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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

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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 decided dominance relationships year-round to avoid conflicts when high-quality food items are available (Wrangham, 1980; Koenig et al., 1998; Archie et al., 2006; Robbins, 2008). Despite this growing body of evidence showing that folivores and herbivores form decided dominance relationships, few studies investigate how their dominance characteristics differ from those of frugivores that may experience more intense competition for food.

To better characterize similarities and differences between species and populations, it is useful to describe dominance hierarchies in terms of several dimensions: hierarchical type, strength or despotism (i.e., if hierarchies are egalitarian or despotic), and tolerance (van Schaik, 1989; Sterck et al., 1997; Isbell & Young, 2002). The first dimension, hierarchical type, describes how females rank in relation to matrilineal female kin (van Schaik, 1989; Sterck et al., 1997). Females form individualistic hierarchies if they do not rank close to female kin (van Schaik, 1989; Sterck et al., 1997), and these females acquire their dominance rank based on individual characteristics such as size and age (e.g., Espmark, 1964; Hrdy & Hrdy, 1976; Creel et al., 1992). Some carnivores, primates and ungulates form these types of dominance hierarchies (e.g., Espmark, 1964; Hrdy & Hrdy, 1976; Creel et al., 1992). Females that form nepotistic hierarchies rank close to female kin (van Schaik, 1989; Sterck et al., 1997). These females rely on coalitionary support from female kin and acquire a rank adjacent to their mothers. Nepotistic hierarchies characterize female philopatric cercopithecines and hyenas (Frank, 1986; Chapais, 1992; Holekamp et al., 1996; Kapsalis, 2004). The second dimension, despotism, is often measured by the degree of hierarchical linearity and hierarchical strength (Sterck et al., 1997; Isbell & Young, 2002). Dominance hierarchies are highly linear when A dominates all group members, B dominates all group members except for A, etc. (Appleby, 1983) and highly linear dominance hierarchies characterize despotic rather than egalitarian species (van Schaik, 1989; Sterck et al., 1997). However, apparent non-linear hierarchies are often an artefact of insufficient data, because the indices that measure linearity are sensitive to the presence of dyads without any recorded interactions (Galimberti et al., 2003; Robbins et al., 2005; Koenig & Borries, 2006). Therefore, a high hierarchical strength (i.e., how strictly enforced the dominance hierarchy is) may be a more informative indicator of despotic relationships. Hierarchical strength is measured by variables linked to the consistency, stability and expression (i.e., how often dominance interactions occur and in what context) of dominance relationships (Isbell & Young, 2002). The third dimension, hierarchical tolerance, describes how dominant animals interact with subordinate animals in despotic species (de Waal, 1989). Tolerant species are characterized by frequent counter-aggression, low kin bias in affiliative behaviours, and high conciliatory tendencies (Thierry, 2000).

These three hierarchical dimensions are predicted to vary with the level of contest competition for food (Isbell, 1991; Sterck et al., 1997). When females directly compete for access to high-quality food items against other group members, they will experience high levels of within-group contest competition for food, and their reproductive success will be correlated with their dominance rank (Janson & van Schaik, 1988). These females will form nepotistic, despotic (i.e., highly linear and strong hierarchies), and intolerant dominance hierarchies (van Schaik, 1989; Isbell, 1991; Sterck et al., 1997). If females also experience high levels of between-group contest competition (i.e., groups' dominance ranks are correlated to mean female reproductive success: Janson & van Schaik, 1988), dominant females will be more tolerant towards subordinates because they rely on the coalitionary support from subordinates during between-group encounters (Sterck et al., 1997). When food is not monopolisable, females will experience low levels of within-group contest competition, and a female's dominance rank will not affect her reproductive success (Janson & van Schaik, 1988). These females will form individualistic dominance hierarchies and egalitarian dominance relationships (i.e., weak dominance hierarchies with low linearity) (van Schaik, 1989; Isbell, 1991; Sterck et al., 1997).

We use the variables mentioned above to investigate current hypotheses of how diet and competitive regime affects dominance relationships in a population of *Colobus vellerosus* (ursine colobus or white-thighed colobus), residing at the Boabeng-Fiema Monkey Sanctuary, Ghana. This population is highly folivorous, and their diet consists mostly of food items that are evenly distributed, relatively low-quality, and have a short processing time (Saj & Sicotte, 2007; Teichroeb & Sicotte, 2009). If using characteristics of common food items as a proxy of competitive regime, there appears to be little potential for within-group contest competition in this population. However, *C. vellerosus* occasionally forage on food items that are contestable (i.e., seed pods of *Parkia bicolor* and palm nuts of *Borassus aethiopum*: E.C.W. & I.B., unpublished data). This population is, therefore, ideal to investigate dominance relationships among females that only occasionally compete aggressively for access to food.

