Published in final edited form as:

Primates. 2013 April ; 54(2): 111–124. doi:10.1007/s10329-012-0335-1.

On folivory, competition, and intelligence: generalism, overgeneralizations, and models of primate evolution

Ken Sayers

Language Research Center, Georgia State University, 3401 Panthersville Rd, Decatur, GA 30034, U.S.A. (lrckas@gsu.edu)

Abstract

Considerations of primate behavioral evolution often proceed by assuming the ecological and competitive milieus of particular taxa via their relative exploitation of gross food types, such as fruits versus leaves. Although this “fruit/leaf dichotomy” has been repeatedly criticized, it continues to be implicitly invoked in discussions of primate socioecology and female social relationships, and explicitly invoked in models of brain evolution. An expanding literature suggests that such views have severely limited our knowledge of the social and ecological complexities of primate folivory. This paper examines the behavior of primate folivore-frugivores, with particular emphasis on gray langurs (traditionally, *Semnopithecus entellus*) within the broader context of evolutionary ecology. Although possessing morphological characters that have been associated with folivory and constrained activity patterns, gray langurs are known for remarkable plasticity in ecology and behavior. Their diets are generally quite broad and can be discussed in relation to “Liem’s paradox,” the odd coupling of anatomical feeding specializations with a generalist foraging strategy. Gray langurs, not coincidentally, inhabit arguably the widest range of habitats for a nonhuman primate, including high elevations in the Himalayas. They provide an excellent focal point for examining the assumptions and predictions of behavioral, socioecological, and cognitive evolutionary models. Contrary to the classical descriptions of the primate folivore, Himalayan and other gray langurs—and, in actuality, many leaf eating primates—range widely and engage in resource competition (both of which have previously been noted for primate folivores) as well as solve ecological problems rivaling those of more frugivorous primates (which has rarely been argued for primate folivores). It is maintained that questions of primate folivore adaptation, temperate primate adaptation, and primate evolution more generally cannot be answered by the frequent approach of broad characterizations, categorization models, crude variables, weakly correlative evidence, and subjective definitions. As a corollary, many current avenues of study are inadequate for explaining primate adaptation. A true understanding of primate ecology can only be achieved through the utilization of mainstream evolutionary ecology, and thorough linkage of both proximate and ultimate mechanisms.

Keywords

Niche breadth; Liem’s Paradox; “fallback foods”; socioecology; day range; group size; brain evolution; evolutionary ecology; *Semnopithecus entellus*; Colobinae

False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for every one takes a salutary pleasure in proving their falseness.

Charles Darwin, *The Descent of Man and Selection in Relation to Sex* (Darwin 1874/1998:629)

Introduction

The foraging strategy of an animal influences virtually every facet of its existence, and it is therefore not surprising that contrasts have frequently been made between primate folivores and those with other dietetic categorizations, such as frugivores, insectivores, and gummivores. Years ago, it was common for primate ecologists to provide explicit generalizations about folivore behavior or evolution influenced by the common premise that “the world is green” (Stephens and Krebs 1986:116), and the greener, or leafier, the diet, the less likely that food will be limiting. With what was considered an abundant resource base, primate folivores were expected (and in some cases found, Clutton-Brock and Harvey 1977) to travel only short distances per day, and exhibit small home ranges and frequent inactivity (Hladik 1975; Oates 1987). Despite increasing evidence to the contrary, leaves were in some cases described as sufficiently plentiful that they were considered an unlikely focus of within or between-group competition (see Wrangham 1980; Isbell 1991; Sterck et al. 1997; Isbell and Young 2002). Since primate folivores exploit items that are hypothetically easy to locate and harvest, they were (and, it must be said, still are) contrasted with frugivores which seek dietary items more scattered in time and space, and also with extractive foragers which exploit foods that are perceptually hidden. Leaf-eaters were thus expected to possess relatively smaller brains, or score lower on various scales of brain complexity, than other primates (Milton 1981; Gibson 1986; Walker et al. 2006).

It could be argued that the preceding paints a straw man, that no one really thinks like this anymore, or that all the wonders and complexity of primate folivory are currently being investigated. But this would be incorrect and—at least for future study of our leaf eating relatives—a horrible miscalculation. As will be detailed, it is true that a dedicated group of workers have battled the idea that leaves are ubiquitous or easy to locate and harvest, and have emphasized instead that primate folivory is more nuanced and variable than once assumed (Glander 1981; Koenig et al. 1998; Snaith and Chapman 2005; Rosenberger et al. 2011). But it is instructive to consider the topics that have or have not been investigated with primate folivores.

Outside of limited investigations related to howler monkey trichromatic color vision (Surridge et al. 2003), the perceptual basis of primate leaf eating has basically remained unstudied, and in contrast to the excellent work performed with frugivores (e.g., Laska et al. 2007). There have been essentially no investigations of the proximate factors determining movement in folivores, particularly as it pertains to spatial memory, and again in decided juxtaposition to more frugivorous primates (Menzel in press). There has, in fact, been little cognitive testing *of any kind* on primate leaf eaters (Rumbaugh et al. 1996; Tomasello and Call 1997; Johnson et al. 2002). In questions of socioecology folivores have fared better (see below), but much of this work has been devoted to demonstrating feeding competition (e.g., Borries et al. 2008). It is sobering that such effort must be expended to simply confirm that resources are limited, as this idea was an extraordinarily modest assumption for essentially all animals even during the birth of modern evolutionary theory (Darwin 1858; Wallace 1858).

It is argued here that the manner in which primate folivores are being studied is often (but not always) related directly to overly broad, written or unwritten assumptions—originated long ago but continued today—about the nature and distribution of all vegetative plant parts. In the case of socioecology, the same assumptions that were once explicit, although since contested, are today still made, only implicitly. In the case of brain evolution, the “fruit/leaf dichotomy” remains decidedly explicit. This paper provides arguments against broad characterizations of niches, foraging strategies, competitive regimes, or intelligence based on the gross food categories that are consumed. As noted, it is an argument that has been

made before in primate socioecology, although certainly not in the same fashion, as this paper takes issue with numerous methodologies popular in current primate research. The argument, in addition, has only rarely been considered in the context of primate brain evolution. Although examples will be freely taken from taxa throughout the order, particular focus will be given to gray langur monkeys, traditionally *Presbytis entellus* or *Semnopithecus entellus* (Napier 1985; Koenig and Borries 2001).

Upon first glance—and even after somewhat detailed anatomical study—gray langurs appear to meet all the requirements for being what were classically deemed specialist primate folivores (Hill 1964). Their thumbs are small, particularly in relation to other phalanges, and this reduces manipulative capabilities to the sort of thumb-to-hand pincer movements that were considered acceptable for harvesting leaves, but little else (Napier and Napier 1967). Like all colobine monkeys, gray langur dentitions are characterized by post-canine teeth with extensive shearing surfaces, long thought to be ideal, in part, for slicing through foliage (Lucas and Teaford 1994; Strait 1997) and they lack the large incisors typical of primate frugivores (Hylander 1975). Also like the other members of their subfamily, and similar to ruminants, gray langurs have a large, sacculated stomach containing symbiotic microbes that aid in the digestion of high-fiber foods (Ayer 1948; Bauchop and Martucci 1968; Chivers and Hladik 1980; Kay and Davies 1994). In short, there is no question that gray langurs have myriad specializations related to leaf consumption, and indeed they include a large amount of foliage in their diet at basically all sites where they have been studied in detail (reviewed in Koenig and Borries 2001; Sayers and Norconk 2008). They are not, however, the “typical” primate folivore—which is scarcely surprising, as there is no such thing.

Gray langurs provide an excellent argument that primate “folivores” and “frugivores” (and any other dietary group) should be studied in essentially the same manner. They are not specialists—indeed, among primates, there are few species that are as ecologically pliable or phenotypically adaptable. Gray langurs, along with many other folivorous primates, also show patterns in ranging and behavior that contrast markedly with past and present (but hopefully not future) dictates of primate socioecological and cognitive evolutionary models. It is argued that questions of primate folivore adaptation, temperate primate adaptation, and primate evolution more generally, cannot be elucidated by the frequent approach of broad characterizations, categorization models, and subjective definitions. They can only be answered by explicit focus on variables long known to be of importance to evolutionary ecology, and by the linking of both proximate and ultimate causes.

Specialization, generalization, Liem’s Paradox, and the notion of “fallback foods”

Although terms like “specialist” and “generalist” are frequently employed in the literature, it is important to stress that these are not truly discrete categories, and are often used for convenience. Specialization and generalization, in reality, refer to two poles on a continuum of ecological strategies, and can be measured with estimates of niche breadth. Pioneering efforts formally defined the ecological niche as an n-dimensional space that denotes the conditions that an organism actually lives in (the realized niche, Hutchinson 1957) or could potentially live in (the fundamental niche, Hutchinson 1965).

