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REVIEW ARTICLE

Special contributions 'Out of the tropics: Ecology of temperate primates'

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

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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 is 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 characteristics 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, engage in resource competition (both of which have previously been noted for primate folivores), and 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 use 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

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surprising that contrasts have frequently been made between primate folivores and those with other dietetic categorizations, such as frugivores, insectivores, and gumnivores. 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, p. 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 being so 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). As 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. However, 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 they 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). However, it is instructive to consider the topics that have or have not been investigated with primate folivores.

Outside of limited investigations related to trichromatic color vision (Surridge et al. 2003; Dominy and Lucas 2004), 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 the more frugivorous primates (Menzel 2012). 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 are freely taken from taxa throughout the order, particular focus is 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 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). As with all colobine monkeys, gray langur dentitions are characterized by postcanine 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 as with 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 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 such as 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 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, as 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). 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, *P. entellus* or *S. 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 (Yoshiba 1967) forest, 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; Maestripieri 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 interannually 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 a 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 anatomical and physiological characteristics 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 (3,000–4,000 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 with 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, whereas Himalayan and other gray langurs are exemplified by morphological and physiological characteristics 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, p. 295; Binning et al. 2009). According to foraging theory, extreme specializations—such as those colobines possess to process high-fiber foods such as some varieties of 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 postcanine 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 identifying a nutritional currency as well as quantifying individual-specific and food-item-specific handling times and encounter rates. Grounded in the observed link between foraging and reproductive fitness (e.g., Ritchie 1990; Altmann 1998), such models predict the set of foods that maximizes long-term gain rate while foraging. They have had great success over a wide range of taxa in predicting changes in diet breadth related to variation in encounter rates with (abundance of) profitable foods. Whereas the fallback foods approach is largely descriptive, the foraging theory approach is predictive, identifies fallback foods when such exist, and necessitates or encourages collection of myriad data relevant to myriad topics—not only dietetic questions, but also those of niche theory, competition, ontogeny of resource use, and 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 nineteenth 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 included variables, particularly predation pressure and resource dispersion, 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 shows many of assumptions of the Crook/Gartlan model to be problematic, including the assertion that forest primates on the whole live in small groups, and, more importantly, 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 characteristics (food distribution and/or predation pressure) or narrow social concerns such as infanticide, whereas Emlen and Oring, in some cases, allow for females to be clumped or dispersed for alternative (e.g., phylogenetic) reasons; (3) the primate socioecological model, as noted, is focused largely or exclusively on females, whereas 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 which it deviates from the treatment by 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). However, other proximate factors, even those directly relevant to the limited universe of the socioecological model, remain little studied (particularly in folivores) and 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 2012) 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. However, 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 the distribution of specific foods in space and time, 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 2012). Despite this, old stereotypes concerning general plant-part categories persist in the literature, even among workers studying folivores. In one example, Vandercone et al. (2012), after finding that *Trachypithecus vetulus* and *S. 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). Whereas 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 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 whereas 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 fraught with difficulty 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 are very selective, often preferring young leaves or nonleaf 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. Whereas 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 are frugivores, but this can be altered when their foods are sufficiently scattered in space. Himalayan gray langurs on average travel >1,000 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 with 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 are 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 (Teichroeb et al. 2003; Teichroeb and Sicotte 2009) colobus. 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 used 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). Whereas 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 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, whereas 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 or less often than during consumption of other food parts, including fruits.
2. Nonalpha 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).
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, p. 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 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 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, p. 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.

Table 1 Rates at which focal Himalayan langurs at Langtang National Park, Nepal, were displaced by other individuals while feeding

Individual(s)	Times displaced per hour of feeding			
	Leaves	Fruits	USOs	All
Adult females	0.65	0.25	0.90	0.69
Alpha male	0.00	0.00	0.00	0.00
Nonalpha adult males	0.26	0.79	1.72	0.68
Immatures	0.32	0.95	–	0.55

Deduced from continuous sampling and arranged by gross plant-part category

Dividing resources by gross type is for illustrative purposes only; within these categories there is tremendous variation in 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), nonalpha males (59, 49, 9, 119), immatures (37, 37, 2, 80). Only rates based on ≥ 5 feeding sessions are included

USO underground storage organ, *all* all food types, including resource categories not listed

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, p. 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 *S. entellus* outperformed the frugivorous *M. 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 used as a surrogate for foraging complexity (Walker et al. 2006, p. 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 used (Deaner et al. 2000). With regard to the famous neocortex ratio, for example, the folivorous *S. 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, 1991, 1999; Garber 1989; Janson 1998; 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 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). However, 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 primates, 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 use 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, and 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; they also manually turn over leaves 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 use as great an eclectic assortment of resource types as does any other primate subfamily (Kirkpatrick 1999). There is, however, a considerable amount of work remaining to be done to advance the study of primate ecology generally and the study of primate folivores in particular. The path that needs to be taken is undoubtedly a complex one but likely involves 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 that, a century after their first pioneering studies, primate cognitive scientists have yet to deal with folivores in an even preliminary fashion. To repeat an earlier point, generalizations regarding the assumed simplicity of folivory have likely stymied such research. 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? Increased attention to quantifying basic resource variables (Krebs and McCleery 1984) such as food energy and nutritional chemistry, individual-specific handling time and intake rate, travel time between patches, patch departure decisions, agonism during feeding, encounter rate with specific foods, and fitness consequences of decision making, regardless of resource type, are critical for a more sophisticated and predictive primate ecology. Some workers have effectively used 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 that determine optimal behavior for particular animals (Menzel 1997; Dominy et al. 2001). It is here that 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.

Whereas descriptors such as frugivore or folivore certainly give information about an animal, they reveal very little relevant information and give almost no insight into 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.

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