We examine two mutually exclusive hypotheses regarding the link between diet and female dominance relationships. Hypothesis one: because these females feed mostly on what appears to be non-contestable food items, there is little incentive to form decided dominance relationships (van Schaik, 1989; Isbell, 1991; Sterck et al., 1997). This hypothesis predicts that females will form individualistic dominance hierarchies with low linearity ($h^{\mathrm{I}} \leqslant 0.5$), consistency (directional consistency index < 0.95), stability, and expression (i.e., low rates of submission, particularly during feeding, and long latencies to detect hierarchies). Hypothesis two: because these females occasionally feed on high-quality, clumped and usurpable food resources, there is some incentive to form decided dominance relationships (Archie et al., 2006). This hypothesis predicts that females will form individualistic dominance hierarchies with high linearity ($h^{\mathrm{I}} \geqslant 0.8$) and intermediate consistency (directional consistency index ≈ 0.95), stability, and expression (i.e., intermediate submission rates and detection latencies). Researchers have not agreed on threshold values to define low versus high stability and expression. We will therefore evaluate our results based on the range of values published from species with egalitarian and despotic hierarchies.

2. Methods

2.1. *Study site and subjects*

Our study site, Boabeng-Fiema Monkey Sanctuary (BFMS), is located in central Ghana (7°43′N, 1°42′W). BFMS consists of a 1.92 km^2 dry semi-deciduous forest (Hall & Swaine, 1981) that is connected to other forest fragments via narrow riparian forest corridors. For more details regarding the study site see Teichroeb & Sicotte (2008). Eight groups were included in this study for different periods of time between 2004 and 2011 (Table 1). The study groups contained nine to thirty animals, but we focused our study on the 75 adult (>5 years) and subadult (4–5 years) females that resided in the groups (Table 1).

2.2. *Data collection*

During all study years, we collected aggressive and submissive interactions ad libitum (Altmann, 1974). We use the term agonistic behaviours when referring to both aggressive and submissive interactions. The agonistic be-

Table 1.
Study years, contact hours, group sizes, years included in the matrices used for analyzing linearity, number of known and unknown dyads, Landau's modified linearity indices (h') and p-values.

Group	Study years	Contact hours	Group size	Adult females	Subadult females	Years in analysis	Number of known/ unknown dyads	h'	p
BO	2008–2010	173	18–21	8	0	2008–2009	19/9	0.7	0.06
BS	2004–2010	1034	7–25	3–5	1–2	2007–2009	14/1	0.9	0.03
DA	2006–2010	489	15–26	5–8	0–3	2007–2009	16/5	0.5	0.30
NP	2007–2010	198	11–14	4–6	0–2	2007–2009	9/1	0.9	–
OD	2007–2010	556	15–20	4–6	0–1	2008–2009	10/5	0.6	0.20
RT	2004–2011	1032	8–27	5–7	0–1	2008–2011	15/0	1.0	0.03
SP	2006–2011	472	9–20	3–5	0–2	2008–2009	10/0	1.0	–
WW	2006–2011	699	23–33	7–9	1–4	2007–2009	37/13	0.6	0.05

haviours we recorded are listed in Appendix A. We noted whether the agonistic interactions occurred during feeding, resting, or social activities. We considered repeated agonistic behaviours as part of the same interaction if they occurred within 3 min of each other (Korstjens et al., 2002). Between 2008 and 2009, ECW also recorded behavioural data during 10-min focal samples (Altmann, 1974) of 54 adult and subadult females. We recorded all social behaviours continuously throughout the focal sample. The focal animal's state behaviour was recorded instantaneously during point samples every 2.5 min. A total of 1101 focal hours were collected with a mean of 17 h per female (range: 1–20 h per female). To ensure inter-observer reliability in identifying animals and coding behaviours among the four observers, observers overlapped for at least one month of data collection every year.

2.3. Data organization and analyses

For each group, we included all interactions during time periods without any rank changes in the same matrix to reduce the number of unknown dyads (i.e., dyads without any recorded dominance interactions). A rank change is a long-lasting rank reversal, which is different from an isolated event of submission in the less common direction (Borries et al., 1991). When natal females turned four years old ($N = 8$) or when females immigrated into the groups ($N = 2$), we added them to the already existing female matrices as long as there were no rank reversals among the other females. This did not lead to a problem of structural zeros because these new females had on average the same number of submissive interactions in the matrix as the previously included females. When females disappeared from the study groups ($N = 3$), we removed them from the matrix. As their disappearances did not affect the relative ranks of the remaining females, we pooled the submissive interactions between the remaining females before and after these disappearances. The females were ranked in relation to each other using 1000 iterations following de Vries (1998). De Vries' method orders the animals in a way that first minimizes intransitive relationships, and then decreases the strength of these relationships by ranking the animals with intransitive relationships as close as possible. For groups with rank changes from which we have several matrices, we chose to analyze linearity and consistency using the matrix with the lowest number of unknown relationships because these will reduce the linearity index (see below). When we analyzed hierarchical stability, we included data from all years.

Based on the submission matrices, we classified dyadic female relationships following the definitions in de Vries (1998), Koenig (2000) and Izar (2006). In linear decided dyads, the majority of submissive interactions are directed up the hierarchy. We considered a dyad as linear decided if there was one more submissive interaction directed from the lower ranking to the higher ranking female. Intransitive dyads have a higher number of submissive interactions down rather than up the hierarchy. Tied dyads have an equal number of interactions up and down the hierarchy. Dyads without any recorded interactions are classified as unknown dyads.

