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Original Article

Causes, mechanisms, and consequences of contest competition among female mountain gorillas in Rwanda

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Socioecological models predict that contest competition will arise when high quality foods can be usurped or monopolized, leading to more favorable energy balances and higher reproductive success for high-ranking females. Gorillas are interesting species for studying such predictions due to the variety of ecological conditions that they experience in different locations. Using data from 23 female mountain gorillas in 3 social groups in the Virunga Massif, we examined food characteristics that may influence contest competition (food site residence times [FSRT]), proximate mechanisms of such competition (aggression and avoidance), and potential consequences of competition (rank-related differences in energy intake rates, travel expenditures, and activity budgets). The average FSRT of each female was significantly correlated with dominance rank, which suggests that high-ranking females may have greater access to foods that are easier to usurp (as predicted with contest competition). High-ranking females were significantly more aggressive than low-ranking females, and both aggression and avoidance were significantly higher while feeding than during other activities. Contrary to predictions for contest competition, however, rank was not significantly correlated with energy intake rates nor with the proportion of time spent traveling versus feeding. Thus, we did not find any energetic benefits to explain why high-ranking females had significantly higher reproductive success in earlier studies. We propose several alternative explanations and discuss the potential complications of assessing contest competition in species with weak dominance relationships.

Key words: **activity budget, aggression, avoidance, energy balance, energy intake, food site residence time, nutritional analyses, proximity, socioecological model, travel expenditure.**

INTRODUCTION

Living in social groups leads to benefits such as enhanced protection from predators, but also incurs costs, including competition over food resources (Alexander 1974; Macdonald 1983; Pulliam and Caraco 1984). The reproductive success of females is constrained by access to food resources because of the substantial energetic demands of gestation and lactation, whereas male reproductive success depends primarily on successful insemination (Trivers 1972; Bradbury and Vehrencamp 1977). Competition for food resources therefore leads to variation in female reproductive success, although female intrasexual competition for access to mates, social partners, and protection from predators is increasingly recognized (Stockley and Bro-Jørgensen 2011; Cheney et al. 2012; Clutton-Brock and Huchard 2013). The quality, distribution, and abundance of food resources influence the strength and type of within-group feeding competition, which in turn influences the nature of female social relationships as well as female reproductive skew (for reviews of these models for primates, see Clutton-Brock and Janson 2012; Koenig et al. 2013).

Contest competition can arise within groups when the distribution of high quality foods allows them to be usurped or monopolized, leading to higher energy intake and/or lower energy expenditure for high-ranking individuals (Wrangham 1980; van

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Schaik 1989; Isbell 1991; Sterck et al. 1997). Conversely, when foods are not easily contested (or not worth contesting), then groups are expected to have egalitarian social relationships without skew in energy balances or fitness (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997). A full assessment of a socioecological model should not merely consider its predictions for species where contest competition is expected to be strong but also for species where such competition is expected to be weak or absent (Archie et al. 2006; Wikberg et al. 2013). Tests of those predictions should ideally include data on food characteristics, the proximate mechanisms of contest competition, as well as energy intake rates and expenditures (Koenig and Borries 2009; Koenig et al. 2013).

The potential for contest competition within groups may depend on food characteristics that determine whether it is worth contesting (i.e., its relative quality) and how easily it can be monopolized or usurped (Janson 1988; Sterck and Steenbeek 1997; Koenig and Borries 2006; Vogel and Janson 2011; Chapman et al. 2012). Quality can vary both between and within food species (Koenig et al. 1998; Snaith and Chapman 2007). Categories such as fruit, leaves, and bark may not adequately reflect the variation in the quality and distribution of foods (Koenig 2000; Murray et al. 2007; Wheeler et al. 2013). For example, leaves have sometimes been described as ubiquitous and evenly distributed, yet they can be patchily distributed in both space and time (Koenig 2000; Murray et al. 2007; Wheeler et al. 2013). Spatial traits such as patch size may influence the ability of high-ranking individuals to monopolize foods by excluding subordinates from an area (Wrangham 1980; van Schaik 1989). Temporal traits such as food site residence times (FSRT) may affect the potential for high-ranking individuals to usurp foods by displacing subordinates from the area (Isbell and Pruetz 1998; Isbell et al. 1998; Mathy and Isbell 2001; Korstjens et al. 2002; Gemmill and Gould 2008; Chancellor and Isbell 2009). In other words, foods may be easier to monopolize when they are concentrated in a small area, and they may be easier to usurp when they take a long time to consume, so both spatial traits and temporal traits can affect the potential for contest competition (Isbell and Young 2002; Chancellor and Isbell 2008). The amount of time that an individual spends at a food site may also reflect the value of the food (Harcourt and Stewart 2007).