As a niche is extraordinarily complex, and may include innumerable ecological, geological, physiological, and behavioral parameters, workers often consider only one or several aspects of a niche at a time, such as the dietary niche (Shipley et al. 2009). Organisms that possess a smaller niche breadth are relatively more specialized than those with a larger, or more generalized, niche breadth. As noted, since this is a continuum, only comparative statements

can be made concerning specialism versus generalism (e.g., taxonomic unit A versus taxonomic unit B, Pianka 1994). And given that organisms undoubtedly vary in relation to, for example, where they can live or what they can eat, recent arguments that “generalism” does not occur in nature (Loxdale et al. 2011) appear to be related to an incomplete understanding of the niche concept. Indeed, in an analogy to life history theory (MacArthur and Wilson 1967), this is tantamount to denying that organisms vary in relation to density-dependent mortality or reproductive effort.

There is little question that gray langurs have a relatively wide niche breadth in terms of both habitat and diet. The traditional taxonomic view of one species of gray langur, *Presbytis entellus* or *Semnopithecus entellus* (e.g., Napier 1985; Koenig and Borries 2001) is followed here. The same arguments, it should be noted, hold for revisionist frameworks, generally based on the phylogenetic species concept, that recognize multiple species of gray langur (Groves 2001; but see Sayers and Norconk 2008) and would necessitate using genus rather than species as the comparator taxonomic unit.

Gray langurs occupy an extraordinary plethora of environments over the Indian subcontinent and Sri Lanka, including moist (Newton 1992) and dry forest (Yoshida 1967), and, aided by provisioning, villages, farmland (Oppenheimer 1978), and desert (Winkler 1988; Holland 2011). Most spectacularly, gray langurs also live in temperate forest and subalpine scrub at high elevations in the Himalayas (provisioning does not occur in the Himalayan regions, but some populations raid potato and other mountain crops, Bishop 1979; Curtin 1982; Sayers and Norconk 2008). Among living primates, this diversity in the environments that are occupied—which relates to realized niche breadth—can be matched only by *Homo sapiens* and possibly *Macaca mulatta* at the species level, and *Homo*, *Macaca*, and possibly *Alouatta* and *Papio* at the genus level (Richard et al. 1989; Rowe 1996; de Marques 2002; Hart and Sussman 2005; Maestripietri 2007).

Gray langurs are also known for their eclectic feeding habits, which extend to basically all general primate food types save vertebrate flesh—including leaves, fruits and seeds, flowers, invertebrates, underground storage organs, algae, gum, and fungi (Ripley 1970; Newton 1992; Koenig and Borries 2001; Sayers and Norconk 2008). This is exemplified by populations living in the temperate/alpine Himalayan regions, as such habitats are characterized by remarkably strong but inter-annually consistent seasonality (Hanya et al. 2012).

According to contingency models from optimal foraging theory (Charnov 1976; Sih and Christensen 2001), a forager’s diet is related to characteristics of the environment (e.g., the nutritional characteristics of food, their associated handling times, and their scatter in the habitat) in addition to the characteristics of the animal (e.g., alimentary features). For a given animal with given morphology, the optimal diet is determined by the profitability (e.g., energy/handling time) of food types, and their availability relative to each other. The predicted diet will thus change as the habitat changes. When highly profitable foods are common, the forager is expected to exploit fewer food types; when they are rare, the diet is expected to expand to include other, less-profitable items (Pyke et al. 1977). Dietary niche breadth (Shipley et al. 2009) is thus related to both the anatomical and physiological characters that determine which foods an animal *can* consume, and the environmental factors that influence which foods an animal *needs to* consume.

In Himalayan regions, shifts in food availability are anything but subtle, and thus illustrate well the pliability of the gray langur diet. At Langtang National Park, Nepal (3000 – 4000 m), for example, spring is characterized by an extensive flush of deciduous leaves, which remain available over the course of a mild monsoon that exhibits an increasing number of

flowering and fruiting events. The availability of these foods—all taken by the langurs—decreases gradually throughout the fall and into the cold, and often snowy, winter. By late winter deciduous leaves and flowers are essentially nonexistent, and ripe fruits are rare and limited to the plant genus *Cotoneaster* (Sayers and Norconk 2008).

An analysis including food profitability (energy/handling time or crude protein/handling time) and encounter rates (specific patch type encountered per unit search time) demonstrates that during the “crunch time” of winter, the Himalayan langur diet expands to include nonseasonal foods of low caloric or protein value—and high fiber content—for the time taken to harvest them, such as certain species of evergreen mature leaves, evergreen mature leaf petioles, bark, and woody roots (Sayers et al. 2010). The annual langur diet at Langtang also includes herbaceous vegetation, young bamboo shoots, mosses and lichens, a small number of invertebrates, and other items. Even in this comparatively barren habitat, with low productivity compared to tropical or subtropical primate sites, plant foods alone come from a minimum of 30 families (Sayers and Norconk 2008). General trends with respect to diet also appear to hold at other Himalayan langur sites in Nepal, such as Melemchi (Bishop 1975) and Junbesi (Curtin 1982), and at Machiara National Park in Pakistan (Minhas et al. 2010).

So while Himalayan and other gray langurs are exemplified by morphological and physiological characters that signal folivory, they are ecological generalists with respect to habitat and diet. In particular, they (and some other colobines, Kirkpatrick 1999) appear to be prime examples of Liem’s Paradox—first identified in cichlid fishes, this is the odd coupling of specialized anatomical features related to diet with a “jack of all trades,” or generalist, feeding strategy (Liem 1980:295; Binning et al. 2009). According to foraging theory, extreme specializations—such as those colobines possess to process high-fiber foods such as mature leaves or bark—can evolve for exploiting foods of low profitability that, while ignored during times of plenty, are critical for survival in periods of dearth (Robinson and Wilson 1998). As another interesting primate example, the extreme post-canine megadontia of robust australopithecines might not reflect a specialization on hard-objects or other difficult-to-process foods, but rather an adaptation for exploiting such items when resource abundance was low, and without eliminating the ability to consume easier-to-process foods (Peters and Vogel 2005; Ungar et al. 2008; contra Cerling et al. 2011).

Much recent attention in primate ecology, and rightly so, has been devoted to identifying such “fallback foods,” often by correlating use and abundance (Marshall and Wrangham 2007). It is crucial to note, however, that the evolutionary importance of such items has long been recognized—and investigated in a much more thorough and informative manner—in the aforementioned diet breadth models from foraging theory (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971; Charnov 1976; Robinson and Wilson 1998). The application of such models involves the identification of a nutritional currency, as well as the quantification of individual-specific, food item-specific handling times and encounter rates. Grounded in the observed link between foraging and reproductive fitness (e.g., Ritchie 1990; Altmann 1998), they predict the set of foods that maximize long term gain rate while foraging, and have had great success, over a wide range of taxa, in predicting changes in diet breadth related to variation in the encounter rates with (abundance of) profitable foods. While the “fallback foods” approach is largely descriptive, the foraging theory approach is predictive, will identify “fallback foods” when such exist, and necessitates or encourages the collection of myriad data relevant to myriad topics—not only dietetic questions, but also those of niche theory, competition, the ontogeny of resource use, and the physiological, sensory, and behavioral bases of decision-making. As exemplified by recent work on feeding perception and cognition (Sherry and Mitchell 2007; Kolling et al. 2012), foraging

theory provides an important link between proximate mechanisms and ultimate causation (Sih and Christensen 2001).

Socioecological models and assumptions reconsidered

Several modifications of a common “socioecological model” have been developed in an attempt to explain primate—or at least female primate—grouping and/or dispersal patterns, and these generally proceed by placing primate populations or species into discrete categories based on risks of predation or infanticide, resource distribution, female bonding, and patterns of resource defense (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; reviewed in Clutton-Brock and Janson 2012). One major component of this gradually morphing model is that (female) social relationships are determined by patterns of resource competition within and between groups—particularly, associating in-group cohesion with out-group hostility—an idea (the amity-enmity complex) that dates back to 19th century sociology (e.g., Spencer 1896) and which anchored popular discussions of human evolution in the 1940s (Keith 1948) and animal territoriality in the 1960s (Ardrey 1966).

The current primate socioecological model (or synthetic model, Thierry 2008) is also influenced by treatments from earlier mainstream ecology (Crook and Gartlan 1966; Emlen and Oring 1977) which considered environmental factors as essential for shaping primate or vertebrate social systems. It is in some ways, however, clearly divorced from them. In comparison with Crook and Gartlan, this is on the whole a good thing—their 1966 paper, while influential, was an admittedly preliminary categorization of primate genera and/or species into five adaptive grades linking broad habitat characteristics with what was then known or assumed about diet, activity patterns, and reproduction. The primary associations with the current primate socioecological model are partial overlap in the variables that are included, particularly predation pressure and the dispersion of resources, and the lack of reference to phylogenetic factors. Differences include the limitation of focus to female behavior and ecology in the current socioecological model, as well as the incorporation of new data from field and, to a far lesser degree, laboratory. Further work has shown many of the assumptions of the Crook/Gartlan model to be problematic, including the assertion that forest primates on the whole live in small groups, and, more important, the assertion that a small list of habitat “types” (forest, forest-fringe, tree-savannah, grassland) adequately convey the ecological complexity of primate environments (Clutton-Brock and Janson 2012).

