

# Primate Group Size and Interpreting Socioecological Models: Do Folivores Really Play by Different Rules?

TAMAINI V. SNAITH AND COLIN A. CHAPMAN

Because primates display such remarkable diversity, they are an ideal taxon within which to examine the evolutionary significance of group living and the ecological factors responsible for variation in social organization. However, as with any social vertebrate, the ecological determinants of primate social variability are not easily identified. Interspecific variation in group size and social organization results from the compromises required to accommodate the associative and dissociative forces of many factors, including predation,<sup>1–3</sup> conspecific harassment and infanticide,<sup>4–6</sup> foraging competition<sup>1,7</sup> and cooperation,<sup>8</sup> dominance interactions,<sup>9</sup> reproductive strategies, and socialization.<sup>10–12</sup> Causative explanations have emerged primarily through the construction of theoretical models that organize the observed variation in primate social organization and group size relative to measurable ecological variation.<sup>1,2,13–16</sup>

tion and group size. We conclude by suggesting future refinements of both empirical inquiry and theoretical models that we hope will improve our ability to adequately characterize the competitive regime and social organization of folivorous primates.

## EXPLANATORY MODELS OF PRIMATE SOCIAL ORGANIZATION

Early assessments of primate socioecology relied primarily on correlational analyses to examine the relationships between ecological and social variation, and generally categorized primates according to group size, the number of males per group, or broad ecological categories based on diet, locomotion, and habitat.<sup>1,3,18,19</sup> This work provided important insights into the variation in primate behavior and the ecological conditions associated with various behavioral traits. The research of behavioral ecologists working on other taxa<sup>8,9,20–22</sup> provided a strong theoretical basis for the development of primate-specific qualitative models grounded in evolutionary theory. In a seminal paper, Wrangham<sup>14</sup> shifted the focus of primate socioecology in two ways. First, rather than relying on correlational analyses, he used an evolutionary approach to generate hypotheses about the adaptive significance of social organization. Second, he focused primarily on female relationships as determined by food competition. This brought primate socioecological theory in line with the basic premise that, for most species, female behavior is affected by

Tamaini Snaith is a Ph.D. candidate in Biology and Anthropology at McGill University in Montreal. Her research has dealt with the behavior, ecology, and conservation of orangutans in Borneo and moose in Nova Scotia, and she worked as a conservation biologist and advocate for the Alberta Wilderness Association. Colin Chapman is a Canada Research Chair Professor of Anthropology and the McGill School of Environment. His current research is focused on the ecological determinants of primate behavior and abundance, emphasizing novel means of promoting primate conservation. Currently, both authors conduct field work in Kibale National Park, Uganda.

Departments of Anthropology and Biology, McGill University, 855 Sherbrooke St. West, Montreal, Canada, H3A 2T7. Phone: 514-398-1242, Fax: 514-398-7476, E-mail: tamaini.snaith@mail.mcgill.ca  
Department of Anthropology and McGill School of Environment, McGill University, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA. E-mail: colin.chapman@mcgill.ca

In the first portion of this paper, we take a historical perspective, reviewing the development of existing models of primate socioecology. We pay particular attention to the manner in which these models have been applied to folivores because, recently, contradictions have emerged between empirical data and longstanding assumptions about food competition in folivores, which challenge conventional interpretations of their competitive regime. In the second part of the paper, we examine how traditional assumptions have led to what has been called the folivore paradox.<sup>4,17</sup> We explicitly examine the context within which this paradox was proposed and critically examine whether folivores experience food competition. Throughout the paper, we focus specifically on ecological variation and the consequent expressions of food competition. While we recognize the potential importance of predation, infanticide, and social factors, no attempt is made to exhaustively review these phenomena or to discuss their effects on social organiza-

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### Box 1. Types of Food Competition<sup>2,31</sup>

**Between-group contest (BGC)** occurs when territories or food patches can be cooperatively defended by group members. This type of competition should favor larger or more aggressive groups that can supplant or exclude smaller groups from feeding sites.

**Between-group scramble (BGS)** results from the common use of food resources by all groups or individuals, and increases in intensity with increasing population den-

sity. The effects of BGS are presumed to be independent of group size and to have little effect on social behavior.

**Within-group contest (WGC)** occurs when food is distributed so that it can be monopolized or defended, resulting in the development of dominance hierarchies, differential access to resources, and skewed energy gains. Behavioral consequences include direct contests over access to food and may

take the form of aggression, displacement, or avoidance.

**Within-group scramble (WGS)** occurs due to the limited nature of the food supply, which must be shared among group members. Competition increases in intensity with group size and smaller groups are favored. Because feeding opportunities are reduced equally for all group members, WGS is unrelated to the development of dominance hierarchies and does not lead to skewed resource acquisition.

ecological variables and food competition, while males are primarily affected by mating competition and the distribution of receptive females.<sup>8,20,23</sup> Female food competition, as the ultimate evolutionary force influencing primate social organization, has provided the fundamental starting point for all subsequent models.