The primary proximate mechanisms of contest competition are aggression and avoidance (Janson 1988; Janson and van Schaik 1988). Dominant females often use aggression to gain greater access to preferred resources, which can lead to positive correlations between rank and rates of aggression (Janson 1985a; van Noordwijk and van Schaik 1987; Vogel 2005), but see Robinson (1981). Rates of agonism are frequently higher during feeding than in other contexts, especially when foods are considered contestable (Wheeler et al. 2013). If the threat of aggression causes subordinates to avoid confrontations with dominant females, however, then negative correlations can arise between rank and proximity to other females (Thouless 1990; Barton and Whiten 1993). In extreme cases, avoidance strategies can cause groups to split apart during foraging (fission–fusion) and individuals may even forage alone (Boesch and Boesch-Achermann 2000; Wittig and Boesch 2003).

The fitness consequences of contest competition within groups can arise from rank-related differences in energy intake rates, energy expenditures for travel, and time budget allocations (Janson and van Schaik 1988; Pusey and Schroepfer-Walker 2013). High-ranking females can have high energy intake rates because they eat more quickly than other females and/or because they eat foods with higher energy concentrations (Barton and Whiten 1993; Murray et al. 2006). Low-ranking females may compensate for lower energy intake rates by spending more time feeding, and they may incur higher energy costs for travel (Pazol and Cords 2005; Schülke and Ostner 2012). Unfortunately, measurements of energy intake rates remain rare, and recent reviews of socioecological models have emphasized the need for further studies of food characteristics as well as the mechanisms and consequences of contest competition (Koenig and Borries 2009; Clutton-Brock and Janson 2012).

This paper examines the potential causes, mechanisms, and consequences of within-group contest competition among female mountain gorillas in the Virunga Volcano region. As socioecological models predict for a species with evenly distributed food, female mountain gorillas form weak and individualistic dominance hierarchies (Watts 1994; Robbins et al. 2005). Competitive interactions are infrequent and generally ineffective, and rates of aggression have not been consistently correlated with dominance rank (Fossey and Harcourt 1977; Watts 1985, 1994). Contrary to predictions, however, rank has been correlated with some aspects of reproductive success, including shorter interbirth intervals, higher rates of giving birth to surviving offspring, and greater longevity for high-ranking females (Robbins et al. 2007a, 2007b, 2011a). If these correlations between rank and reproductive success arise from contest competition, they may explain why female mountain gorillas form dominance hierarchies, but further investigation is required to determine which food characteristics facilitate such competition. Alternatively, rank and reproductive success in mountain gorillas could both covary with the physical condition of the mothers, even if those variables are not strongly influenced by contest competition for food (Pusey et al. 2005; Robbins et al. 2007b).

To further examine whether the correlations between rank and reproductive success arise from contest competition among female mountain gorillas in the Virungas, we examined food characteristics that are temporal rather than spatial, proximate mechanisms based on avoidance versus aggression, and potential consequences based on energy intake rates and time budget allocations. Firstly, to examine opportunities for usurpation of food resources, we looked for correlations between FSRT versus aggression rates and dominance rank. If contest competition primarily occurs over foods that are easier to usurp, then we expect higher aggression rates for species that have longer FSRT, and we expect high-ranking females to have greater access to those foods (i.e., higher-ranking females will have longer FSRT). Secondly, to examine the potential mechanisms of contest competition, we tested whether rank is correlated with aggression rates and patterns of spatial proximity. If aggression is the primary mechanism for contest competition, then we expect high-ranking females to have higher rates of aggression given. If avoidance is the primary mechanism for contest competition, then we expect high-ranking females to have fewer individuals in close proximity compared with low-ranking females (low-ranking females avoid high-ranking females, enabling the high-ranking females to occupy better feeding spots). Thirdly, to examine the potential consequences of contest competition, we tested whether rank is correlated with energy intake rates, the time spent traveling between food sites, and the proportion of time spent feeding. If contest competition is strong enough to have detectable consequences, then we expect high-ranking females to have significantly higher energy intake rates, lower energy expenditures due to travel, and a smaller proportion of time spent feeding.