The current primate socioecological model, while agreeing on the importance of the environment, contrasts with Emlen and Oring’s (1977) landmark paper on mating systems in the following respects: 1) phylogenetic factors, a first-step determinant of individual capacity to exploit the “environmental potential for polygyny” (EPP) in Emlen and Oring’s analysis, are, as noted above, ignored, 2) female distribution is generally assumed to be based on ecological characters (food distribution and/or predation pressure) or limited social concerns such as infanticide, while Emlen and Oring, in some cases, allow for females to be clumped or dispersed for alternative (e.g., phylogenetic) reasons, and 3) the primate socioecological model, as noted, is focused largely or exclusively on females, while Emlen and Oring shift their focus from males to females based on factors such as the operational sex ratio (OSR).

It is interesting to note that criticisms (or polite suggestions for improvement) of the socioecological model (e.g., Sussman et al. 2005; Koenig et al. 2006; Sussman et al. 2006; Thierry 2008; Koenig and Borries 2009; Clutton-Brock and Janson 2012) are often related to those very points from where it deviates from the treatment of Emlen and Oring (1977). This

includes specifically the lack of attention to male ecological or social concerns—or their potential importance for female distribution and behavior—including the observation that males often take the lead role during resource defense or between-group encounters (Fashing 2007; Thierry 2008). Recent workers have also emphasized the critical role of phylogenetic inertia (Thierry 2007; Chapman and Rothman 2009; Shultz et al. 2011), which was actually evident (albeit not discussed) in the essentially *scala naturae* progression of the five adaptive grades of Crook and Gartlan (1966).

It is also evident that the popularity of the socioecological model has focused attention on certain proximate mechanisms at the expense of others. The clear winner in this regard is the study of competition (e.g., Janson 1985; Janson 1990; Snaith and Chapman 2008) to the dismay of some workers (Sussman et al. 2005). But other proximate factors, even those directly relevant to the limited universe of the socioecological model, remain little studied (particularly in folivores) or infrequently cited. Relatively little-studied topics are the perceptual and cognitive factors by which primates estimate predation danger (Cheney and Seyfarth 1992) or food distribution (Menzel in press) and the physiological and behavioral underpinnings of primate dispersal (Crockett 1984; Stumpf et al. 2009). Remaining largely uncited are key experimental studies related to group formation (e.g., Kummer 1975) and the voluminous psychological and physiological literature on social bonding and attachment, of which there is an excellent primate focus (reviews in Mendoza and Mason 1989; Mendoza et al. 2002). In this regard, it is interesting to note that there is surprisingly little evidence in nonhuman primates for the socioecological model's core assumption that within-group cohesion is accentuated by increasing conflicts between groups (Mason 1976; Cheney 1992; Cords 2002).

One unfortunate repercussion of the early work concerning the socioecological model was a stereotyping of leaves as abundant compared with other gross plant parts in terms of scarcity, "patchiness," and defensibility. It was noted, for example, that the biomass of reproductive plant parts, such as flowers and fruits, are much lower than vegetative plant parts, such as leaves (Oates 1987). The repercussions of this are: 1) that leaves can be exploited over a much smaller spatial scale, and 2) that leaves are also less likely to be the targets of feeding competition (Janson and Goldsmith 1995; Kamilar and Ledogar 2011).

Data does indeed show that folivores on average (Clutton-Brock and Harvey 1977) travel shorter distances per day than similarly-sized frugivores, but there are likely many exceptions to this rule (see below). More important is that this correlation tells us essentially nothing about the mechanisms of foraging. The abstraction of feeding behavior to a two-dimensional scale (as it is generally measured) may or may not relate to the complexities of real foraging in n-dimensional space. A hypothetical example will help illustrate this point. Suppose a spider monkey gorges itself on fruit and then travels for 700 m and randomly encounters another fruit tree, where it commences to eat again (see Ramos-Fernandez et al. 2004 and Boyer et al. 2006 for models of random and memory-based encounter; it is likely a mixture of both are important in reality). A hypothetical howler monkey, in contrast, spends minutes in a tree visually inspecting leaves, gaining sensory information on them through touch, and eating only the choicest examples. After reducing the availability of "good" leaves, it travels 20 m to the next visible tree of that species and repeats the process. Based just on the ranging criterion, some primate ecologists might say that the spider monkey has a more complex foraging strategy. But in this hypothetical case, most psychologists would likely opt for the howler monkey. This example highlights why obtaining data on the proximate mechanisms of food choice is vitally important for understanding foraging strategy.

It has been repeatedly argued that it is not the general food types (e.g., leaves, fruit) that are important, but rather the distribution of specific foods, how and by what means animals respond to such heterogeneity (of which we know some, Terborgh 1983; Menzel and Juno 1985; Koenig et al. 1998; Snaith and Chapman 2007), and the perceptual and memory information that is manipulated during the foraging process (of which we know very little, Dominy et al. 2001; Sayers and Menzel 2012; Menzel in press). Despite this, old stereotypes concerning general plant part categories persist in the literature, even among workers studying folivores. In one example, Vandercone and colleagues (2012), after finding that *Trachypithecus vetulus* and *Semnopithecus entellus* prefer fruits and flowers over other gross plant parts, argue that this “supports the increasing recognition that we should not regard colobines as subsisting primarily on leaves and *hence not being food limited*, as this is an oversimplification” (emphasis added). While it is indeed an oversimplification to categorize colobines as strict folivores, it is equally an oversimplification to exclude leaves of any type as a possible limiting resource.

Indeed, the “fruit/leaf dichotomy,” in relation to the socioecological model, is still frequently employed, although its use is becoming more implicit rather than explicit. A recent review, for example, examined the socioecological model’s prediction that female dispersal is related to resource competition and food distribution (Clutton-Brock and Janson 2012). The prediction is examined not by presenting quantitative data, but instead by noting (in addition to other comparisons of gross dietetic categorizations) that “folivorous” gorillas and frugivorous chimpanzees have similar dispersal patterns. The authors contend that this argues against the prediction of the model; the underlying assumption, of course, is that leafy food resources and fruits are inherently different in their dispersion as well as their capacity to generate competition. This assumption may not always hold, however, and indeed may be dangerous to apply in the absence of detailed, quantitative data (see below).

Another example of the implicit application of a fruit/leaf dichotomy is the frequent contrast drawn between the “nutritional value” or “quality” of these resource categories. The common wisdom is that fruits are of higher quality than leaves (Aiello and Wheeler 1995; Fish and Lockwood 2003; Allen and Kay 2012), which implicitly suggests, in the context of the socioecological model, that fruits are more likely to be targets of competition (Wrangham 1980). There are several serious objections to such assertions. The first is that while leaves on average contain higher levels of fiber than fruits (and higher levels of protein, Milton 1999), there is tremendous variation within and between species of fruit or leaf—and thus certainly within and between these gross plant part categories—in all major nutritional components, including, but not limited to, proteins, sugars, fats, fiber, and energy (e.g., Rothman et al. 2007). Statements about general quality should ideally be expressed in relation to particular quantifiable factors (e.g., energy, fiber) based on detailed nutritional work, and preferentially in association with handling time data. When such work is done, clear distinctions between gross plant part categories are not as clear-cut as is often simplified in the literature (e.g., Koenig et al. 1998; Nakagawa 2009; Sayers et al. 2010).

In addition, general food value or quality cannot be compared or contrasted across animal species unless: 1) the species in question are sufficiently similar in anatomy and physiology as to assure similar assimilation of the chemical contents of foods, or 2) corrections in “biologically usable” nutrient contents are made to account for such differences in assimilation (note that very little primate data currently exists for such precise corrections). The specific nutritional contents of foods can of course be compared (Conklin-Brittain et al. 1998) but general statements concerning value cannot be made across species without these considerable reservations. The profitability of a particular leaf to a colobine monkey, for example, will differ from that of a hominoid or cercopithecine (i.e., may be more valuable) because of characteristics of their dentition and digestive tract. Generalizations about food

quality between animals of differing morphology—even between certain closely related species such as spider and howler monkeys—are uninformative and potentially misleading, particularly when related to competitive regimes.

In relation to general foraging strategy and range use, it is well known that primate folivores do not feed indiscriminately, but rather are very selective, often preferring young leaves or non-leaf resources when available (reviewed in Kirkpatrick 1999). In some cases time may be expended “sampling” leaves from particular trees, presumably to gain sensory information about them, before returning at a later time (mantled howler monkeys, Glander 1981). In addition, regardless of gross food category, when resources are sufficiently rare—such as small patch sizes or large between-patch distances—animals irrespective of taxa are expected to respond in similar ways in terms of diet selection, patch residence time, or search time. While such issues have long been investigated in traditional evolutionary ecology (Emlen 1966; MacArthur and Pianka 1966; Stephens and Krebs 1986), they are addressed only rarely in primate studies (Grether et al. 1992; Nakagawa 2009).