Wrangham<sup>14</sup> proposed an ecological mechanism for the formation of female-bonded primate groups; specifically, females will live in groups when the benefits of cooperative resource defense outweigh the costs of within-group feeding competition. Females will form bonds with their relatives to cooperatively defend access to food resources. Large groups will out-compete smaller groups and obtain greater fitness by excluding neighboring groups from food sources. This requires that high-quality food is distributed in discrete, defensible patches, and that fallback foods (those eaten when preferred high-quality foods are unavailable), occur in large, uniform patches that minimize within-group competition. When feeding sites within food patches are limited or vary in quality, competition within groups will lead to the formation of female dominance hierarchies. For these female-bonded species, between-group competition will select for group formation and create a selective advantage for larger groups, while within-group competition (in nonterritorial species) or the

ability to defend a home range of appropriate size (in territorial species) will ultimately constrain group size. Non-female bonded species were classified into two categories. One category includes species that rely almost exclusively on high-quality, patchy resources and display short-term variation in group size so that individuals can respond to fluctuations in food availability and competition intensity, as do chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles spp.*). The second category includes those whose preferred foods occur in low-quality uniform patches with a large number of feeding sites (i.e., leaves, particularly mature leaves), and thus live in cohesive groups with little or no feeding competition. Many non-female bonded folivores were placed in this category.

By highlighting the social consequences of food competition, Wrangham<sup>14</sup> refocused the attention of primatologists. Empirical work has supported the importance of between-group competition, among other factors, in determining group size and social organization among primates,<sup>24–26</sup> birds,<sup>22</sup> carnivores,<sup>27</sup> and humans.<sup>1</sup> Over the next decade, a clearer understanding of food competition was developed, which led to expanded ecological models of primate social organization. Building on the work of population and behavioral ecologists,<sup>28–30</sup> Janson and van Schaik<sup>2,31</sup> defined four types of food competition (Box 1) that pro-

vided conceptual clarity in subsequent models. The type and intensity of food competition have important implications for group size, social behavior, dominance relationships, and dispersal patterns. Depending on the distribution and abundance of food resources, individuals in groups will experience either contest or scramble competition, or both. When individuals or groups can exclude others from resources, contest competition results in differential access to food and ultimately leads to skewed fitness. Scramble competition occurs because all individuals must forage from the same limited resource base and results in equally reduced feeding opportunities for all individuals. Because the cost of scramble competition intensifies as groups grow larger, within-group scramble competition is expected to impose a limit on group size, while contest competition between groups may favor larger groups.<sup>14,31</sup>

Various authors built on Wrangham's work to make predictions about the outcome of competition on group size and social relationships.<sup>2,15,16,32</sup> van Schaik<sup>2</sup> modified Wrangham's model, suggesting that predation risk was the ultimate factor forcing females to live in groups despite the costs imposed by feeding competition. Building on previous work,<sup>1,13,14</sup> van Schaik argued that the costs of within-group competition far outweigh any advantages resulting from communal resource defense and that resource defense cannot be invoked as the pri-

mary selective force for grouping. Rather, the threat of predation puts a lower limit on group size, while within-group food competition sets the upper limit. If food is uniformly distributed in small patches of even quality that cannot be monopolized, or in very large patches where the whole group can feed, then competition will be by scramble. Female fitness will be affected primarily by group size and individuals will not be able to increase food acquisition through overt behaviors. If food occurs in well-defined, defensible patches that vary in quality and are not large enough for all group members, then contest competition will occur within groups. If high-quality food is clumped and patches are large enough for all group members, then between-group competition will be important.

van Schaik outlined a series of predictions regarding female dispersal and social relationships under various competitive regimes. This model was among the first to draw a sharp distinction between frugivores and folivores in terms of food distribution, competitive regime, and social outcomes. Within groups, folivores were classified as scramblers and frugivores as contesters, while between-group contests were assumed to occur only among frugivores. This distinction has been maintained in the literature and has been amplified so that applications of some later models assume that folivores experience no feeding competition at all.<sup>15</sup>

Sterck, Watts, and van Schaik<sup>16</sup> expanded van Schaik's model to explicitly integrate social variables and to define more clearly the possible social outcomes. By incorporating the effects of male behavior (particularly sexual coercion and infanticide), habitat saturation, and the cost of dispersal, along with predation and food distribution, this model seems to explain more of the observed variation in primate grouping patterns and social organization. With respect to folivores, Sterck, Watts, and van Schaik<sup>16</sup> suggested that infanticide in particular may have important social consequences for some species.

Isbell<sup>15</sup> and Isbell and Young<sup>33</sup> advanced ideas about how the social

### Box 2. Behavioral Indicators of Food Competition<sup>15</sup>

Type of Competition	Behavioral Indicator
<b>Between-group contest</b>	<ul style="list-style-type: none"> <li>● Between-group aggression among females</li> </ul>
<b>Between-group scramble</b>	<ul style="list-style-type: none"> <li>● Positive relationship between home range size and group size</li> </ul>
<b>Within-group contest</b>	<ul style="list-style-type: none"> <li>● Strong female dominance hierarchies</li> </ul>
<b>Within-group scramble</b>	<ul style="list-style-type: none"> <li>● Positive relationship between day range (daily travel distance) and group size</li> <li>● Negative relationship between female reproductive rates and group size</li> </ul>

and ecological cost of dispersal may act as a major determinant of social organization, proposing that when food is clumped, both WGS and WGC occur and, when food is dispersed, neither occurs. In constructing this model, Isbell<sup>15</sup> provided valuable methodological clarification by explicitly defining five behavioral indicators of food competition (Box 2), which can be used to assess the competitive regime of a species. Interestingly, although separate indicators were proposed for contest and scramble competition, Isbell<sup>15</sup> linked them together by presenting data demonstrating that they covary; that is, among species having home ranges that increase in size with group size, females are aggressive between groups. Similarly, among species with strong female dominance hierarchies, day range (daily travel distance) increases with group size. In contrast, species with weak or no female dominance hierarchies demonstrate no relationship between day range and group size. This is an important point because the model precludes the possibility of scramble competition without contest competition. The model does not allow the possibility that foods may be limiting but not defensible, or patchy but not monopolizable and that competition could be by scramble alone, as suggested in earlier models.<sup>2,14</sup>

Furthermore, Isbell<sup>15</sup> presented empirical data from a wide range of studies to demonstrate that many folivores experience no food competi-

tion. Notably, however, Isbell raised the possibility that ranging and group size may be poor indicators of competition among folivores and that previous attempts to measure these variables may have been confounded by food availability. This foresight is now proving to be very important.