METHODS

Data collection

This study was conducted in Volcanoes National Park, Rwanda, between September 2009 and December 2010 on groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center.

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We used 2 types of protocols to collect data from 3 study groups (PAB, BWE, & NTA). Our "food intake protocol" involved focal sampling of adult females for intervals of 30 min to collect data for dietary intake. Our "behavioral protocol" followed the long-term monitoring protocol of the Karisoke Research Center and consisted of 50-min focal sessions during which all agonistic interactions involving the focal subject were recorded. The behavioral protocol also involved taking an instantaneous scan every 10 min to record the activity of the focal female (feeding, traveling, resting, grooming, or playing) along with the number of other adult females within 2 and/or 5 m. For the 23 adult females in the 3 study groups combined, we collected 657 h of data with the food intake protocol and 931 focal hours with the behavioral protocol, which represent 28.5 and 39.9 h per female, respectively. Focal females were chosen following a predetermined order to ensure a balanced data set. As required by the Rwanda Development Board, observations were limited to 4 h/day to minimize anthropogenic disturbance.

Dominance hierarchies for each group were computed from the outcomes of dyadic approach–retreat interactions (displacements) using David's score (de Vries et al. 2006). We define a displacement as when 1 female made a nonaggressive approach to a stationary female, who watched the approacher and moved away in direct response to the approaching individual. Displacements were collected ad lib during the contact time with the group. The steepness of each hierarchy was significantly greater than expected by chance ($P < 0.005$ for each group). The females within each group were given an ordinal ranking (R) based on their David's score from the dominance hierarchy. We standardized those ordinal rankings using Equation 1:

$$\text{Standardized rank} = (N - R) / (N - 1) \tag{1}$$

where N is the number of females in the matrix. The standardized rank of each female equals the proportion of other females who were below her in the matrix, so the lowest female in each matrix has a standardized rank of 0, and highest female has a standardized rank of 1 (Robbins et al. 2005). We calculated only 1 value for the dominance rank of each female throughout the study, partly because interactions are too infrequent to calculate hierarchies for shorter time intervals, and partly because dominance relationships often remain stable for many years (Robbins et al. 2005).

Metabolic energy content of gorilla foods

To determine the metabolic energy content of gorilla foods, we collected samples of 33 different plant parts from 25 different species (Table 1), preferably on the same day that such foods were consumed, either from the exact plant eaten by the gorillas or from several adjacent plants of the same species. The samples were processed in a way similar to the feeding behavior of the gorillas, and only the ingested sections of the plant were sampled. All samples were weighed immediately after collection to determine their total mass, then dried at 40–45 °C using a fruit dryer, and then weighed again to determine their dry mass. Samples were stored in paper bags within small canisters/Ziplocs filled with silica gel globuli or sachets. Dried samples were sent to the Leibniz Institute for Zoo and Wildlife Research in Berlin for measurements of crude protein (CP), lipids (L), neutral detergent fiber (NDF), and total ash (TA) as a percentage of dry matter (Ortmann et al. 2006). We estimated the percentage of total nonstructural carbohydrates (TNC) by difference:

$$\%\text{TNC} = 1 - \%\text{CP} - \%\text{L} - \%\text{NDF} - \%\text{TA} \tag{2}$$

If the %TNC is close to zero, then Equation 2 is calculating a small difference between larger numbers, and imprecision from the other components can lead to negative estimates. The equation produced a negative estimate for bamboo leaves, so we assumed that the %TNC was zero and we normalized the percentages of the other components for that sample. Our correction changed the estimated metabolic energy content for bamboo leaves by approximately 1%.