Daily travel distance can be influenced by a number of factors, both ecological and social, but food distribution is often one of its prime determinants. As noted, folivorous primates are generally expected to traverse shorter distances in a given day than frugivores, but this can be altered when their foods are sufficiently scattered in space. Himalayan gray langurs on average travel over 1000 m per day at the three sites where this variable has been measured: Junbesi, Nepal (Curtin 1975), Langtang National Park, Nepal (Sayers and Norconk 2008), and Machiara National Park, Pakistan (Minhas et al. 2012). Similar to some lowland gray langur populations (Newton 1992; Koenig et al. 1997), these are comparable to the day ranges of some highly frugivorous primates (Di Fiore and Campbell 2007), including those with similar group sizes (Pombo et al. 2004), and may include a greater degree of three-dimensional, altitudinal movement.

Daily path length, however, is a crude measure with little inherent value unless the factors predicting its variation are elucidated. At Langtang, Himalayan langur ranging patterns are closely linked to resource availability (Sayers and Norconk 2008). During late fall and winter, when path lengths are the longest, deciduous leaves—which are preferred over evergreen leaves and higher in energy/protein and lower in fiber—are rare or absent in the environment, and encounter rates with food patches per unit search time are decidedly low (Sayers et al. 2010). It is clear that the seasonal increase in between-patch distances, with associated increases in between-path travel times, is a major factor driving movement patterns in this population. Indeed, it has been argued that deciduous leaves are, at least seasonally, far more “patchily” distributed at Langtang than ripe fruits at many or most tropical or subtropical primate sites (Sayers and Norconk 2008).

Although it is still sometimes downplayed (Kamilar and Ledogar 2011), feeding competition, including what are loosely termed as scramble and contest competition, occurs regularly in gray langurs and other folivorous primates (see Rank et al. 2006 for a discussion of the gray area between these two “types” of competition). Scramble competition generally relates to resources being exploited on a first-come basis; early arrivers to certain patches will benefit by consuming items that are then unavailable to latecomers (van Schaik 1989). With all other variables held constant, such competition could be expected to increase with group size (but see Sussman and Garber 2007), and influences of group size on daily path length, group spread, feeding time, and/or female reproductive fitness—all potential responses to or indicators of scramble competition—have been documented in red (Snaith and Chapman 2008) and ursine colobus (Teichroeb et al. 2003; Teichroeb and Sicotte 2009). In a similar vein, Phayre’s leaf monkeys living in larger groups are categorized by later age of weaning and slower female reproduction (Borries et al. 2008). These variables, however,

are all far removed from what individual animals are actually doing in and between individual food patches, and it is sometimes advisable to go directly to the horse's (or monkey's) mouth. For example, the quantification of patch depression (as opposed to patch depletion, see Charnov et al. 1976; Stephens and Krebs 1986)—the reduction of intake rates in a patch over time unrelated to satiation effects—has been utilized effectively to argue for scramble competition in red colobus (Snaith and Chapman 2005).

Contest competition, as usually defined, is more straightforwardly observable, and involves direct, antagonistic exclusion of certain individuals, usually of comparatively lower rank, from certain resources (Janson 1985; van Schaik 1989; Isbell 1991; Sussman et al. 2005). While this definition makes contest competition comparatively easy to quantify, it unfortunately excludes certain behaviors that are clearly related, such as avoidance (see Koenig and Borries 2006). At Ramnagar in the southern terai (lowland) region of Nepal, for example, female gray langurs have a linear dominance hierarchy, and an analysis of patch distribution and the nutritional content of foods suggests that their resources, even leaf resources, can profitably be exploited by contest. High-ranking females have access to high-quality patches, while low ranking females generally feed peripherally in resources of lower quality (Koenig et al. 1998; Koenig and Borries 2001).

In the Himalayas, where productivity is low and many plant species are small in size and widely spaced—and the monkeys likely run on an energy deficit over a significant portion of the year—similar contests can be expected. This is well exemplified by the rates at which focal langurs at Langtang National Park were displaced (chased) from feeding sites, as determined from continuous recording of foraging bouts (Sayers et al. 2010) over the course of a year (Table 1). Several important points can be made from this data set: 1) displacements during leaf feeding bouts do not necessarily occur more nor less often than during consumption of other food parts, including fruits, 2) non-alpha adult males are displaced from feeding sites (almost exclusively by more dominant males) at rates nearly identical to which adult females are displaced, contradicting the frequent but rarely tested assumption (Sterck et al. 1997) that feeding competition is necessarily greater in female primates, 3) intriguingly high rates of displacement are related to foods (underground storage organs; all displacements were related to valued cultivated varieties) high in profitability (cf. Janson 1985), as defined by metabolizable energy to handling time (Sayers et al. 2010), and 4) the rates of agonism during feeding for Himalayan langurs are broadly similar to, if not greater than, those of more frugivorous primates (Sussman and Garber 2007). In addition, 34/374 (9.1%) of langur departures from feeding patches were precipitated by active displacement or interference by another individual. Himalayan langurs thus provide yet another example that gross food categories are insufficient for predicting competitive regimes or for making generalizations about feeding behavior.

The future of the primate socioecological model remains uncertain. One worker has argued that it “impedes the development of new lines of thought,” does not fit with existing data, and should be abandoned (Thierry 2008:93). Others have countered that much of the requisite data for adequately testing the model has yet to be collected (Koenig and Borries 2009) and/or that the model can be salvaged with moderate modification (Clutton-Brock and Janson 2012). There is a case to be made for all of these perspectives. Certainly the practice of ignoring phylogeny or individuals carrying Y chromosomes should be thrown in the dustbin of history (although the latter remains dogma, Clutton-Brock and Janson 2012). On the other hand, phylogenetic concerns can be addressed to some degree by altering the level of taxonomic analysis (e.g., from populations or species to genera or families) and the collection of detailed data on food availability, competition, kinship, affiliative behaviors, and especially individual fitness will be useful whether or not one accepts the tenets of the socioecological model (Koenig and Borries 2009).

It is also important, however, that other avenues of research be explored (Thierry 2008). This is not necessarily due to a perceived unimportance of competition, but rather due to an incomplete knowledge of how the proximate mechanisms related to food exploitation or defense—particularly physiological and psychological—in primates as a whole, are actually structured (Overdorff and Parga 2007). It must be remembered that “the basic unit in the primate social system is indeed an *individual*, with all that this implies about the uniqueness, unity, and complexity of behavioral organization” (emphasis in original, Mason 1976:437). If the behavior of individuals is not understood at both a proximate and evolutionary level, it is unlikely that the mysteries of primate sociality can be solved.

Models of brain evolution

Primates, compared to most other mammals, are well known for possessing relatively large, complex brains, and much work has been devoted to unraveling the factors related to cognitive evolution in our order (reviewed in Allman 1999). The ultimate causation models related to prosimian and anthropoid brain evolution can conveniently be divided into social and ecological hypotheses (even though intelligence is not unidimensional, see Menzel 1997), and the latter class of models, not surprisingly, often evince a rather low opinion of the cognitive abilities required to be a primate folivore. The assumption, in general, is that leaves are relatively simple to locate and consume, and other food types, such as fruits or hidden resources, are more difficult (Potts 2004).

Unlike some recent treatments of the socioecological model, accounts of primate brain evolution continue to use an explicit fruit/leaf dichotomy. The notion that there exist “greater cognitive abilities in frugivorous compared to folivorous primates” (Walker et al. 2006:481) remains common in this literature, despite the fact that almost no cognitive testing of folivorous primates has yet been performed. Indeed, in a meta-analysis of primate cognition studies intending to construct a linear scale of intelligence, only one study (out of 30) included a colobine monkey (Johnson et al. 2002). Interestingly, in that solitary study, the folivorous *Semnopithecus entellus* outperformed the frugivorous *Macaca mulatta* in visual pattern and object discrimination tasks (Manocha 1967). It is argued here that the notion that the foraging landscape of primate frugivores is necessarily more complex than primate folivores is based on assumption rather than hard evidence.

Perhaps the most influential ecological model of primate brain evolution contrasted relatively large-brained, frugivorous spider monkeys with relatively small-brained, folivorous howler monkeys (Milton 1981). From that time forward, the measure of “percent fruit and seeds” has frequently been utilized as a surrogate for “foraging complexity” (Walker et al. 2006:481) and some studies (but not all) have found a significant effect of this rubric on measures of relative brain size or complexity (see Barton 1996; Walker et al. 2006; Allen and Kay 2012). Gross brain measures, however, are hardly the last word in matters of cognitive evolution (Holloway 1966), and putative fruit-brain relationships are heavily dependent on how taxa are sampled, as well as the measure of “brain complexity” that is utilized (Deaner et al. 2000). With regards to the famous neocortex ratio, for example, the folivorous *Semnopithecus entellus* scores higher than capuchins, spider monkeys, and most of its fellow Old World monkeys (Kudo and Dunbar 2001).