To investigate whether dominance hierarchies were individualistic or nepotistic, we performed Spearman rank correlations using the standardized ranks of mothers and daughters. The standardized rank is calculated as a female's rank subtracted from the number of females in the group, divided by the number of female opponents (Robbins et al., 2005). Mother-daughter relationships were determined based on demographic and genetic data (Wikberg et al., 2012).

To investigate hierarchical linearity, we computed Landau's modified linearity index (h') (de Vries, 1995). The index ranges from zero to one, and higher indices imply more linear hierarchies with a greater number of known transitive relationships. Although the index takes unknown relationships into account (de Vries, 1995), it cannot fully compensate for the lack of data, and unknown relationships still reduce the linearity index (Koenig & Borries, 2006). Tied and intransitive dyads will also lead to lower linearity indices, especially when there is a large rank difference between the females in these dyads (de Vries, 1995).

For the first component of hierarchical strength, expression, we used three sets of variables: agonistic rates, context of submission, and latency to detect a linear hierarchy (Isbell & Young, 2002). First, we used Wilcoxon signed rank tests to compare focal rates of submission during different contexts. For each focal female, we calculated submission rates during different contexts as the number of interactions during context A divided by the time spent in context A. The time spent in context A was estimated as the proportion of point samples in context A multiplied by the number focal hours. For each group, we calculated mean submission rates during feeding and during other activities (i.e., resting and social activities). We did not perform this analysis on aggression due to limited sample size. Second, we calculated standardized rates of submissive and aggressive interactions during focal samples (number of events/number of focal hours and females in the study group). Although displacements have both an aggressive and a submissive component, we considered them as submissive behaviours (Rowell, 1974). We only included displacements when calculating rates of submission to make our results comparable to other studies. We used a Spearman rank correlation to investigate if a female's age affected rates of received and directed aggression or submission. Third, we calculated the latency to detect a highly linear hierarchy as the minimum number of observation hours required to order females into a linear hierarchy divided by the number of females in the group (Isbell & Young, 2002).

For the second variable of hierarchical strength, directionality or consistency, we calculated two indices: the directional consistency index and the dyads-up index. The directional consistency index indicates the proportion of interactions in the more common direction in each dyad. It is calculated by subtracting the number of interactions in the less common direction from the number of interactions in the more common direction divided by the total number of interactions (van Hooff & Wensing, 1987). The dyads-up index is the percentage of known dyads that form intransitive relationships (Berman et al., 2004).

For the third variable of hierarchical strength, stability, we examined the rates of changes in group composition and in dominance ranks. We calculated stability in group membership as female entry (i.e., number of females that entered the hierarchy due to immigration or maturation each year) and female exit (i.e., number of females that left the hierarchy due to emigration or death each year) following Bergstrom & Fedigan (2010). When calculating the rank change, we only included active rank changes during which females' rank positions changed in relation to each other. For example, if a female increased one rank position due to the disappearance of a higher ranking female, this increase would not be labeled as a rank change. None of the rank changes occurred as an immediate response to females entering or leaving the hierarchy, and females occupied the lowest rank immediately after entering the hierarchy. We calculated the mean rate of rank change for each female as the number of positions she increased or decreased per year (Cheney et al., 1988). We also present the percentage of dyads that changed ranks each year (Borries et al., 1991) in the groups in which we observed a sufficient number of interactions to determine the rank order each year of study (BS, RT, SP, WW). We investigated if the changes in rank were due to females entering and/or leaving the hierarchy using Mann–Whitney U-tests. We used the software Matman (Noldus Information Technology, 1998) for computing rank orders and linearity indices. All other tests were computed in R 2.13.2 (R Development Core Team, 2011). We set the significance level to $p \leqslant 0.05$, and tests were two-tailed.

3. Results

Out of the 529 recorded agonistic bouts, 12% consisted of aggression only, 25% contained submission only and 63% included both aggression and submission. We were not able to identify the animals involved in the agonistic interaction in 55 of these bouts.

3.1. Hierarchical type

Only one out of nine adult daughters occupied a rank adjacent to her mother, and the ranks of mothers and their adult daughters were not correlated ($r_S = -0.075$, $N = 9$, $p = 0.84$). Five daughters ranked above their mother and four below. Females that ranked below their mothers may not have attained a stable position in the hierarchy yet because all of them were young adults, between 5 and 7 years old.

3.2. Hierarchical linearity

Four groups (BS, NP, RT and SP) showed highly linear dominance hierarchies with a modified linearity index ranging between of 0.9 and 1 (Table 1). The linearity index was significant for BS and RT groups. We could not evaluate the result statistically for NP and SP groups because these groups had only five females, which is lower than the minimum number required for statistical analysis (Appleby, 1983). The hierarchy in WW group was significantly and moderately linear with a modified linearity index of 0.6. The hierarchy in BO group showed a trend toward moderate linearity ($h' = 0.7$). The remaining two groups (DA and OD) did not show significantly linear hierarchies. The indices in the latter four groups were probably negatively affected by a large percentage of unknown dyads, which ranged between 24% and 32%.