We estimated the metabolic energy concentration of the dry matter (MEC_{DRY}) by using conversion factors of 4 kcal/g for crude protein and total nonstructural carbohydrates, 9 kcal/g for lipids, 1.6 kcal/g for neutral detergent fiber, and 0 kcal/g for ash (Conklin-Brittain et al. 2006; Wright et al. 2014). We used a coefficient 4.184 to convert kilocalories (kcal) into kilojoules (kJ), so the overall calculation is expressed by Equation 3:

$$\text{MEC}_{\text{DRY}}(\text{kJ}/\text{g}) = 4.184 \times [(4 \times \%\text{TNC}) + (4 \times \%\text{CP}) + (9 \times \%\text{L}) + (1.6 \times \%\text{NDF})] \tag{3}$$

The MEC of the original undried samples ($\text{MEC}_{\text{UNDRIED}}$) equaled the energy concentration of the dried samples (MEC_{DRY}) times their proportion of dry mass per total mass.

For each part of each plant species, we chose a "unit" (e.g., 1 berry, 1 leaf, or 1 segment of a stem), which we used to record the quantity of food consumed by the gorillas (Rothman et al. 2007; Nakagawa 2009). For example, a single leaf was chosen as the food unit for *Basella alba*, so when we observed a female gorilla eating *Basella alba*, we recorded the number of leaves that she consumed. To obtain an average total mass per food unit, we collected and weighed 50 samples of each food unit. The energy content (kJ) per food unit was calculated as $\text{MEC}_{\text{UNDRIED}}$ (kJ per gram of total mass) times the average total mass per food unit.

Characteristics of food sites

We defined the FSRT as the elapsed time from when a female settled at a food site and commenced eating, until she stopped eating and/or moved more than 1 m (Wright and Robbins 2014). Previous studies have defined FSRT to end when an individual engaged in locomotion with both hind limbs, and such movements could not merely involve turning in place or taking a step with 1 foot to reach for food (Chancellor and Isbell 2009). Our 1-m criterion is merely an additional attempt to disregard movements in which a female essentially reoriented herself within the same location. Both approaches are intended to provide a temporal perspective on the potential for usurpation, rather than a spatial perspective on the potential for monopolization (Isbell and Young 2002; Chancellor and Isbell 2008). Although the Virunga mountain gorillas are considered to have evenly distributed food, our current emphasis on a temporal measurement is not intended to reject the potential importance of spatial distributions; we merely chose to focus our limited resources for this particular study on a perspective that is less thoroughly investigated (Watts 1984, 1985; McNeilage 2001).

We define a food site as the location where a FSRT elapsed, but again, we did not attempt to specify its boundaries because our perspective is temporal rather than spatial. For each food site, the total energy intake (kJ) equaled the sum of the energy content for all food units consumed at the site. For example, if a female consumed 2 units of a food with 10.1 kJ/unit, and 4 units of a food with 12.8 kJ/unit, then the total energy intake at the site would be $(2 \times 10.1) + (4 \times 12.8) = 71.4$ kJ. Thus, the total energy intake at the food site is essentially an equivalent term for the total energy intake by the focal female while the FSRT elapsed.

We classified each food site according to the main food species that the gorilla consumed (i.e., the species that accounted for the largest proportion of energy intake at the site). The gorillas