“Frugivory equals complexity” was an acceptable viewpoint during the first generation of primate brain evolution models, as it generated useful discussion; e.g., how features such as long-term memory could be used to solve problems relating to resource distribution. Today, however, it appears to be a barren approach, and far less exciting than studies that actually investigate the specific mechanisms relating cognition to foraging (Menzel 1973; Garber

1989; Menzel 1991; Janson 1998; Menzel 1999; Menzel et al. 2002), and which have been, unfortunately, almost ignored in folivores.

Critically, the “frugivory equals complexity” approach overlooks the previous point that not all leaves are the same, nor are all fruits, and this holds for any other dietary category. Again, the focus should be on the distribution of resources and how the forager exploits them, rather than the gross plant part categories that are consumed. The gray langur habitat at Langtang National Park, Nepal and other Himalayan sites are “simple” in the sense that productivity is likely lower than at many tropical or subtropical sites, and being temperate/alpine, plant species diversity may be reduced (Sayers and Norconk 2008). But there are few a priori reasons to assume that the foraging problems faced by Himalayan langurs, even given their anatomical advantages, are any less challenging than those faced by spider monkeys, Barbary macaques, or even African apes. Himalayan langur foods at Langtang, at least seasonally, are widely dispersed and many occur as shrubs or other diminutive patch types, and for almost half of the year, deciduous leaves (along with most other food types) are rare or absent. As with other largely leaf-eating primates, including lowland gray langurs, fruits, seeds and myriad other resources are also exploited (Newton 1992). Indeed, for many species of stereotypically “folivorous” primate, fruit/seeds actually constitute the plurality or majority of the diet at some sites, which argues against the idea that these items, from a cognitive perspective, are too difficult for them to exploit (reviews in Campbell et al. 2007; Dela 2007).

The other major ecological model for primate brain evolution is the extractive foraging hypothesis, which suggests that the utilization of hidden food resources was a prime mover in cognitive change (Parker and Gibson 1977). These are foods that cannot be seen or otherwise perceived and must be removed from inedible coverings, such as seeds from shells, underground storage organs from the ground, and insects from mounds. Colobine monkeys have long been considered the exemplar of the “nonextractive” primate forager (Gibson 1986; Dunbar 1995) and, to be sure, gray langurs have not been observed removing foods with tools. There are, however, many examples of gray langurs extracting hidden foods with the hands or mouth. Himalayan langurs at Langtang National Park, Nepal dig up underground storage organs, remove pericarp from seeds, peel off leaf sheaths from young bamboo, among other extractive behaviors (Sayers and Norconk 2008). At the highland site of Junbesi, monkeys dig for underground storage organs and root through moss and lichens, possibly for insects (Curtin 1975). Similar behaviors are found at lowland gray langur sites. At Kahna Tiger Reserve in India, for example, langurs induce gum flow by enlarging holes in trees or by removing hardened gum with canines, and also manually turn over leaves in order to find and consume caterpillars (Newton 1992). Indeed, extractive foraging (as defined by Gibson 1986) in some variety occurs in many, if not most or all, colobine monkeys (e.g., Kirkpatrick 1999; Ren et al. 2008; Grueter et al. 2009). This fact has yet to be appreciated in treatments of primate brain evolution.

Ultimately, the assumption that primate frugivores face foraging challenges that folivores do not remains just that—an assumption. It is an assumption that has almost certainly discouraged researchers interested in psychological topics from studying taxa that stereotypically consume large quantities of leaves. It is an assumption that, before being repeated again in another article on brain evolution, needs to be tested.

Concluding remarks

Broad characterizations and sweeping definitions certainly have a proper place in science, but it is generally assumed that, at some point, a discipline will move beyond them. As has been detailed, some areas of primate ecology and behavior have fortunately become

increasingly sophisticated in their treatment of dietetic categorizations. It is now well-established that not all primate folivores are specialists, and the notions that leaves are ubiquitously distributed, easy to find, and unworthy of competition are at best oversimplified, and at worst nonsensical (Snaith and Chapman 2007). For example, it could be argued that folivorous howler monkeys (*Alouatta*) are the most “generalized” platyrrhine genus based on their expansive geographical distribution and habitat plasticity (Di Fiore and Campbell 2007) or that colobine monkeys as a whole utilize as an eclectic assortment of resource types as any other primate subfamily (Kirkpatrick 1999). There is, however, a considerable amount of work remaining to be done to truly elevate the study of primate ecology generally, and the study of primate folivores in particular. The path which needs to be taken is undoubtedly a complex one, but likely involves the expansion of investigations, and methodologies, beyond those of the limited research areas that are currently popular. Popularity does not necessarily equate to quality.

The key to investigations of primate, including human, anatomical or behavioral evolution lies in the fundamentals of evolutionary theory (Tooby and DeVore 1987; Sayers and Lovejoy 2008) and, importantly, in relating ultimate causation to proximate mechanisms. Animals should obviously not be defined simply by the resource category they consume most frequently; nor should the research program for animals be dictated by such ecological stamp collecting. Such “stamp collecting,” indeed, is likely a primary reason why, a century after their first pioneering studies, primate cognitive scientists have yet to deal with folivores in an even preliminary fashion. Such “avoidance behavior,” to draw a phrase from competition theory, is unwarranted, as there are innumerable varieties of fruits, leaves, flowers, gums, fungi, and fauna, and in each habitat individual prey species are distributed in varying combinations of patch sizes, within-patch densities, and between-patch distances. Foods of all types vary nutritionally within and between species—and, in the case of flora, even within particular plants—and individual animals will harvest them at different rates (Sullivan 1988; Houle et al. 2007; Sayers and Menzel 2012). There is complexity in the feeding behavior of all primates.

So what is the course for the future? An increased attention to quantifying such basic resource variables (Krebs and McCleery 1984) as food energy and nutritional chemistry, individual-specific handling time and intake rate, the travel time between patches, patch departure decisions, agonism during feeding, encounter rate with specific foods, and the fitness consequences of decision-making, regardless of resource type, are critical for a more sophisticated and predictive primate ecology. Some workers have effectively utilized such data, particularly with respect to competition (e.g., Janson 1985; Snaith and Chapman 2005; Borries et al. 2008; Nakagawa 2009). Just as basic, however, or even more so, are the anatomical, physiological, perceptual, and cognitive factors that underlie primate foraging and movement, and which determine optimal behavior for particular animals (Menzel 1997; Dominy et al. 2001). It is here where many current methodologies will fall short of truly explaining and predicting ecology and sociality, as such “optimal behavior” cannot be determined by food species lists, by considering only crude factors such as day range or group size, or by assuming resource characteristics without measuring the pertinent variables.

While descriptors such as “frugivore” or “folivore” certainly give information about an animal, they do not reveal very much relevant information, and give almost no insight on mechanism. Although some have moved beyond such dichotomies, the movement has not been very far beyond it, and it is probable that the popularity of such categorizations, and the acceptance of their explanatory value for primate behavior, have seriously impeded the study of social relationships, foraging complexity, and cognition in leaf-eating primates. A true understanding of primate adaptation will come only as we look beyond the

generalizations, get back to proximate mechanisms, and begin linking them with evolutionary causation.

Acknowledgments

I would like to thank Goro Hanya, Cyril Grueter, and Yamato Tsuji for inviting me to contribute to the temperate primates special issue and for providing critical comments on an earlier version of this manuscript, as well as Andreas Koenig for providing a valuable and detailed critique. Charles Menzel, Marilyn Norconk, Owen Lovejoy, and Richard Meindl engaged in useful conversations concerning the ideas expressed in the paper; Menzel also provided comments on an early version of the article. Field work at Langtang was supported by the L.S.B. Leakey Foundation and Kent State University. The writing of this article was supported in part by grants HD-38051, HD-060563, HD-056352, and 1F32HD061177 from the National Institutes of Health (NIH). The contents of this article do not necessarily represent the official views of NIH, the Leakey Foundation, or any of the individuals named above.