Developed alongside these models was one that simply proposed to explain variation in group size. The ecological constraints model, or scramble competition hypothesis, suggests that group size is a function of travel costs.<sup>34–37</sup> Within-group competition is associated with increasing day range because when food is patchy, larger groups will deplete patches more quickly, individuals will obtain less food per patch, and groups will have to visit more patches in a day.<sup>38,39</sup> The energetic cost of travel between food patches is the mechanism whereby scramble competition imposes a cost on individuals and limits group size. The model is well supported by empirical data, particularly among frugivorous primates that compete for patchy, high-quality food resources.<sup>34,35,40–43</sup> Variation in group size is not a simple function of food abundance, however, but is a response to the interaction of the size, density, and distribution of food patches as well as individual differences in energy budget, travel costs, and foraging strategy. Nevertheless,



Figure 1. Black-and-white colobus monkey, *Colobus guereza*, from Kibale, Uganda.

existing evidence clearly demonstrates *i*) the cost of grouping to individuals, *ii*) the limiting effect of food competition on group size, and *iii*) the mechanism behind the relationship between group size and day range. While acknowledging that observed group sizes will be confounded by variables such as predation risk, resource defense, and mating strategies, the ecological constraints model proposes that the upper limit on group size is set by the increasing costs of travel imposed in larger groups. The application of this model to folivores has rarely been examined, but see Gillespie and Chapman<sup>44</sup> and Ganas and Robbins.<sup>45</sup>

### THE FOLIVORE PARADOX

In applications of socioecological models, many authors have implicitly or explicitly assumed that food

competition within folivore groups is inconsequential and that populations and groups are not limited by the availability of food (but see Koenig and colleagues<sup>26</sup> and Borries<sup>46</sup>). This inference is based primarily on studies that have found no relationship between group size and day range among folivores. For example, Clutton-Brock and Harvey<sup>3</sup> found that feeding group weight was not related to day-range length across diurnal, arboreal folivore genera. Similarly, Yeager and colleagues<sup>47,48</sup> found that across 17 Asian colobine species, day range did not increase with increasing group size. More specifically, early data for red colobus (*Procolobus rufomitratu tephrosceles*) in Kibale, Uganda, showed no relationship between group size and day range.<sup>49</sup> More recently, Fashing<sup>50</sup> found no relationship between group size and day range across five groups of black-and-white colobus (*Colobus guereza* see Fig. 1). In general, the

flat relationship between group size and day range, in combination with the longstanding assumption that leaf resources are abundant and evenly dispersed, has been used to infer that within-group food competition is weak or absent among folivores.<sup>4,14–16,33,37</sup>

Given this assumed reduction in feeding competition, folivores are theoretically free to form larger groups. If protection from predation is a major aggregative force,<sup>1,2,10,13</sup> then folivores should take advantage of this reduction in feeding competition to form large groups. However, many folivores live in surprisingly small groups relative to similarly sized frugivores, which should be more constrained by the patchy distribution of fruit.<sup>37,51</sup> This apparent contradiction has been referred to as the folivore paradox.<sup>4,17</sup>

Social factors, such as the risk of infanticide, have been invoked to solve the problem. For example,

Crockett and Janson<sup>51</sup> found that the rate of infanticide increased with group size in red howlers (*Alouatta seniculus*), but only until a group was large enough to create paternity confusion; at that point, WGS became more costly. These authors suggested that infanticide avoidance could constrain group size below the level where WGS imposes a cost. Steenbeek and van Schaik<sup>4</sup> suggested that among Thomas' langurs (*Presbytis thomasi*),<sup>4</sup> group size was limited by the risk of infanticide because larger groups were more at risk of male takeover. Although demonstrable effects of WGS were observed (day range increased with group size and females in larger groups ate less fruit and more leaves) the authors concluded that WGS was not limiting group size because dietary switching was marginal and there was no effect on activity budget or birth rate. Koenig and Borries<sup>17</sup> found that both feeding competition and infanticide risk constrained group size in hanuman langurs (*Semnopithecus entellus*): As group size increased, female nutritional condition was compromised, birth rates decreased, and the risk of infanticide increased due to immigrating males. However, Treves and Chapman<sup>52</sup> found that infanticide avoidance did not limit group size in different populations of hanuman langurs, but that increasing group size may have been a counter-strategy to prevent takeovers and infanticide. The available evidence indicates that in some populations infanticide may constrain group size, but might not provide a complete solution to the folivore paradox. Furthermore, the data do not rule out the possibility that ecological factors also play an important role in limiting folivore group size in some populations.

### Do Folivores Experience Within-Group Scramble Competition?

Nine lines of evidence suggest that folivores experience within-group scramble competition and that group size may be ecologically constrained. This evidence implies that current

interpretations of primate socioecology inadequately characterize the competitive regime of folivores, and that, although social factors are no doubt also important, the folivore paradox may be resolved for some species on ecological grounds.

