



## Individualistic female dominance hierarchies with varying strength in a highly folivorous population of black-and-white colobus

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### Abstract

Females that do not experience strong contest competition for food are presumed to form 'egalitarian' relationships (i.e., lacking strong, linear dominance hierarchies). However, recent studies of *Gorilla beringei beringei* (mountain gorilla) have documented relatively strong, linear female dominance hierarchies despite them having a highly folivorous diet that generates relatively low levels of within-group contest competition (Robbins et al., 2005, 2007). To investigate if this pattern holds true for other highly folivorous species that may experience low levels of contest competition, we examined the linearity and strength of female dominance hierarchies in a population of *Colobus vellerosus* (ursine colobus or white-thighed colobus) at Boabeng-Fiema, Ghana. From 2004 to 2011, we collected data via ad libitum and focal sampling of 75 adult and subadult females in eight groups. Half of the study groups had few unknown submissive relationships, and females formed individualistic hierarchies with high linearity indices ranging from 0.9 to 1. There was between-group variation in all components of hierarchical strength (i.e., hierarchical expression, consistency, and stability). Groups showed varying rates of submission, and there was a short latency to detect a linear hierarchy in some groups and a long latency in other groups (i.e., varying levels of hierarchical expression). Females in most groups formed unidirectional and stable relationships. Maturing females challenged older females in some groups, and these groups had more non-linear relationships (i.e., dyads with more submissive interactions down rather than up the hierarchy) and higher rates of individual rank change than other groups. Based on low rates of submission, long latencies, and/or some inconsistencies, we conclude that most groups form relatively

weak dominance hierarchies, similar to other egalitarian primates. However, a few groups formed strong dominance hierarchies, similar to some despotic primates. *Colobus vellerosus* occasionally forage on contestable food items, and this may provide enough incentive for females to establish individualistic dominance hierarchies of varying strength.

### Keywords

dominance, individualistic hierarchies, hierarchical linearity, hierarchical strength, egalitarian, female relationships, dominance continuum, *Colobus vellerosus*.

## 1. Introduction

The most important resource for female reproductive success is usually food (Trivers, 1972), and females in social groups compete aggressively for access to high-quality food items when they are contestable on a spatial (i.e., monopolisable) and temporal (i.e., usurpable) scale (Janson & van Schaik, 1988; Isbell, 1991; Janson & Chapman, 2000). To avoid repeated and escalated conflicts for access to these high-quality foods, females should form linear dominance hierarchies (Guhl & Allee, 1944; Maynard Smith & Price, 1973; Bernstein et al., 1974; Maynard Smith, 1974; Sapolsky, 1983). High-ranking females benefit from greater access to food and show higher reproductive success than low-ranking females in several species including *Rangifer tarandus* (reindeer) (Espmark, 1964; Barrette & Vandal, 1986), *Papio anubis* (olive baboons) (Barton, 1993; Barton & Whiten, 1993), *Crocuta crocuta* (spotted hyenas) (Holekamp et al., 1996, 2012), *Chlorocebus pygerythrus* (vervet monkeys) (Whitten, 1983), and *Cebus capucinus* (white-faced capuchins) (Vogel, 2005).

Females are not expected to form dominance hierarchies if their diets consist mostly of food items that are not contestable according to several socioecological models (Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Sterck et al., 1997). Some colobines, gorillas and elephants that eat mostly leaves or grass were thought to fit this pattern because of low rates of agonistic interactions. However, detailed, long-term observations show that these species form stable and/or consistent female dominance hierarchies (e.g., *Semnopithecus entellus*: Koenig, 2000; *Trachypithecus phayrei*: Koenig et al., 2004; *Gorilla beringei beringei*: Robbins et al., 2005; *Loxodonta africana*: Archie et al., 2006). Many of these species occasionally forage on high-quality food items, which may only be available seasonally (reviewed in Snaith & Chapman, 2007). If these food items are contestable (i.e., it is possible to monopolize access to the food patch), it may be important to maintain