3.3. Hierarchical expression

The context was clear in 162 out of 163 submissive interactions, and the most common context was feeding ($N = 125$). The highest median rates of submission occurred during feeding in all groups (Figure 1). Submission rates were significantly higher during feeding than resting and social activities

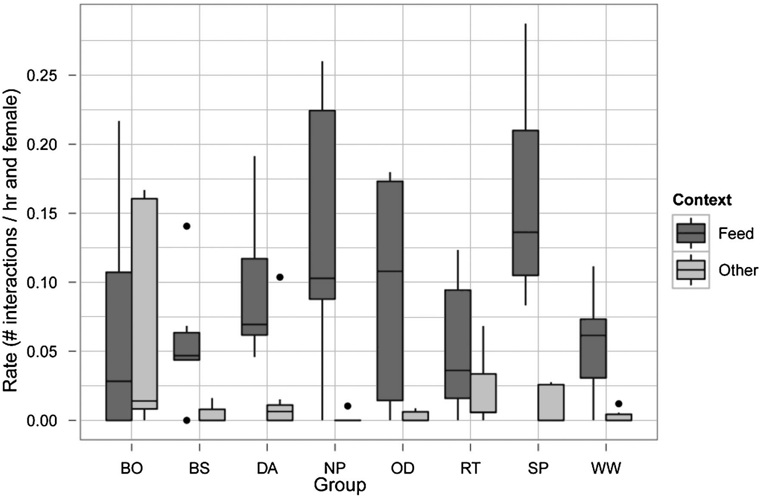

Figure 1. Standardized rates of submission during feeding and other activities (i.e., rest and social). The box represents the 1st and 3rd quartiles and the median is marked with a horizontal bar. The whiskers represent the range of the data with the exception of outliers that are indicated with a dot.

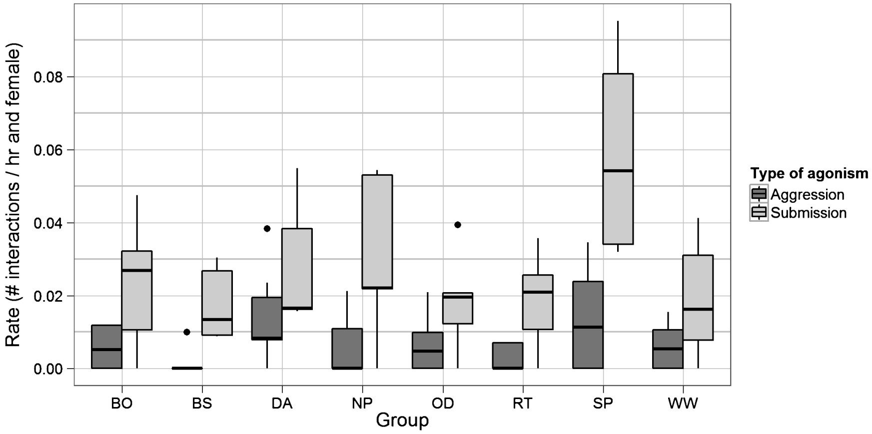

Figure 2. Standardized rates of aggression and submission. The box represents the 1st and 3rd quartiles, and the median is marked with a horizontal bar. The whiskers represent the range of the data with the exception of outliers that are indicated with a dot.

(Wilcoxon signed rank test: $Z = -2.4$, $N = 8$, $p < 0.001$). The individual rates of submission varied from low to intermediate (0 to 0.1 interactions per focal hour and female). Aggression was rare, and the rates of aggression ranged from 0 to 0.04 interactions per focal hour and female. Female age was negatively correlated with rates of received and directed submission ($r_S = -0.28$, $N = 62$, $p < 0.05$) but not aggression ($r_S = -0.11$, $N = 62$, $p = 0.45$). The mean rates across groups were low with 0.03 submissive interactions and 0.007 aggressive interactions per focal hour and female (Figure 2). In most groups with high linearity indices, the mean latency to detect a linear hierarchy was relatively short with a mean of 34 observation hours per female (BS 53 h, NP 28 h, RT 18 h and SP 38 h). We did not detect highly linear hierarchies in the remaining four groups during our study, which indicates that the detection time will be longer than the current observation time per female (BO > 22 h, DA > 44 h, OD > 28 h and WW > 44 h).

3.4. Hierarchical consistency

Of the 125 known dyads, 119 formed linear decided relationships (i.e., dyads with at least one more submissive interaction directed from the lower ranking to the higher ranking female than the other way around). Only two dyads in the large WW group and one dyad in the small OD group formed tied relationships. Each of the tied dyads had one interaction in each direction, and these dyads consisted of old adult females that were long-term residents in the groups. One dyad in the large DA group and two dyads in the large WW group were intransitive, and each of these dyads contained one young adult natal female that had recently entered the hierarchy. The intransitive dyads in WW group changed rank, but we do not know if rank changes occurred in DA group. The dyads-up index was relatively high (6%) in DA and WW groups, while it was 0% in the other six groups because they lacked intransitive dyads. Eighteen dyads showed submission in both directions. The directional consistency index ranged from low to high (BO 0.92, BS 0.99, DA 0.95, NP 1.00, OD 0.92, RT 0.95, SP 0.95 and WW 0.98) with a mean of 0.96.