### *Folivore foods vary in distribution and quality*

Folivores have traditionally been defined as those primate taxa with morphological adaptations specialized for the efficient digestion of leaves.<sup>53</sup> A significant proportion of their diet was thought to be com-

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posed of leaf matter. Recent evidence suggests the need to reassess the assumption that folivores rely on ubiquitous and evenly distributed food resources of relatively low and uniform nutritional quality. It is now clear that folivores feed selectively and that their food resources vary in quality, availability, and spatial distribution. Many folivores primarily select high-quality young leaves, seeds, flowers, and unripe fruits.<sup>26,48,54-56</sup> These resources are often patchily distributed in both

space and time, and vary in nutritional quality.<sup>54,57-60</sup> Thus, they may provide the ecological conditions typically associated with food competition. It is probably only mature leaves that are distributed superabundantly and continuously, and even these vary dramatically in nutritional quality.

Koenig<sup>25</sup> and Koenig and colleagues<sup>26</sup> have demonstrated that forest-living hanuman langurs preferentially exploited mature leaves that occurred in low-density clumps that were not large enough for all group members to feed simultaneously, and were higher in protein and soluble sugar than other available foods. Black-and-white colobus (*C. guereza* see Fig. 1) in Kibale are among the most highly folivorous primates known, and yet they are selective eaters; they more frequently choose young than old leaves, select certain tree species, alter their range use to obtain certain foods, and eat foods of varied nutritional content.<sup>61-63</sup> Similarly, *C. guereza* and *A. palliata* do not forage continuously as they move through the canopy, but feed only in certain trees, often traveling directly from one source to another.<sup>59,61</sup> Finally, for many folivores, mature leaves are heavily consumed only when other foods are scarce.<sup>48</sup> These studies suggest that the simple designation "folivore" is insufficient for characterizing the diet of primate species<sup>26,60</sup> or for making behavioral inferences.

### *Folivores may deplete patches of food*

An important assumption underlying current interpretations of competition among folivores is that they do not deplete food patches. This assumption necessarily underlies the idea that folivores do not need to increase day range to compensate for increasing patch depletion rates in larger groups and thus do not experience scramble competition. However, a recent study found that red colobus monkeys functionally depleted patches of high-quality foods (young leaves) and that patch occupancy

time was related to the size of the feeding group and the size of the patch.<sup>64</sup> Similar patch-size effects have been demonstrated for howling monkeys.<sup>43,65</sup> If patches are depleted more quickly by larger groups, day range is expected to increase. However, this relationship may not always be simple; alternate responses may exist. For example, if larger groups cannot compensate for increased depletion rates by increasing travel distance, they may increase group spread to maintain fewer individuals per patch.<sup>43,64–66</sup> Alternatively, individuals may deplete patches further, possibly by feeding on less desirable plant parts. This idea is based on the logic of Charnov's<sup>67</sup> marginal value theorem, which proposed that giving-up times should occur after more depletion (at a lower intake rate) when the time required to find another food patch is high. There has been no examination of whether folivores use such compensatory measures. However, the observations that folivores demonstrably deplete patches and that patch size is related to feeding group size are consistent with the assumptions of the ecological-constraints model and suggest that WGS occurs among folivores.

#### *Group size is related to habitat quality*

It has recently been demonstrated that folivore group size can be predicted by habitat variables. For example, across the geographical range of red colobus, group size tended to be larger in rainforests and moist woodlands than in drier seasonal habitats.<sup>68,69</sup> Across 10 sites, red colobus group size ranged from 7 to 83 individuals ( $n = 60$ ) and was affected by the tree density, degree of deciduousness, degree of forest disturbance, and forest block size.<sup>70</sup> Similarly, across four study sites in Kibale, groups were larger where food-tree density was greater.<sup>44,71</sup> Furthermore, although black-and-white colobus monkeys typically form much smaller groups than often-sympatric red colobus, in Nyungwe, black-and-whites (*C. angolensis*) form exceptionally

large groups of more than 300 individuals.<sup>72</sup> This has been attributed to the almost unrestricted availability of unusually high-quality mature leaves that are a source of high protein and low fiber. However, this result must be interpreted with caution because fiber content was determined using a different technique than those used in other studies. Furthermore, Dunbar<sup>73</sup> reported that *C. guereza* group size was related to territory quality. Groups permanently fissioned into smaller groups when group size exceeded 10 trees per individual and territory size could not be increased. These results suggest that folivore group size may be ecologically constrained and that large groups form only when food conditions mitigate the costs of within-group competition.

#### *Day range may be related to group size*

As described, evidence for the absence of scramble competition among folivores comes primarily from studies that have found no relationship between group size and day range, and is based on the assumption that folivores rely on ubiquitous and evenly distributed food resources. However, using these studies<sup>3,47–50</sup> to infer that there is no within-group competition is problematic because they generally lack sufficient controls for ecological variation through time, among study groups, or across species. If group size can be adjusted to ecological conditions, then scramble costs can be avoided, negating the need to increase day range. Ecological variation can thus confound correlational studies, making it difficult to interpret previous comparisons across groups, and especially across species. Several recent studies that controlled for ecological variation found that day range did increase with group size for some folivores (*Gorilla beringei*,<sup>45</sup> *P. tephrosceles*,<sup>44</sup> *P. thomasi*<sup>4</sup>). If folivore day range has the potential to be affected by group size in the manner suggested by the ecological constraints model, inferences drawn on the basis of ear-

lier studies that lacked ecological controls must be reassessed.

