–85.
- Chivers DJ. 1977. The feeding behaviour of siamang (*Symphalangus syndactylus*). In: Clutton-Brock TH, editor. Primate ecology: Studies of feeding and ranging behaviour in lemons, monkeys, and apes. London: Academic Press. p 355–382.
- Conklin-Brittain N-L, Wrangham RW, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int J Primatol* 19:971–998.
- Cuozzo FP, Sauter ML. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *J Hum Evol* 51:490.
- Cutler P. 1986. Famine warning, famine prevention and nutrition. *Nutr Bull* 11:23–28.
- Dominy NJ, Vogel ER, Yeakel JD, Constantino P, Lucas PW. 2008. Mechanical properties of plant underground storage

- organs and implications for dietary models of early hominins. *Evol Biol* 35:159–175.
- Ellis F. 1982. Agricultural price policy in Tanzania. *World Dev* 10:263–283.
- Fossey D, Harcourt AH. 1977. Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. London: Academic Press. p 415–447.
- Fox EA, Sitompul AF, van Schaik CP. 1999. Intelligent tool use in wild Sumatran orangutans. In: Parker ST, Mitchell RW, Miles HL, editors. *The mentalities of gorillas and orangutans*. Cambridge: Cambridge University Press. p 99–116.
- Grant PR, Grant BR. 2006. Evolution of character displacement in Darwin's finches. *Science* 313:224–226.
- Grine FE. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. *J Hum Evol* 15:783–822.
- Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006. Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *J Hum Evol* 51:297–319.
- Hanya G, Kiyono M, Yamada A, Suzuki K, Furukawa M, Yoshida Y, Chijiwa A. 2006. Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. *Primates* 47:275–278.
- Hatley T, Kappelman J. 1980. Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of belowground food resources. *Hum Ecol* 8:371–387.
- Hernandez-Aguilar RA, Moore J, Pickering TR. 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. *P Natl Acad Sci* 104:19210–19213.
- Hladik CM. 1973. Alimentation et activite d'un groupe de chimpanzes reintroduits en foret gabonaise. *Terre Vie* 27:343–443.
- Hladik CM. 1977. Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. London: Academic Press. p 481–501.
- Hladik CM. 1988. Seasonal variations in food supply for wild primates. In: de Garine I, Harrison GA, editors. *Coping with uncertainty in food supply*. Oxford: Clarendon Press. p 1–25.
- Laden G, Wrangham R. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopithecine origins. *J Hum Evol* 49:482–498.
- Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *Am J Phys Anthropol* 125:363–368.
- Leighton M, Leighton DR. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. *Tropical rain forest: ecology and management*. Oxford: Blackwell Scientific Publications. p 181–196.
- Liem KF. 1990. Aquatic versus terrestrial feeding modes: possible impacts on the trophic ecology of vertebrates. *Am Zool* 30:209–221.
- MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. *Am Nat* 100:603.
- Malenky RK, Wrangham RW. 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. *Am J Primatol* 32:1–12.
- Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. *Int J Primatol* 28:1219–1235.
- Matsumoto-Oda A, Hosaka K, Huffman MA, Kawanaka K. 1998. Factors affecting party size in chimpanzees of the Mahale Mountains. *Int J Primatol* 19:999–1011.
- Mills LS, Soule ME, Doak DF. 1993. The keystone-species concept in ecology and conservation. *Bioscience* 43:219–224.
- Paine RT. 1969. A note on trophic complexity and community stability. *Am Nat* 103:91–93.
- Peres CA. 2000. Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *J Trop Ecol* 16:287–317.
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystones. *Bioscience* 46:609–627.
- Primack RB. 1993. *Essentials of conservation biology*. Sunderland, MA: Sinauer Associates Inc.
- Robinson BW, Wilson DS. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. *Am Nat* 151:223–235.
- Rodman PS. 1977. Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. London: Academic Press. p 383–413.
- Rogers ME, Abernethy K, Bermejo M, Cipolletta C, Doran D, McFarland K, Nishihara T, Remis M, Tutin CE. 2004. Western gorilla diet: a synthesis from six sites. *Am J Primatol* 64:173–192.
- Rosenberger A, Kinzey W. 1976. Functional patterns of molar occlusion in platyrrhine primates. *Am J Phys Anthropol* 45:281–298.
- Teaford MF, Oyen OJ. 1989. In vivo and in vitro turnover in dental microwear. *Am J Phys Anthropol* 80:447–460.
- Terborgh J. 1986. Keystone plant resources in the tropical forest. In: Soule ME, editor. *Conservation biology: the science of scarcity and diversity*. Sunderland, MA: Sinauer Associates, Inc. p 330–344.
- Tutin C, Fernandez M, Pierce AH, Williamson EA. 1985. Foods consumed by sympatric populations of *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon: some preliminary data. *Int J Primatol* 6:27–43.
- Tutin CEG, Ham RM, White LJT, Harrison MJS. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *Am J Primatol* 42:1–24.
- Ungar P. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *J Hum Evol* 46:605–622.
- Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE* 3:e2044.
- Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *J Hum Evol* 55:60–74.
- Waser P. 1975. Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). *Afr J Ecol* 13:249–263.
- White FJ. 1998. Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. *Int J Primatol* 19:1013–1027.
- Wrangham RW. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. London: Academic Press. p 503–538.
- Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew WC, Marchant L, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 45–57.
- Wrangham RW, Conklin NL, Chapman CA, Hunt KD, Milton K, Rogers E, Whiten A, Barton RA. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. *Philos Trans Biol Sci* 334:171–178.
- Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int J Primatol* 19:949–970.
- Xiang ZF, Huo S, Xiao W, Quan RC, Grueter CC. 2007. Diet and feeding behavior of *Rhinopithecus bieti* at Xiaochangdu, Tibet: adaptations to a marginal environment. *Am J Primatol* 69:1141–1158.
- Yamakoshi G. 1998. Dietary response to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *Am J Phys Anthropol* 106:283–295.