3.5. Hierarchical stability

The mean rates of entry and exit into the dominance hierarchy across groups were relatively low. Rates of entry into the dominance hierarchy by immigrant and maturing females ranged from 0.33 to 1.60 females per year while rates of exit by disappearing females ranged from 0.17 to 1.80 females per year (Table 2). Although only four out of thirty-one females had the same rank throughout the study, rates of individual rank change were low in most cases. The individual rate of rank change varied between females from 0 to 2 positions per year, and the mean rank change across all groups was 0.33 positions per year (Table 2). The percentage of dyads with rank changes was also low in most groups, and the mean across groups was 4.5% (Table 2).

Table 2.
Changes in group membership and dominance rank.

Group	Entry rate (no. of maturing and immigrating females/year)	Exit rate (no. of emigrating and disappearing females/year)	Individual rank change (no. of positions/year)	Dyadic rank change change (% dyads with rank changes/year)
BO	1.50	0.50	–	–
BS	0.33	0.17	0.20	4.0
DA	1.25	1.75	–	–
NP	0.67	0.67	–	–
OD	0.67	0.67	–	–
RT	0.43	0.29	0.13	3.4
SP	0.60	0.20	0.28	4.0
WW	1.60	1.80	0.71	6.9
Mean	0.77	0.75	0.33	4.5

The small SP group showed the highest hierarchical stability, as the five females occupied the same ranks for four years despite two females maturing and one female disappearing during this time period. During the fifth year of study, one of the recently matured females increased in rank. The highest individual rank stability occurred in the small RT group, where the alpha female kept her position for over seven years despite changes in group membership. None of the observed rank changes were due to changes in group composition when females emigrated or immigrated.

The majority of rank changes occurred when young females (i.e., 4–9 years old) challenged older females and increased in rank. However, this was a slow process, and only two out of eight maturing females increased their rank within a year of entering the adult dominance hierarchy. Only one older female increased in rank by challenging other females. Young females showed a positive median rank change (0.5 ranks/year) while older females had a negative median rank change (-1 rank/year), and the difference in rank change between young and old females was significant ($N_{\text{Young}} = 12$, $N_{\text{Old}} = 16$, $U = 57.5$, $p < 0.01$).

4. Discussion

This study found the most support for hypothesis two: occasional foraging on contestable food items leads to the formation of individualistic dominance hierarchies of intermediate strength in female *C. vellerosus*. However, all four measures of hierarchical strength varied between groups. Some groups showed high hierarchical linearity, intermediate agonistic rates and consistency, and long-term hierarchical stability. The hierarchies of other groups were characterized by intermediate linearity due to unknown relationships, long detection time, and more inconsistencies. We suggest that these between-group differences might be partly explained by demographic factors.

4.1. Hierarchical type

Female hierarchies were individualistic as we predicted based on the low frequency of coalitionary support (Saj et al., 2007). A female is unlikely to inherit her mother's rank if she lacks coalitionary support (Broom et al., 2009), because this is the primary mechanism by which rank inheritance occurs in primates (Chapais, 1992) and hyenas (Engh et al., 2000). The lack of matrilineal rank inheritance is consistent with the pattern reported in elephants (Archie et al., 2006) and folivorous primates without frequent and/or consistent coalitionary support (Hrdy & Hrdy, 1976; Borries et al., 1991; Korstjens et al., 2002; Koenig et al., 2004).

4.2. Hierarchical linearity

We used significant linearity indices to classify weakly ($h^{\mathrm{I}} < 0.5$), intermediately ($h^{\mathrm{I}} = 0.5$–0.8) and strongly linear hierarchies ($h^{\mathrm{I}} > 0.8$) (Bergstrom & Fedigan, 2010). Based on this classification scheme, two study groups showed strongly linear hierarchies. The two smallest study groups also had modified linearity indices in the range of strongly linear hierarchies, but it was not possible to test for significance due to the small group size.

High linearity indices are reported in a variety of folivorous and frugivorous animals (reviewed in Jackson & Winnegrad, 1988). In fact, whenever hierarchies are weakly or moderately linear, they usually have a high percentage of unknown relationships (e.g., Rutberg, 1986; Isbell & Pruetz, 1998; Cafazzo et al., 2010). Therefore, it is not surprising that our study groups with several unknown relationships showed weak or moderate linearity. Three of the four groups with low linearity indices also contained maturing females that challenged older females, and it is possible that these groups form dominance hierarchies with higher (and significant) linearity indices during time periods when there are no maturing females. We were not able to limit our analyses to periods without maturing females partly due to low submissive rates, which made it necessary to include data from several months or years to detect a linear hierarchy. Thus, the combination of a large group size, maturing females, and low submissive rates made it difficult to detect linear hierarchies in some groups. Comparing linearity across groups is further complicated by varying group sizes. The linearity index is negatively affected by group size, as one animal is less likely to be dominant over all other group members in larger groups (Mesterton-Gibbons & Dugatkin, 1995). In contrast, large groups are more likely to show significant linearity indices despite a high number of unknown relationships than small groups (demonstrated by hypothetical data sets: Koenig & Borries, 2006). These issues call into question the usefulness of this variable when comparing the degree of despotism between differently sized groups (Isbell & Young, 2002; Koenig & Borries, 2006).