#### *Day range may be related to food availability*

Several studies have found that folivore groups increase day range during periods of food scarcity or in areas with lower food availability (*G. beringei*,<sup>45</sup> *C. satanas*,<sup>74</sup> *C. angolensis*<sup>75</sup>), presumably due to the need to increase travel between patches. This can be interpreted as an effect of scramble competition because, if group size is constrained by local ecological conditions, then a given group might be expected to respond to temporal fluctuations in food availability by increasing its range when food becomes scarce. However, other studies have documented either no relationship (*C. guereza*<sup>50</sup>) or the reverse pattern (*C. satanas*<sup>76</sup>). Careful examination of the relationship among food abundance, the distribution of food patches, and ranging behavior is required to clarify these patterns. Relationships between food abundance and day range are likely to be confounded by food distribution. For example, some groups may travel long distances to reach specific resources<sup>50,62,77,78</sup> or may change their diet to rely on more evenly distributed foods during periods of scarcity.<sup>48</sup>

#### *Fission-fusion occurs*

Studies have found that some folivore species exhibit fission-fusion behavior, with large groups temporarily dividing into smaller foraging groups that vary in size and composition.<sup>48,54,70,72,79,80</sup> Studies suggest that this pattern occurs in response to low food availability associated with low tree density, particularly in degraded habitat. Such short-term variation in group size is a well-documented response to variable ecological conditions among frugivores, including chimpanzees,<sup>40,42</sup> bonobos (*P. paniscus*),<sup>11</sup> orangutans (*Pongo pygmaeus*),<sup>12,81</sup> and spider monkeys.<sup>82,83</sup> This strategy is advantageous for individuals that rely on patchy and unpredictable food resources because the ability to adjust

group size allows greater flexibility in response to ecological conditions, and can mitigate the costs of food competition.

### *Reproductive success is related to group size*

There is evidence that female reproductive success may be compromised as group size increases, presumably because increasing food competition leads to nutritional stress. This reasoning is based on the relationship between female nutritional status and fecundity, birth rate, and early infant survival. There is a very clear causative chain linking energy balance to fecundity in humans and apes,<sup>84,85</sup> as well as a documented relationship between female nutritional status (food intake) and both birth rate and early infant survival in many primates.<sup>10,86–89</sup> Although careful empirical work is required to separate the effects of compromised fecundity from those of infanticide,<sup>51</sup> there appears to be a group-size effect on birth rate in folivores. Gorillas in larger groups spent more time feeding, suggesting a social foraging cost.<sup>90</sup> Struhsaker and coworkers<sup>70</sup> found that habitat quality was the most important factor affecting birth rate across 19 groups of red colobus. Koenig<sup>17,25</sup> found that as group size increased, female nutritional condition was compromised among hanuman langurs. Dunbar<sup>73</sup> documented the same relationship across four populations of *C. guereza* and suggested that stress and competition led to reproductive suppression in larger groups. More generally, van Schaik<sup>10</sup> demonstrated that folivore birth rate (number of infants per female) decreased with increasing group size, and that this relationship was stronger for folivores than frugivores. However, there is disagreement regarding this use of unadjusted birth rates.<sup>51,87</sup>

This effect may be related to the energetics of a folivorous diet. Due to their dietary specialization for the digestion of low-quality foods, folivores must devote a large portion of their time to resting and digesting.<sup>91,92</sup> This may prevent individuals from

increasing food intake to compensate for increasing energetic costs, which may effectively prevent folivores from increasing day range as group size increases, even if food competition intensifies. This may ultimately result in compromised nutrition, fecundity, and birth rates. Measures of female reproductive success and hormonal markers of fecundity may provide important indices of within-group competition costs when changes in day range are not observed.

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**...folivores engage in contests for food both within and between groups, challenging the longstanding notion that their diet is not worth fighting over and raising further questions about the apparent lack of dominance relations in some species. Although further investigation is certainly required, the findings reviewed here suggest that group size is probably constrained by ecological factors for some species of folivores...**

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### *Food-related contest competition occurs*

Recent research suggests that food-related contest competition occurs both within and between some groups of folivores. We believe that this finding is important for two reasons. First, it challenges previous notions that folivores generally do not or cannot engage in contests for food. Second, it raises the possibility that the benefits of BGC compensate for the costs of WGS or WGC in some larger folivore groups,<sup>14,32</sup> which may lead to the appearance of no competition and the

apparent absence of a group-size effect. Koenig<sup>25,26</sup> documented linear dominance hierarchies within groups of hanuman langurs that fed on high-quality clumped resources that were too small for all group members. Higher-ranking females attained higher net energy gain and were in the best physical condition, indicating WGC. Furthermore, between-group differences in condition indicated BGC. Remarkably, the benefits of BGC were shown to compensate to some degree for the demonstrated costs of WGC and WGS, with the result that females in mid-sized groups were in the best physical conditions.

Some populations of black-and-white colobus monkeys rely on fruit for some portion of their diet and both males and females may participate in food defense.<sup>93</sup> Several authors have concluded that in more leaf-dependent populations of black-and-white colobus, males competitively defend food resources as an indirect means of defending access to females.<sup>50,61,62,94</sup> A dominance hierarchy between groups has been demonstrated for *C. guereza* at Kibale.<sup>62,63</sup> Dominant groups roared more, won more fights, were avoided by subordinate groups, and maintained core areas with food resources of greater quantity and quality. This case is particularly interesting because this population is highly folivorous,<sup>61,62,95</sup> suggesting that leaves are indeed worth fighting over. In general, this new evidence indicates that folivore groups may compete to monopolize access to food sources even without overt fighting or displacements and without strict territoriality. As suggested by Wrangham,<sup>14</sup> avoidance is a possible manifestation of contest competition in primates. Dominant groups or individuals may maintain preferential, if not exclusive, access to the best resources simply because they are avoided by subordinate groups or individuals.

