Re-evaluating the Ecological Constraints model with red colobus monkeys 
(*Procolobus rufomitratus tephrosceles*)

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Abstract
The Ecological Constraints model was proposed to explain limits to group size and the observation that larger groups of primates often travel farther per day than smaller groups. It argues that larger groups are forced to travel to more patches of food to compensate for more rapid patch depletion. While the evidence from highly frugivorous primates is consistent with this argument, evidence from folivorous primates is contradictory. Many folivorous species, including the extremely folivorous red colobus (*Procolobus rufomitratus tephrosceles*), have long been thought to show no group size-adjusted changes in daily travel distance (DTD). More recent research suggests, however, that larger groups of red colobus do travel farther per day than smaller groups, and it has been argued that earlier research obscured real effects of group size on DTD because of differential but unacknowledged habitat quality. This study challenges that explanation with a comparison of red colobus feeding and ranging behavior and activity budgets in two distinct compartments of Kibale Forest, Uganda, one of which was selectively logged 11 years earlier. Logging would have accentuated natural floristic differences that might have existed between compartments, thus increasing the likelihood that DTD would differ significantly between compartments. Findings reveal, however, that although there were compartmental differences in canopy cover, understory density, size of trees, and food tree species, the group did not respond to these differences by altering DTD (or their activity budgets). If the floristic differences between compartments are interpreted as insufficient to affect DTD, then it weakens the explanation that earlier studies were confounded by habitat differences. Alternatively, if the differences between compartments are interpreted as theoretically or ordinarily sufficient to affect DTD (e.g., in primates that routinely adjust DTD to group size), then the mechanism underlying the Ecological Constraints model must be questioned for red colobus. Feeding behavior coupled with group movements suggest that the group did not feed in discrete patches, an important element of the Ecological Constraints model. Instead, the group typically fed from multiple tree species per 0.25-ha quadrat and moved slowly, suggesting that their food trees were more uniformly distributed. Estimates from botanical transects and behavioral data also support the interpretation of a more uniform food distribution. Nearly all stems were food tree
species and food trees occurred at a density much higher than for folivorous primates that do show a group size effect on DTD. The group increased its DTD more when funneling across gaps in the forest. Funneling is a group movement that is expected to occur more frequently during travel when group size is large, travel routes are few and narrow, and target locations are sparse or patchy and small relative to group size. It is proposed here to be more fundamental than patch depletion as a mechanism to explain group size-adjusted DTD in other primates.

**Keywords**
folivores, primates, feeding behavior, ranging behavior, daily travel distance, Kibale National Park, Uganda.

### 1. Introduction

Primates display wide dietary and social diversity that can help shed light on ecological and social influences on female reproductive success, group size, and population dynamics. For instance, in Old World monkey (cercopithecoid) species whose diet includes a high proportion of fruit, females tend to live throughout their lives in their natal groups (Pusey & Packer, 1987; Isbell & Van Vuren, 1996), whereas in Old World monkey species whose diets include a high proportion of leaves, females are apparently less constrained socially and can join other groups (Isbell & Van Vuren, 1996; Fashing, 2011). Similarly, a positive relationship between group size and daily travel distance (DTD) exists for most frugivorous primates (Clutton-Brock & Harvey, 1977; Isbell, 1991; Wrangham et al., 1993; Janson & Goldsmith, 1995) (guenons, *Cercopithecus* spp., are exceptions: Struhsaker & Leland, 1988; Butynski, 1990), whereas no such relationship has historically been found in folivory-adapted primates (Clutton-Brock & Harvey, 1977; Struhsaker & Leland, 1987; Isbell, 1991; Janson & Goldsmith, 1995; Fashing, 2001).

A group size effect on DTD suggests that there can be energetic consequences of living in larger groups. The logic and mechanism behind a group size effect on DTD is detailed in the Ecological Constraints model, which posits that as groups increase in size, for any patch of a given size, there will be less food per individual. This leads to faster depletion of available food, forcing larger groups to travel farther to get sufficient food for the entire group if they cannot spread out (Waser, 1977; Chapman, 1990; Isbell, 1991; Chapman et al., 1995; Chapman & Chapman, 2000a,b; Wrangham, 2000; Snaith & Chapman, 2005). For this to occur, foods would necessarily occur in discrete patches, commonly defined for primates as an individual tree or group of trees of the same species separated from other trees of that species.