4.3. Hierarchical expression

Species with highly expressed hierarchies should show more frequent submission during feeding than expected at random (Isbell & Young, 2002). Following this definition, all but two of our study groups formed well-expressed hierarchies as the most common context for submissive interactions was feeding. However, this is not a very useful variable when comparing the expression of dominance relationships across species because feeding is the most common context for submission in most other animals (e.g., Cords, 2000, 2002; Koenig, 2000; Korstjens et al., 2002; Koenig et al., 2004; Bergstrom & Fedigan, 2010; Cafazzo et al., 2010; but see Isbell & Pruetz, 1998). Instead, it might be more informative to compare agonistic rates during feeding between species. Such a comparison shows that the agonistic rates during feeding in *C. vellerosus* fall within the documented range for some folivorous primates (*Colobus polykomos* and *Procolobus badius badius*: Korstjens et al., 2002; *G. b. beringei*: Robbins, 2008). However, submissive rates during feeding in *C. vellerosus* were lower than those reported for despotic Asian colobines (reviewed in Sterck, 1999).

Females with highly expressed hierarchies should also show high rates of aggression and submission (Isbell & Young, 2002), but there are no set threshold values for what should be considered as low, intermediate and high rates. To facilitate future comparisons, we used previously published data to categorize low, intermediate, and high rates. Agonistic rates below 0.1 interactions per focal hour and female may be considered as low rates (*C. polykomos* and *P. b. badius*: Korstjens et al., 2002; *T. phayrei*: Koenig et al., 2004; *Colobus guereza*: Harris, 2005; *Nasalis larvatus*: Matsuda et al., 2012). Intermediate rates may fall within the range of 0.1 and 1.0 interactions per focal hour and female (*Macaca fascicularis*: Sterck & Steenbeek, 1997; *Alouatta palliata*: Zucker & Clarke, 1998; *Cercopithecus mitis stuhlmanni*: Cords, 2000; *C. capucinus*: Bergstrom & Fedigan, 2010). Agonistic rates above 1.0 interaction per focal hour and female may indicate high rates (*Papio ursinus*: Seyfarth, 1976; *Macaca mulatta*: de Waal & Luttrell, 1989; *C. capucinus*: Bergstrom & Fedigan, 2010). Based on this classification, all of our study groups showed low mean rates. However, variation between individuals (this study) or groups (Bergstrom & Fedigan, 2010) makes it difficult to determine if the hierarchical expression of groups or populations should be classified as low, intermediate, or high. Furthermore, it is difficult to determine cut-off values for characterizing weakly versus highly expressed hierarchies. For example, *Presbytis thomasi* (Thomas langurs) show low aggression rates similar to species with weakly expressed hierarchies but high submission rates similar to species with highly expressed hierarchies (Sterck & Steenbeek, 1997) while the opposite is true for *G. b. beringei* (Robbins, 2008). Because species with stronger hierarchies do not always show higher agonistic rates than species with weaker hierarchies (de Waal & Luttrell, 1989; Sterck & Steenbeek, 1997), agonistic rates may not always be reliable indicators of hierarchical strength (Koenig, 2002; Koenig & Borries, 2006).

Finally, well-expressed hierarchies have a short latency to detect a highly linear hierarchy (Isbell & Young, 2002). We considered a latency of less than 22 h per female as very short (*C. capucinus*: Bergstrom & Fedigan, 2010), and only one study group had such a short latency. Two study groups had a latency between 22 and 50 h per female, which may be considered as an intermediate latency (*Chlorocebus pygerythrus*: Isbell & Pruetz, 1998). One study group had a long latency and required over 50 h per female before a highly linear hierarchy was detected, which indicates low hierarchical expression (*Erythrocebus patas*: Isbell & Pruetz, 1998). We did not find a highly linear hierarchy for the remainder of the study groups, and their detection latencies remain unknown. The three groups with the longest detection times (>44 h per female) also had the lowest submission rates during ad libitum data collection (E.C.W., unpublished data) and/or the highest group spread (Teichroeb & Sicotte, 2009). Thus, some of the between-group variation may be explained by submission rates and group spread affecting the likelihood of observing submission in all dyads. Some authors also argue that between-group comparisons can be complicated by the fact that detection times may depend on observation conditions (i.e., visibility, number of observers, and group size) rather than hierarchical strength (Koenig, 2002; Koenig & Borries, 2006). Despite these issues, we believe that the latency to detect a linear hierarchy is a good complement to rates of agonism because these two variables may not always correspond to each other. For example, a group with low submission rates might have a latency that is as short, or even shorter, as a group with high submission rates if the latter has a higher level of bidirectionality. However, to make it easier to compare detection latencies across groups or species with different observation conditions, this variable should not be calculated from ad libitum data but from data collected via focal sampling. If all submissive interactions are recorded continuously during focal samples, latencies calculated from focal data should be less affected by differences in observation conditions. We were not able to calculate hierarchical detection latencies using focal data alone because of a low number of submissive interactions during focal samples, and this is likely the case in other studies as well.