### *Population density is related to habitat quality or food availability*

Folivore biomass can be predicted by the distribution of mature leaves with a high protein-to-fiber ra-

tio.<sup>72,95–98</sup> Although this does not directly suggest that there will also be constraints on group size, it does provide further support that folivores may be limited in important ways by the quality, availability, and distribution of food resources, and suggests that the potential for food competition exists. Previous assumptions that folivore food resources are nutritionally uniform and not limiting have formed the basis for general inferences about food competition in folivores.

## DISCUSSION

Folivores have traditionally been seen as living without food competition or social stratification within or between groups, but this was largely based on the notion that they exploited ubiquitous and invariable food sources. These assumptions have been implicitly or explicitly incorporated into applications of socioecological models and have led to the folivore paradox. However, recent empirical data are increasingly exposing folivores as competitive and socially variable. Many folivore populations exploit high-quality, patchily distributed, temporally variable food resources, and display many of the expected responses to food competition. The emerging picture is complex. Folivore strategies vary across populations and species, indicating adaptive flexibility in response to local conditions. Folivores appear to be subject to the same ecological constraints as frugivores and may respond with similar competitive regimes when food conditions are similar. However, rather than simply increasing day range to compensate for increasing group size, folivores may display alternate responses to the costs imposed by scramble competition or may incur fitness costs in larger groups. Perhaps most surprisingly, folivores engage in contests for food both within and between groups, challenging the longstanding notion that their diet is not worth fighting over and raising further questions about the apparent lack of dominance relations in some species. Although further investigation is certainly required, the find-

<b>Box 3. Expanded List of Behavioral Indicators of Food Competition</b>	
<b>Type of Competition</b>	<b>Behavioral Indicator</b>
<b>Between-group contest</b>	<ul style="list-style-type: none"> <li>● Food-related between-group aggression involving females and/or males</li> <li>● Between-group dominance hierarchy</li> <li>● Between-group displacements or avoidance</li> </ul>
<b>Between-group scramble</b>	<ul style="list-style-type: none"> <li>● Positive relationship between habitat quality and population density</li> </ul>
<b>Within-group contest</b>	<ul style="list-style-type: none"> <li>● Female dominance hierarchies</li> <li>● Food-related within-group aggression, avoidance, displacements and/or agonistic alliances</li> <li>● Rank-related skew in food acquisition, nutritional status, fecundity, and reproductive success</li> </ul>
<b>Within-group scramble</b>	<ul style="list-style-type: none"> <li>● Positive relationship between group size and day range and/or home-range size and/or habitat quality</li> <li>● Negative relationship between habitat quality and day range and/or home-range size</li> <li>● Fission-fusion related to temporal variation in resource availability</li> <li>● Positive relationship between patch depletion rate and group size, and/or negative relationship between depletion rate and patch size</li> <li>● Positive relationship between group size and normalized group spread, and/or nonpositive relationship between total group size and feeding group size</li> <li>● Longer giving-up time in larger groups and/or poorer habitat</li> <li>● Negative relationship between group size and female nutritional status, fecundity, and reproductive success</li> </ul>

ings reviewed here suggest that group size is probably constrained by ecological factors for some species of folivores just as has been demonstrated for many frugivores. Undoubtedly, folivore group size is also influenced by social factors like infanticide. The interaction of social factors and ecological constraints requires further investigation. These results provide important insights into the folivore paradox and may be used to refine the assumptions behind current interpretations of the

competitive regime of leaf-eating monkeys.

In practical terms, we believe there are two areas where efforts are required to provide theoretical clarification and direction for empirical research. First, the terms used to describe resource characteristics and the methods used to measure them need to be consistently and explicitly defined,<sup>66,99</sup> particularly if resource characteristics are used to infer particular competitive regimes. Second, a wider range of indicators of food competition, including social, be-





Figure 2. Female aggression during between group encounters as illustrated by female Hanuman langurs (*Semnopithecus entellus*) from Jodhpur, India. Photo by Carola Borries.

havioral, and energetic, needs to be recognized.

The abundance and distribution of food determines the type, intensity, and social outcomes of feeding competition. However, the distribution of food varies in a number of interacting dimensions and on many scales. Wrangham<sup>14</sup> wrote that BGC requires that high-quality food is distributed in discrete, defensible patches, and that fallback food occurs in large, uniform patches. This is a complex statement that incorporates five separate issues: food source size, quality, patchiness, defensibility, and variability. Separating these ideas, clarifying the spatial and temporal scales at which they operate, and standardizing measurement methods will go a long way toward clarifying ecological measures and their competitive outcomes in future models. Furthermore, Wrangham drew attention to the need to recognize not only the difference

between preferred and fallback foods, but that both may influence social organization. That primates can modify their feeding strategies in response to food availability, exploiting different foods with different nutritional and distributional characteristics at different times, may be a major issue affecting our ability to construct realistic models.