References

- Aiello LC, Wheeler P. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr Anthropol*. 1995; 36:199–221.
- Allen KL, Kay RF. Dietary quality and encephalization in platyrrhine primates. *Proc R Soc B Bio*. 2012; 279:715–721.
- Allman, JM. *Evolving brains*. WH Freeman & Co; New York: 1999.
- Altmann, SA. *Foraging for survival: yearling baboons in Africa*. The University Of Chicago Press; Chicago: 1998.
- Ardrey, R. *The territorial imperative*. Atheneum; New York: 1966.
- Ayer, AA. *The anatomy of Semnopithecus entellus*. The Indian Publishing House Ltd; Madras: 1948.
- Barton RA. Neocortex size and behavioural ecology in primates. *Proc R Soc B Bio*. 1996; 263:173–177.
- Bauchop T, Martucci RW. Ruminant-like digestion of the langur monkey. *Science*. 1968; 161:698–700. [PubMed: 4969750]
- Binning SA, Chapman LJ, Cosandey-Godin A. Specialized morphology for a generalist diet: evidence for Liem's paradox in a cichlid fish. *J Fish Bio*. 2009; 75:1683–1699. [PubMed: 20738642]
- Bishop, NH. Ph.D. University of California; Berkeley: 1975. Social behavior of langur monkeys (*Presbytis entellus*) in a high altitude environment.
- Bishop NH. Himalayan langurs: temperate colobines. *J Hum Evol*. 1979; 8:251–281.
- Borries C, Larney E, Lu A, Ossi K, Koenig A. Costs of group size: lower developmental and reproductive rates in larger groups of leaf monkeys. *Behav Ecol*. 2008; 19:1186–1191.
- Boyer D, Ramos-Fernandez G, Miramontes O, Mateos JL, Cocho G, Larralde H, Ramos H, Rojas F. Scale-free foraging by primates emerges from their interaction with a complex environment. *Proc R Soc B*. 2006; 273:1743–1750.
- Campbell, CJ.; Fuentes, A.; MacKinnon, KC.; Panger, M.; Bearder, SK., editors. *Primates in perspective*. Oxford University Press; Oxford: 2007.
- Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, Sponheimer M, Uno KT. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc Natl Acad Sci*. 2011; 108:9337. [PubMed: 21536914]
- Chapman CA, Rothman JM. Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates*. 2009; 50:12–22. [PubMed: 19142700]
- Charnov E, Orians G, Hyatt K. Ecological implications of resource depression. *Am Nat*. 1976; 110:247–259.
- Charnov EL. Optimal foraging: attack strategy of a mantid. *Am Nat*. 1976; 110:141–151.
- Cheney DL. Intragroup cohesion and intergroup hostility: the relation between grooming distributions and intergroup competition among female primates. *Behav Ecol*. 1992; 3:334–345.
- Cheney, DL.; Seyfarth, RM. *How monkeys see the world: inside the mind of another species*. University of Chicago Press; Chicago: 1992.

- Chivers DJ, Hladik CM. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *J Morphol.* 1980; 166:337–386. [PubMed: 7441763]
- Clutton-Brock T, Janson C. Primate socioecology at the crossroads: past, present, and future. *Evol Anth.* 2012; 21:136–150.
- Clutton-Brock TH, Harvey PH. Primate ecology and social organization. *J Zool.* 1977; 183:1–39.
- Conklin-Brittain NL, Wrangham RW, Hunt KD. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. macronutrients. *Int J Primatol.* 1998; 19:971–998.
- Cords M. Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour.* 2002; 139:291–314.
- Crockett, CM. Emigration by female red howler monkeys and the case for female competition. In: Small, MF., editor. *Female primates: studies by women primatologists*. Alan R. Liss; New York: 1984. p. 159-173.
- Crook JH, Gartlan JS. Evolution of primate societies. *Nature.* 1966; 210:1200–1203. [PubMed: 6007804]
- Curtin, RA. The socioecology of the common langur, *Presbytis entellus*, in the Nepal Himalaya. University of California; Berkeley: 1975.
- Curtin RA. Range use of gray langurs in highland Nepal. *Folia Primatologica.* 1982; 38:1–18.
- Darwin C. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. I. Extract from an unpublished work on species, II. Abstract of a letter from C. Darwin, Esq., to Prof. Asa Gray. *J Proc Linn Soc Zool.* 1858; 3:45–53.
- Darwin, C. The descent of man, and selection in relation to sex [second edition; originally published in 1874]. Prometheus Books; Amherst: 1874/1998.
- de Marques AAB. Use of space by *Alouatta guariba clamitans* Cabrera, 1940, in temperate and subtropical habitats in southern Brazil. *Neotropical Primates.* 2002; 10:31.
- Deaner RO, Nunn CL, Van Schaik CP. Comparative tests of primate cognition: different scaling methods produce different results. *Brain Behav Evol.* 2000; 55:44–52. [PubMed: 10773625]
- Dela JDS. Seasonal food use strategies of *Semnopithecus vetulus nestor*, at Panadura and Piliyandala, Sri Lanka. *Int J Primatol.* 2007; 28:607–626.
- Di Fiore, A.; Campbell, CJ. The atelines: variation in ecology, behavior, and social organization. In: Campbell, CJ.; Fuentes, A.; MacKinnon, KC.; Panger, M.; Bearder, SK., editors. *Primates in perspective*. Oxford University Press; New York: 2007. p. 155-185.
- Dominy NJ, Lucas PW, Osorio D, Yamashita N. The sensory ecology of primate food perception. *Evol Anth.* 2001; 10:171–186.
- Dunbar RIM. Neocortex size and group size in primates: a test of the hypothesis. *J Hum Evol.* 1995; 28:287–296.
- Emlen JM. The role of time and energy in food preference. *Am Nat.* 1966; 100:611–617.
- Emlen ST, Oring LW. Ecology, sexual selection, and the evolution of mating systems. *Science.* 1977; 197:215–223. [PubMed: 327542]
- Fashing, PJ. African colobine monkeys: patterns of between-group interaction. In: Campbell, CJ.; Fuentes, A.; MacKinnon, KC.; Panger, M.; Bearder, SK., editors. *Primates in perspective*. Oxford University Press; New York: 2007. p. 201-224.
- Fish JL, Lockwood CA. Dietary constraints on encephalization in primates. *Am J Phys Anthropol.* 2003; 120:171–181. [PubMed: 12541334]
- Garber PA. Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. *Am J Primatol.* 1989; 19:203–216.
- Gibson, KR. Cognition, brain size and the extraction of embedded food resources. In: Else, JG.; Lee, PC., editors. *Primate ontogeny, cognition and social behaviour*. Cambridge University Press; Cambridge: 1986. p. 93-103.
- Glander, KE. Feeding patterns in mantled howling monkeys. In: Kamil, AC.; Sargent, TD., editors. *Foraging behavior: ecological, ethological, and psychological approaches*. Garland STPM Press; New York: 1981. p. 231-257.
- Grether GF, Palombit RA, Rodman PS. Gibbon foraging decisions and the marginal value model. *Int J Primatol.* 1992; 13:1–17.

- Groves, CP. Primate taxonomy. Smithsonian University Press; Washington, D.C.: 2001.
- Grueter CC, Li D, Ren B, Wei F, Van Schaik CP. Dietary profile of *Rhinopithecus bieti* and its socioecological implications. *Int J Primatol*. 2009; 30:601–624. [PubMed: 19816538]
- Hanya G, Grueter CC, Tsuji Y. Out of the tropics: ecology of temperate primates. *Primates*. 2012
- Hart, D.; Sussman, RW. Man the hunted: primates, predators, and human evolution. Westview Press; New York: 2005.
- Hill WCO. The maintenance of langurs (Colobidae) in captivity; experiences and some suggestions. *Folia Primatol*. 1964; 2:222–231.
- Hladik, CM. Ecology, diet, and social patterning in Old and New World primates. In: Tuttle, RH., editor. *Socioecology and psychology of primates*. Mouton Publishers; The Hague: 1975. p. 3-35.
- Holland JS. A monkey that knows no bounds. *Natl Geogr*. 2011; 220:86–95.
- Holloway RL. Cranial capacity, neural reorganization, and hominid evolution: a search for more suitable parameters. *Am Anthropol*. 1966; 68:103–121.
- Houle A, Chapman CA, Vickery WL. Intratree variation in fruit production and implications for primate foraging. *Int J Primatol*. 2007; 28:1197–1217.
- Hutchinson GE. Concluding remarks. *Cold Spring Harb Sym*. 1957; 22:415–427.
- Hutchinson, GE. *The ecological theater and the evolutionary play*. Yale University Press; New Haven: 1965.
- Hylander WL. Incisor size and diet in anthropoids with special reference to Cercopithecidae. *Science*. 1975; 189:1095–1098. [PubMed: 808855]
- Isbell LA. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol*. 1991; 2:143–155.
- Isbell LA, Young TP. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour*. 2002; 139:177–202.
- Janson C. Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behav Ecol Sociobiol*. 1985; 18:125–138.
- Janson CH. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *An Behav*. 1990; 40:922–934.
- Janson CH. Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *An Behav*. 1998; 55:1229–1243.
- Janson CH, Goldsmith ML. Predicting group size in primates: foraging costs and predation risks. *Behav Ecol*. 1995; 6:326–336.
- Johnson VE, Deaner RO, Van Schaik CP. Bayesian analysis of rank data with application to primate intelligence experiments. *J Am Stat Assoc*. 2002; 97:8–17.
- Kamilar JM, Ledogar JA. Species co-occurrence patterns and dietary resource competition in primates. *Am J Phys Anthropol*. 2011; 144:131–139. [PubMed: 20740497]
- Kay, RNB.; Davies, AG. Digestive physiology. In: Davies AG and Oates JF (eds). *Colobine monkeys: their ecology, behaviour and evolution*. Cambridge University Press; Cambridge: 1994. p. 229-249.
- Keith, A. *A new theory of human evolution*. Watts & Co.; London: 1948.
- Kirkpatrick, RC. Colobine diet and social organization. In: Dolhinow, P.; Fuentes, A., editors. *The nonhuman primates*. Mayfield; Mountain View: 1999. p. 93-105.
- Koenig A, Beise J, Chalise MK, Ganzhorn JU. When females should contest for food—testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behav Ecol Sociobiol*. 1998; 42:225–237.
- Koenig A, Borries C. Socioecology of Hanuman langurs: the story of their success. *Evol Anthropol*. 2001; 10:122–137.
- Koenig, A.; Borries, C. The predictive power of socioecological models: a reconsideration of resource characteristics, agonism, and dominance hierarchies. In: Hohmann, G.; Robbins, MM.; Boesch, C., editors. *Feeding ecology in apes and other primates*. Cambridge University Press; Cambridge: 2006. p. 263-284.
- Koenig A, Borries C. The lost dream of ecological determinism: time to say goodbye? Or a white queen's proposal? *Evol Anthropol*. 2009; 18:166–174.