Our study population of *C. vellerosus* appears to have low or intermediate hierarchical expression based on mean values. These results are difficult to interpret because the three different variables of hierarchical expression did not always co-vary in a consistent way, and there was considerable between-group variation in hierarchical expression. The variation may be partly explained by the methodological issues raised earlier. However, there were some consistent patterns across groups, which indicate that females in some groups formed more well-expressed hierarchies than others. For example, females in SP group formed a more well-expressed hierarchy than females in BS group based on a higher rate of agonism and a shorter latency to detect a linear hierarchy.

4.4. Hierarchical consistency

Female *C. vellerosus* showed few tied and intransitive relationships, which is indicative of strong dominance hierarchies (sensu Isbell & Young, 2002) and supports hypothesis two. The low dyads-up indices (i.e., the low percentage of known dyads with intransitive relationships) in this study were similar to those reported for more frugivorous species with intermediately strong hierarchies such as *Macaca thibetana* (Berman et al., 2004) and *M. radiata* (Silk et al., 1981). However, other studies report a complete absence of intransitive dyads (e.g., Seyfarth, 1976; Harris, 2005; Robbins et al., 2005; Bergstrom & Fedigan, 2010). Thus, the dyads-up indices in *C. vellerosus* may reflect intermediate hierarchical strength in support of hypothesis two. However, data from a wider range of species are needed to determine the cut-off value between species with strong versus weak hierarchies.

The mean directional consistency index in this study was above the 0.95 threshold for defining strong hierarchies (sensu Isbell & Young, 2002), which also supports hypothesis two. Although the mean index in *C. vellerosus* was high, it was below the 0.95 cut-off in two groups. One of these groups was only studied during one year. The second group showed extreme rank instability, and the female that appeared to be the alpha female fell to the bottom of the hierarchy within a year. Unfortunately, we did not observe a sufficient number of interactions before and after this event to be able to calculate rates of rank changes. We suggest that bidirectional interactions may reflect temporary hierarchical instability rather than persistent bidirectional dominance relationships in *C. vellerosus*. Further research is needed to confirm this suggestion. Other studies also report low directional consistency indices during temporary instability, while hierarchies are well-defined during stable periods (Isbell & Pruetz, 1998; Zucker & Clarke, 1998; Koenig, 2000). These results illustrate that longitudinal data from several groups are informative when interpreting dominance relationships.

4.5. Hierarchical stability

The mean rate of entry and exit in our study was slightly lower than that reported for female philopatric and despotic *C. capucinus* (Bergstrom & Fedigan, 2010) and female dispersed and more egalitarian *G. b. beringei* (Robbins et al., 2005). Possibly due to low rates of female immigration (Teichroeb et al., 2009) and a lack of age-graded hierarchies (E.C.W., unpublished data), the rates of rank change were lower in *C. vellerosus* than in other species with individualistic hierarchies (Hrdy & Hrdy, 1976; Borries et al., 1991; Zucker & Clarke, 1998; Robbins et al., 2005). The dyadic rank change in *C. vellerosus* was comparable to some nepotistic and despotic cercopithecines (*Macaca nemestrina*: Bernstein, 1969; *C. pygerythrus*: Seyfarth, 1980) and cebines (*C. capucinus*: Bergstrom & Fedigan, 2010). Thus, female *C. vellerosus* form stable dominance relationships, which indicates a high hierarchical strength (sensu Isbell & Young, 2002). These results provide stronger support for hypothesis two (intermediate hierarchical strength) than hypothesis one (low hierarchical strength).

4.6. Egalitarian to despotic dominance continuum

It is difficult to categorize *C. vellerosus* as either despotic or egalitarian because this population showed high values for some but not all dominance variables investigated. Instead of using two discrete categories, we suggest using graphing techniques that can organize species or groups based on several variables along a dominance continuum ranging from highly egalitarian to highly despotic. In our example here, we focus on population averages of agonism and directional consistency. Although rank stability is also an informative dominance characteristic, we omitted it from our between-species comparison due to a lack of published data. We plotted the population averages in a heatmap with a dendrogram function that clusters populations