In the 1980s and 1990s, the work of Wrangham,<sup>14</sup> van Schaik,<sup>2</sup> Isbell,<sup>15</sup> Sterck,<sup>16</sup> and others was instrumental in defining primate competitive regimes and highlighting the ultimate importance of ecological factors in determining the adaptive strategies of individuals and the consequent social organization of groups. Perhaps most critically, these authors emphasized the importance of applying clear definitions of the types of food competition experienced by individuals in groups, made predictions regarding the social and behavioral consequences of competi-

tion, and identified measurable behavioral indicators by which the competitive regime of a species can be assessed. It is now becoming increasingly apparent that primates possess a suite of responses to food competition and that any single index may be confounded by a variety of ecological and social factors. Here and in Box 3 we propose an expanded set of behavioral indicators of competition. The necessity of incorporating multiple indices of competition into both theory and empirical studies was highlighted by our exploration of the folivore paradox, where failure to document the simple expectation of increasing day range with increasing group size led to premature conclusions about food competition.

The most commonly used evidence of food-related between-group contest competition has been female aggression during between-group encounters (see Fig. 2)<sup>2,14,15,100</sup> and was the

indicator originally proposed by Isbell (see Box 2) to measure this phenomenon. This follows from sexual selection theory,<sup>23</sup> which suggests that because female reproductive success is limited by access to resources, females should compete for and defend food, while males should compete for and defend mates. However, a lack of female participation in between-group encounters should not be used as evidence that BGC is *not* related to food. Males may also participate in BGC in defense of food resources as an indirect means to defend access to females.<sup>8</sup> Furthermore, overtly aggressive between-group interactions are not required; avoidance behaviors may also indicate BGC.<sup>14,100</sup>

Between-group scramble competition results from the common use of food resources by all groups or individuals; it can thus occur only when groups occupy overlapping ranges. In habitat of constant quality, BGS will increase in intensity with increasing population density. Earlier work<sup>15,87</sup> suggested that an increase in home-range size as a result of an increase in group size could be used to indicate BGS. However, because between-group scramble is an effect of population density and is independent of group size, this is not an appropriate measure. Rather, a positive relationship between population density (cumulative group size) and habitat quality indicates that BGS competition occurs.

Female dominance hierarchies have traditionally been used as the primary indicator of within-group contest competition. Because contest competition results in skewed energy acquisition,<sup>2,9,31</sup> interindividual differences in fitness, as indicated by skew in birth rate, body condition, and other physiological measures may also indicate WGC. Such measures must be used with care because individual differences in fitness will be affected by many factors such as genetic and ontogenetic variation. Nevertheless, these measures may prove useful in cases where overt contests and dominance hierarchies are rare or difficult to observe (for example, subtle avoidance behavior

or the ability to occupy the best feeding sites). For example, it has been shown that there may be a demonstrable WGC effect on food intake and reproductive success without the expected agonistic alliances and nepotistic affiliative patterns<sup>25</sup> or without clear behavioral contests over relevant food items.<sup>89</sup> Measures of birth rate and body condition have the additional advantage of being more direct indicators of fitness and, if they can be related to differences in rank, may provide an index of the ultimate effects of food competition on the reproductive success of individuals.<sup>25</sup>

A positive relationship between day range and group size has long been used as the primary indicator of within-group scramble competition. However, the relationship between day range and group size can be obscured by ecological variation. Moreover, increasing day range is not the only possible behavioral response to scramble competition in groups. Group size itself may be constrained by local habitat quality, so that individuals may avoid the need to increase day range. Furthermore, within groups, individuals may compensate for temporal fluctuations in competition intensity caused by ecological variation by adjusting day range through time or by fissioning. Individuals may also avoid the travel costs associated with increasing day range by altering group spread or patch depletion thresholds and giving-up times. If individuals are unable to compensate for grouping costs, then fitness will decrease in larger groups. Such considerations substantially broaden the list of potentially observable indicators of within-group scramble competition.

Expanding the list of acceptable indicators of food competition provides measurable, quantifiable variables for field studies and may provide direction for the development of hypotheses that will further our understanding of primate socioecology. Furthermore, by constructing this list we acknowledge that primates may employ a variety of possible responses to food competition and that univariate analyses will often be

insufficient for describing the competitive regime of a species.

Based on the issues addressed in this paper, Figure 3 outlines a working-version model of the potential competitive outcomes of variation in resource characteristics. The logic and predictions of this model are essentially no different from those of van Schaik<sup>2</sup> or Wrangham.<sup>14</sup> We attempt to build on these models by offering a more detailed tool for addressing the multidimensional nature of ecological variation and possible competitive outcomes. The availability, distribution, size, quality, and contestability of food resources are addressed as separate ecological variables that can vary independently of one another. There are no *a priori* assumptions about the mutual exclusion of different types of competition. For example, WGS may occur alone or along with BGC and/or WGC. When the empirical evidence presented here regarding the distribution, quality, and abundance of folivore foods is applied to this model or to previous models, it leads to the prediction that many folivores will compete by scramble and/or contest.

Perhaps the most important development presented here, from the perspective of understanding ecological constraints on folivores, is the distinction between patchy (that is, depletable) and continuous food distribution at the second level of classification. This allows for the possibility of WGS without contest competition. Scramble can still be important when food is neither variable in quality nor defensible, a likely scenario for many folivores. We provide examples of folivore populations on as many branches as possible, including branches representing competitive regimes that have traditionally been reserved for frugivores. Further research is required to determine whether the ideas presented in Figure 1 are a useful and accurate way to depict the ecological pressures influencing the evolution of primate social organization.