- Koenig A, Borries C, Chalise MK, Winkler P. Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *J Zool.* 1997; 243:215–235.
- Koenig A, Borries C, Doran-Sheehy D, Janson C. How important are affiliation and cooperation? A reply to Sussman et al. *Am J Phys Anthropol.* 2006; 131:522–523. [PubMed: 16883567]
- Kolling N, Behrens TEJ, Mars RB, Rushworth MFS. Neural mechanisms of foraging. *Science.* 2012; 336:95–98. [PubMed: 22491854]
- Krebs, JR.; McCleery, RH. Optimization in behavioural ecology. In: Krebs, JR.; Davies, NB., editors. *Behavioural ecology: an evolutionary approach*. Sinauer; Sutherland: 1984. p. 91-121.
- Kudo H, Dunbar RIM. Neocortex size and social network size in primates. *An Behav.* 2001; 62:711–722.
- Kummer, H. Rules of dyad and group formation among captive gelada baboons (*Theropithecus gelada*); *Proc Symp 5th Int Cong Primatol*; Tokyo: Japan Science Press. 1975;
- Laska M, Freist P, Krause S. Which senses play a role in nonhuman primate food selection? A comparison between squirrel monkeys and spider monkeys. *Am J Primatol.* 2007; 69:282–294. [PubMed: 17146790]
- Liem KF. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am Zool.* 1980; 20:295–314.
- Loxdale HD, Lushai G, Harvey JA. The evolutionary improbability of ‘generalism’ in nature, with special reference to insects. *Biol J Linnean Soc.* 2011; 103:1–18.
- Lucas, PW.; Teaford, MF. Functional morphology of colobine teeth. In: Davies, AG.; Oates, JF., editors. *Colobine monkeys: their ecology, behavior and evolution*. Cambridge University Press; Cambridge: 1994. p. 173-203.
- MacArthur RH, Pianka ER. On optimal use of a patchy environment. *Am Nat.* 1966; 100:603–609.
- MacArthur, RH.; Wilson, EO. *The theory of island biogeography*. Princeton University Press; Princeton: 1967.
- Maestripieri, D. *Macchiavellian intelligence: how rhesus macaques and humans have conquered the world*. University of Chicago Press; Chicago: 2007.
- Manocha S. Discrimination learning in langurs and rhesus monkeys. *Percept Motor Skill.* 1967; 24:805–806.
- Marshall AJ, Wrangham RW. Evolutionary consequences of fallback foods. *Int J Primatol.* 2007; 28:1219–1235.
- Mason, WA. Primate social behavior: pattern and process. In: Masterton, RB.; Bitterman, ME.; Campbell, CBG.; Hotton, N., editors. *Evolution of brain and behavior in vertebrates*. Lawrence Erlbaum Associates; Hillsdale: 1976. p. 425-455.
- Mendoza, SP.; Mason, WA. Primate relationships: social dispositions and physiological responses. In: Seth, PK.; Seth, S., editors. *Perspectives in primate biology volume 2. Today & Tomorrow's Printers and Publishers*; New Delhi: 1989. p. 129-143.
- Mendoza SP, Reeder DM, Mason WA. Nature of proximate mechanisms underlying primate social systems: simplicity and redundancy. *Evol Anthropol.* 2002; 11:112–116.
- Menzel CR. Cognitive aspects of foraging in Japanese monkeys. *Anim Behav.* 1991; 41:397–402.
- Menzel, CR. Primates' knowledge of their natural habitat: As indicated in foraging. In: Whiten, A.; Byrne, R., editors. *Machiavellian intelligence II: extensions and evaluations*. Cambridge University Press; Cambridge: 1997. p. 207-239.
- Menzel CR. Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays. *J Comp Psychol.* 1999; 113:426–434. [PubMed: 10608566]
- Menzel, CR. Solving ecological problems. In: Mitani, JC.; Silk, JB.; Palombit, RA.; Call, J.; Kappeler, PM., editors. *The evolution of primate societies*. The University of Chicago Press; Chicago: in press
- Menzel CR, Savage-Rumbaugh ES, Menzel EW Jr. Bonobo (*Pan paniscus*) spatial memory and communication in a 20-hectare forest. *Int J Primatol.* 2002; 23:601–619.
- Menzel EW Jr. Chimpanzee spatial memory organization. *Science.* 1973; 182:943–945. [PubMed: 17737534]

- Menzel EW Jr, Juno C. Social foraging in marmoset monkeys and the question of intelligence [and discussion]. *Philos T Roy Soc B*. 1985; 308:145–158.
- Milton K. Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *Am Anthropol*. 1981; 83:534–548.
- Milton K. Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition*. 1999; 15:488–498. [PubMed: 10378206]
- Minhas RA, Ahmed KB, Awan MS, Dar NI. Habitat utilization and feeding biology of Himalayan grey langur (*Semnopithecus entellus ajax*) in Machiara National Park, Azad Jammu and Kashmir, Pakistan. *Zool Res*. 2010; 2:177–188. [PubMed: 20545008]
- Minhas RA, Ali U, Dar NI, Awan MS, Khan MN, Qamar QZ, Ali H, Ahmed MS. Ranging behavior of Himalayan gray langur (*Semnopithecus ajax*) in Machiara National Park, Azad Jammu and Kashmir, Pakistan. *Primates*. 2012
- Nakagawa N. Feeding rate as valuable information in primate feeding ecology. *Primates*. 2009; 50:131–141. [PubMed: 19205830]
- Napier, JR.; Napier, PH. A handbook of living primates. Academic Press; London: 1967.
- Napier, PH. Part III: family Cercopithecidae, subfamily Colobinae. British Museum (Natural History); London: 1985. Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles.
- Newton P. Feeding and ranging patterns of forest Hanuman langurs (*Presbytis entellus*). *Int J Primatol*. 1992; 13:245–285.
- Oates, JF. Food distribution and foraging behavior. In: Smuts, BB.; Cheney, DL.; Seyfarth, RM.; Wrangham, RW.; Struhsaker, TT., editors. Primate societies. The University of Chicago Press; Chicago: 1987. p. 197–209.
- Oppenheimer, J. Aspects of the diet of the Hanuman langur. In: Chivers, DJ.; Herbert, J., editors. Recent advances in primatology. Volume I: behaviour. Academic Press; London: 1978. p. 337–342.
- Overdorff, DJ.; Parga, J. The new era of primate socioecology: ecology and intersexual conflict. In: Campbell, CJ.; Fuentes, A.; MacKinnon, KC.; Panger, M.; Bearder, SK., editors. Primates in perspective. Oxford University Press; New York: 2007. p. 466–482.
- Parker ST, Gibson KR. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *J Human Evol*. 1977; 6:623–641.
- Peters CR, Vogel JC. Africa's wild C4 plant foods and possible early hominid diets. *J Human Evol*. 2005; 48:219–236. [PubMed: 15737391]
- Pianka, ER. Evolutionary ecology (fifth edition). HarperCollins College Publishers; New York: 1994.
- Pombo, AR.; Waltert, M.; Mansjoer, SS.; Mardiasuti, A.; Muhlenberg, M. Home range, diet and behaviour of the Tonkean macaque (*Macaca tonkeana*) in Lore Lindu National Park, Sulawesi. In: Gerold, G.; Fremery, M.; Guhardja, E., editors. Land use, nature conservation and the stability of rainforest margins in Southeast Asia. Springer; Berlin: 2004. p. 313–325.
- Potts R. Paleoenvironmental basis of cognitive evolution in great apes. *Amer J Primatol*. 2004; 62:209–228. [PubMed: 15027093]
- Pyke GH, Pulliam HR, Charnov EL. Optimal foraging: a selective review of theory and tests. *Q Rev Biol*. 1977; 52:137–154.
- Ramos-Fernandez G, Mateos JL, Miramontes O, Cocho G, Larralde H, Ayala-Orozco B. Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behav Ecol Sociobiol*. 2004; 55:223–230.
- Rank NE, Yturalde K, Dahlhoff EP. Role of contests in the scramble competition mating system of a leaf beetle. *J Insect Behav*. 2006; 19:699–716.
- Ren B, Li M, Wei F. Preliminary study on digging and eating underground plant corms by wild Yunnan snub-nosed monkeys at Tacheng, Yunnan, China. *Acta Theriologica Sinica*. 2008; 28:237–241.
- Richard A, Goldstein S, Dewar R. Weed macaques: the evolutionary implications of macaque feeding ecology. *Int J Primatol*. 1989; 10:569–594.