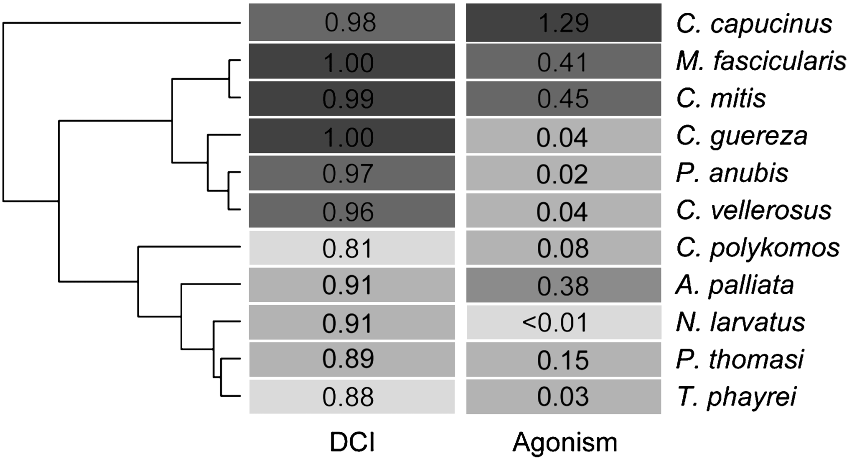

Figure 3. The heatmap shows directional consistency indices (DCI) and rates of agonism (interactions per hour and female). Darker colours indicate higher values. Species have been organized according to similarities in these two variables. References: *C. capucinus*: Bergstrom & Fedigan (2010); *M. fascicularis* and *P. thomasi*: Sterck & Steenbeek (1997); *C. mitis*: Cords (2000, 2002); *C. guereza:* Harris (2005); *P. anubis*: Barton & Whiten (1983); *C. vellerosus*: this study; *C. polykomos*: Korstjens et al. (2002); *A. palliata*: Zucker & Clark (1988); *N. larvatus*: Matsuda et al. (2012); *T. pharei*: Koenig et al. (2004).

with the most similar values (using the R package ggplot2: Wickham, 2009). Darker colours represent higher values, which indicate a higher degree of despotism. Of the primate species with comparable published data that we included in Figure 3, *T. pharei* is the most egalitarian and *C. capucinus* is the most despotic species. Our study population lies in the middle of the dominance continuum in this preliminary between-species comparison (Figure 3). To facilitate future cross-species comparisons, we urge researchers to use a similar methodology and report standardized variables. With this information available from a wide range of species, future classification schemes will be able to determine more precisely where populations lie on the dominance continuum.

4.7. Conclusions regarding the effect of occasional foraging on contestable food items

This study demonstrated that female *C. vellerosus* form individualistic dominance hierarchies with relatively low expression and moderate to high linearity, consistency, and stability. These findings support the second hypothesis, which predicts that females will form linear, individualistic dominance hierarchies of intermediate strength if they at least occasionally forage on contestable food items. Hierarchical strength in *C. vellerosus* was similar to those of several other species that only occasionally forage on contestable food items. However, our study and other comparative studies of folivorous primates show considerable variation in hierarchical strength, both within and between species. Some of the variation in hierarchical expression may be explained by the percentage of contestable food items in their diet (Robbins, 2008). Although dominance characteristics in our study did not appear to be affected by habitat type or percentage of frugivory (results not shown), more subtle variation in quality or distribution of food items may affect dominance characteristics in groups of *C. vellerosus*. In our study population, hierarchical expression is sometimes greater in large groups (Teichroeb et al., 2009) and when new females establish themselves in the adult hierarchy (this study). The latter means that lower frequencies of female immigration may lead to higher hierarchical stability (see discussion above). Only one of our study groups (WW group) did not contain any recent female immigrants (Wikberg et al., 2012), but the potential stabilizing effect of no female immigration may have been counteracted by a high proportion of maturing females. Based on these results, we suggest that dominance characteristics are likely shaped by demographic factors in addition to the competitive regime. To investigate if the variation in hierarchical strength between our study groups also reflects differences in competitive regimes, future studies should focus on the effect of dominance rank on food intake and reproductive success.

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Appendix A.
Definitions of aggressive and submissive behaviours recorded in this study.

Type	Behaviour	Definition
S	Avoid or displace	An animal moves away before another approaches to one meter, and the approaching animal does not pursue the leaving animal; an animal approaches to one meter and takes the spot of another that leaves within five seconds; an animal takes over a resource from another animal that was within one meter for more than five seconds either before or after the resource was taken over; or an animal directs aggression towards another animal that was within one meter for more than five seconds, and the victim leaves while the aggressor stays in the spot[1, 2, 3, 4, 5].
A, S	Chase and flee	One animal rapidly moves away from another animal in pursuit, not in a playful manner[3].
A	Contact aggression	Includes any offensive behaviour where an animal establishes physical contact with another. For example, this category includes bite, hit, pinch, pounce, shove, and wrestle[3].
S	Grimace	An animal opens the mouth and pulls back the lips so that the teeth are visible[3], and it often occurs when a subordinate animal approaches a dominant animal.
A	Other aggressive	Any offensive behaviours behaviour that is not defined here, such as a swipe at and lunge at.
S	Present	An animal turns the back and rump towards another while standing on all four[3], and this is typically directed from a subordinate to a dominant animal.
S	Snuffling vocalization	An animal produces a series of rough, noisy snorts of short duration, often while grimacing[3]. This vocalization often occurs when a subordinate animal approaches a dominant animal or when a dominant animal is aggressing or displacing a subordinate animal.

A, aggressive; S, submissive. The definitions are modified from: [1]Berman et al. (2004); [2]Borries et al. (1991); [3]Oates (1977); [4]Palombit et al. (2001); [5]Rowell (1974).