The evidence presented here suggests several profitable directions for future field research. First, it is important to understand individual behavioral strategies. Data regarding

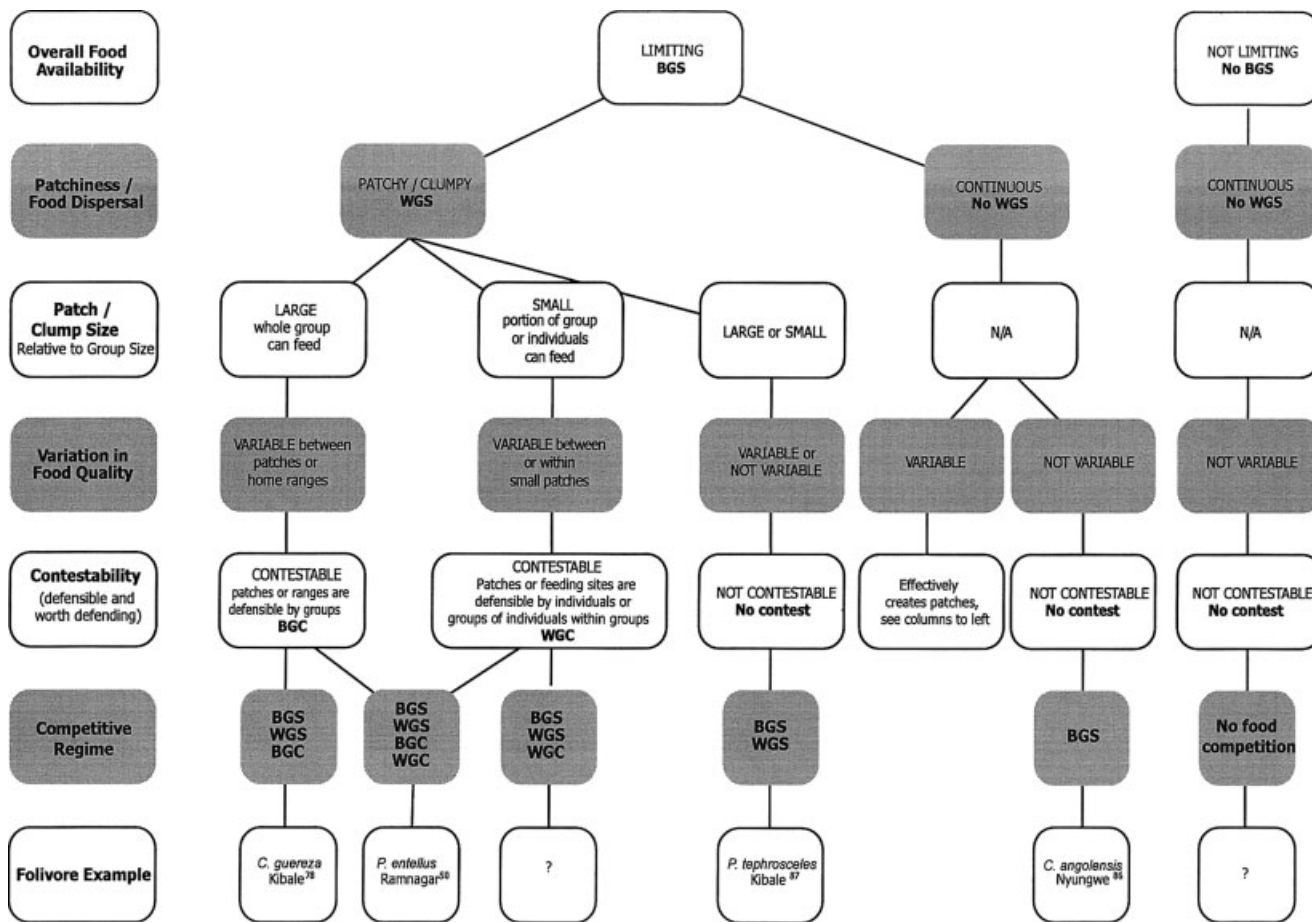


Figure 3. Working model of how resource abundance and distribution affect competitive regime in primates. Legend: BGS: Between-group scramble competition; BGC: Between-group contest competition; WGS: Within-group scramble competition; WGC: Within-group contest competition.

the activity budgets, nutrient gain, and reproductive success of recognizable individuals in groups of different sizes are required to quantify the fitness costs of food competition. Second, attention should be focused on subtle expressions of contest competition, such as avoidance or the consistent attainment of better feeding sites by certain individuals or groups, and whether these have fitness consequences. Third, to unravel how primate social organization is shaped by ecological conditions and whether different species and populations respond in the same manner to ecological variation, we need quantitative ecological data based on carefully defined measures for a wide range of species. For example, we need comparable descriptions of the spatial and temporal distribution of food resources, variation in food

quality within and between patches and through time, patch size relative to group size, and patch attributes such as contestability. Because these factors are presumed to be of primary importance in determining the nature of within- and between-group competition, we need to investigate their social outcomes in hypothesis-driven field studies.

It is unlikely that any model will ever capture the entire range of social variability among primates, and we recognize that our focus on feeding competition captures only part of the puzzle. Many other factors, including predation, infanticide, dispersal costs, and social dynamics must also be incorporated. But we hope that the issues brought to light by this ecological examination of the folivore paradox will contribute to the next generation of models by

increasing our understanding of the adaptive significance of particular competitive regimes and the selective forces shaping primate food competition and social organization.

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