- Ripley, S. Leaves and leaf-monkeys: The social organization of foraging in gray langurs *Presbytis entellus thersites*. In: Napier, JR.; Napier, PH., editors. Old World monkeys: evolution, systematics and behavior. Academic Press; New York: 1970. p. 481-509.
- Ritchie ME. Optimal foraging and fitness in Columbian ground squirrels. *Oecologia*. 1990; 82:56–67.
- Robinson BW, Wilson DS. Optimal foraging, specialization, and a solution to Liem's paradox. *Am Nat*. 1998; 151:223–235. [PubMed: 18811353]
- Rosenberger AL, Halenar L, Cooke SB. The making of platyrrhine semifolivores: models for the evolution of folivory in primates. *Anat Rec*. 2011; 294:2112–2130.
- Rothman JM, Plumptre AJ, Dierenfeld ES, Pell AN. Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. *J Trop Ecol*. 2007; 23:673–682.
- Rowe, N. The pictorial guide to the living primates. Pogonias Press; East Hampton: 1996.
- Rumbaugh DM, Savage-Rumbaugh ES, Washburn DA. Toward a new outlook on primate learning and behavior: complex learning and emergent processes in comparative perspective. *Japanese Psychol Res*. 1996; 38:113–125.
- Sayers K, Lovejoy CO. The chimpanzee has no clothes: a critical examination of *Pan troglodytes* in models of human evolution (with comments and reply). *Curr Anthropol*. 2008; 49:87–114.
- Sayers K, Menzel CR. Memory and foraging theory: chimpanzee utilization of optimality heuristics in the rank-order recovery of hidden foods. *Anim Behav*. 2012; 84:795–803. [PubMed: 23226837]
- Sayers K, Norconk MA. Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: Diet, Activity Patterns, and Resources. *Int J Primatol*. 2008; 29:509–530.
- Sayers K, Norconk MA, Conklin-Brittain NL. Optimal foraging on the roof of the world: Himalayan langurs and the classical prey model. *Amer J Phys Anthropol*. 2010; 141:337–357. [PubMed: 19844998]
- Schoener TW. Theory of feeding strategies. *Ann Rev Ecol Syst*. 1971; 2:369–404.
- Sherry, DF.; Mitchell, JB. Neuroethology of foraging. In: Stephens, DW.; Brown, JS.; Ydenberg, RC., editors. Foraging: behavior and ecology. The University of Chicago Press; Chicago: 2007. p. 61-102.
- Shipley LA, Forbey JS, Moore BD. Revisiting the dietary niche: when is a mammalian herbivore a specialist? *Integr Comp Biol*. 2009 doi:10.1093/icb/icp1051.
- Shultz S, Opie C, Atkinson QD. Stepwise evolution of stable sociality in primates. *Nature*. 2011; 479:219–222. [PubMed: 22071768]
- Sih A, Christensen B. Optimal diet theory: when does it work, and when and why does it fail? *Anim Behav*. 2001; 61:379–390.
- Snaith TV, Chapman CA. Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*). *Behav Ecol Sociobiol*. 2005; 59:185–190.
- Snaith TV, Chapman CA. Primate group size and interpreting socioecological models: do folivores really play by different rules? *Evol Anthropol*. 2007; 16:94–106.
- Snaith TV, Chapman CA. Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. *Behav Ecol*. 2008; 19:1289–1296.
- Spencer, H. The principles of ethics. Vol. 1. D. Appleton & Company; New York: 1896.
- Stephens, DW.; Krebs, JR. Foraging theory. Princeton University Press; Princeton: 1986.
- Sterck EHM, Watts DP, van Schaik CP. The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol*. 1997; 41:291–309.
- Strait SG. Tooth use and the physical properties of food. *Evol Anthropol*. 1997; 5:199–211.
- Stumpf R, Emery Thompson M, Muller M, Wrangham R. The context of female dispersal in Kanyawara chimpanzees. *Behaviour*. 2009; 146(4):629–656.
- Sullivan KA. Age-specific profitability and prey choice. *Anim Behav*. 1988; 36:613–615.
- Surridge AK, Osorio D, Mundy NI. Evolution and selection of trichromatic vision in primates. *Trends Ecol Evol*. 2003; 18:198–205.
- Sussman, RW.; Garber, PA. Cooperation and competition in primate social interactions. In: Campbell, CJ.; Fuentes, A.; MacKinnon, KC.; Panger, M.; Bearder, SK., editors. Primates in perspective. Oxford University Press; New York: 2007. p. 636-651.

- Sussman RW, Garber PA, Cheverud JM. Importance of cooperation and affiliation in the evolution of primate sociality. *Amer J Phys Anthropol.* 2005; 128:84–97. [PubMed: 15778981]
- Sussman RW, Garber PA, Cheverud JM. How important are affiliation and cooperation? A response to Koenig et al. *Amer J Phys Anthropol.* 2006; 131:524.
- Teichroeb JA, Saj TL, Paterson JD, Sicotte P. Effect of group size on activity budgets of *Colobus vellerosus* in Ghana. *Int J Primatol.* 2003; 24:743–758.
- Teichroeb JA, Sicotte P. Test of the ecological-constraints model on ursine colobus monkeys (*Colobus vellerosus*) in Ghana. *Amer J Primatol.* 2009; 71:49–59. [PubMed: 18828147]
- Terborgh, J. Five new world primates: a study in comparative ecology. Princeton University Press; Princeton: 1983.
- Thierry, B. The macaques: a double-layered social organization. In: Campbell, CJ.; Fuentes, A.; MacKinnon, KC.; Panger, M.; Bearder, SK., editors. *Primates in perspective*. Oxford University Press; New York: 2007. p. 224-239.
- Thierry B. Primate socioecology, the lost dream of ecological determinism. *Evol Anthropol.* 2008; 17:93–96.
- Tomasello, M.; Call, J. *Primate cognition*. Oxford University Press; Oxford: 1997.
- Tooby, J.; DeVore, I. The reconstruction of hominid behavioral evolution through strategic modeling. In: Kinzey, WG., editor. *The evolution of human behavior: primate models*. State University of New York Press; New York: 1987. p. 183-237.
- Ungar PS, Grine FE, Teaford MF. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PloS One.* 2008; 3:e2044. [PubMed: 18446200]
- Vandercone RP, Dinadh C, Wijethunga K, Ranawana K, Rasmussen DT. Dietary diversity and food selection in Hanuman langurs (*Semnopithecus entellus*) and purple-faced langurs (*Trachypithecus vetulus*) in the Kaludiyapokuna Forest Reserve in the dry zone of Sri Lanka. *Int J Primatol.* 2012 DOI 10.1007/s10764-012-9629-9.
- van Schaik, CP. The ecology of social relationships amongst female primates. In: Standen, V.; Foley, RA., editors. *Comparative socioecology: the behavioral ecology of humans and other mammals*. Blackwell; Oxford: 1989. p. 195-218.
- Walker R, Burger O, Wagner J, Von Rueden CR. Evolution of brain size and juvenile periods in primates. *J Human Evol.* 2006; 51:480–489. [PubMed: 16890272]
- Wallace AR. On the tendency of varieties to depart indefinitely from the original type. *J Proc Linn Soc Zool.* 1858; 3:53–62.
- Winkler, P. Feeding behavior of a food-enhanced troop of Hanuman langurs (*Presbytis entellus*) in Jodhpur, India. In: Fa, JE.; Southwick, CH., editors. *Ecology and behavior of food-enhanced primate groups*. Liss; New York: 1988. p. 3-24.
- Wrangham RW. An ecological model of female-bonded primate groups. *Behaviour.* 1980; 75:262–300.
- Yoshida K. An ecological study of Hanuman langurs, *Presbytis entellus*. *Primates.* 1967; 8:127–154.

Table 1

The rates at which focal Himalayan langurs at Langtang National Park, Nepal were displaced by other individuals while feeding, deduced from continuous sampling, and arranged by gross plant part category.

Individual(s)	Times displaced per hour of feeding			
	<i>leaves</i>	<i>fruits</i>	<i>uso_s</i>	<i>all</i>
adult females	0.65	0.25	0.90	0.69
alpha male	0.00	0.00	0.00	0.00
non-alpha adult males	0.26	0.79	1.72	0.68
immatures	0.32	0.95	-----	0.55

uso = underground storage organ, *all* = all food types, including resource categories not listed. Dividing resources by gross type is for illustrative purposes only; within these categories there is tremendous variation in the abundance, nutritional quality, average between-patch distances, and within-patch densities of foods (see text). Sample sizes (number of feeding sessions continuously recorded, listed in the order of leaves, fruits, usos, and all) were as follows: adult females (95, 64, 16, 181), alpha male (30, 18, 16, 66), non-alpha males (59, 49, 9, 119), immatures (37, 37, 2, 80). Only rates based on 5 feeding sessions are included.