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Table 1

Nutritional analysis for the energy concentration of gorilla foods

Species	Unit	g/unit	%DM	Protein	Lipids	NDF	Ash	kJ/g
Basella alba	Leaf	2.6	8.2%	23.3%	2.0%	30.0%	21.8%	0.86
Carduus leptacanthus	Leaf	28.9	10.7%	25.8%	1.6%	35.7%	23.3%	1.02
Carduus nyassanus	Flower	0.6	32.3%	19.3%	3.0%	60.7%	4.5%	3.40
Carduus nyassanus	Leaf	28.9	11.6%	28.8%	1.4%	51.6%	13.7%	1.11
Carduus nyassanus	Root	29.3	14.3%	13.7%	0.6%	33.6%	9.6%	1.70
Carduus nyassanus	Stem	33.2	4.6%	10.9%	0.4%	36.1%	30.4%	0.38
Carex bequaertii	Leaf	18.2	12.3%	15.4%	0.5%	58.2%	12.3%	1.10
Crassocephalum ducis-aprutii	Dry leaf	0.3	79.4%	19.5%	1.7%	46.8%	10.8%	8.40
Cyperus karisimbiensis	Leaf	35.8	12.2%	16.3%	1.4%	64.6%	12.7%	1.02
Dendrosenecio erici-rosenii	Pith	10.4	6.1%	5.6%	0.2%	24.6%	29.1%	0.57
Discopodium penninervium	Pith	5.6	8.4%	13.6%	0.9%	35.3%	26.7%	0.75
Droguetia iners	Leaf	3.5	31.6%	19.5%	1.4%	30.1%	17.9%	3.48
Echinops hoehnelii	Leaf	18.2	15.4%	17.3%	4.3%	48.5%	17.2%	1.52
Eucalyptus sp.	Bark	3.9	24.6%	5.6%	0.0%	68.5%	4.8%	2.23
Galium sp.	All	53.8	12.0%	24.0%	1.1%	46.2%	14.6%	1.19
Helichrysum cf. formossissimum	Leaf	7.0	15.6%	19.4%	3.0%	53.9%	12.8%	1.53
Laportea alatipes	Leaf	11.4	25.2%	26.2%	0.8%	43.0%	16.5%	2.47
Laportea alatipes	Stem	4.8	8.8%	22.2%	0.8%	41.1%	15.8%	0.89
Lobelia giberroa	Bark	0.9	60.0%	5.3%	1.5%	82.5%	4.0%	4.86
Lobelia stuhlmannii	Pith	18.5	10.6%	4.2%	0.5%	36.6%	9.8%	1.22
Lobelia wollastonii	Pith	18.5	10.8%	2.9%	0.2%	19.7%	5.6%	1.50
Pentarrhinum insipidum	Leaf	1.2	13.4%	26.5%	1.8%	33.1%	13.9%	1.54
Peucedanum kerstenii	Stem	5.0	9.6%	9.9%	2.1%	36.5%	18.1%	1.01
Peucedanum kerstenii	Root	5.0	10.7%	5.9%	0.7%	46.5%	15.7%	1.03
Peucedanum linderi	Stem	37.4	10.1%	6.7%	0.3%	61.1%	14.6%	0.83
Rubus runssorensis	Fruit	15.5	20.1%	14.2%	6.0%	45.3%	5.2%	2.53
Rubus runssorensis	Leaf	2.6	48.1%	18.7%	1.3%	54.5%	5.0%	5.14
Rubus runssorensis	Stem	3.1	14.6%	14.4%	0.7%	57.6%	5.8%	1.48
Rumex ruwenzoriense	Stem	20.7	5.3%	18.5%	0.4%	21.5%	19.0%	0.61
Senecio subsessilis	Stem	21.3	5.2%	9.7%	0.5%	27.0%	33.1%	0.45
Vernonia adolfi-frederici	Flower	2.1	40.4%	13.7%	1.5%	58.0%	5.9%	4.14
Yushania alpina	Leaf	13.4	42.8%	21.2%	1.1%	62.7%	15.0%	3.49
Yushania alpina	Shoot	32.7	10.9%	28.8%	1.5%	43.0%	14.0%	1.13
Average		15.0	19.6%	16.0%	1.4%	45.3%	14.5%	1.96
SD		13.7	17.2%	7.6%	1.2%	14.8%	7.8%	1.71

For each part of the 25 plant species, we report the average total mass (g/unit) and the percentage of dry matter per total mass (%DM). The concentrations of crude protein, lipids, neutral detergent fiber (NDF), and total ash are expressed as a percentage of dry matter. The MEC is expressed per total weight (kJ/g).

consumed only 1 food species in 2671 of the 3681 sites where energy intake was measured (72.6%), and the main food species accounted for at least half of the total energy intake in 3635 of the 3681 sites (98.8%). Of the 25 species that were measured for nutritional analyses—which together represent >95% of the gorilla diet (Grueter et al. 2013; Wright et al. 2015)—23 (92%) were the main species for at least 1 food site (Table 2). Almost all of the foods in this study are considered terrestrial herbaceous vegetation, so we did not consider categories such as fruit versus leaves as in some other papers (e.g., Wright et al. 2014).

To test the hypothesis that high-ranking females have greater access to sites that can be usurped, we aggregated the food site data into a single point for each female. We then examined the correlation between the average FSRT of each female versus her rank. Our level of aggregation was chosen primarily because we have only 1 value for the dominance rank of each female throughout the study, so we can examine differences among females but not any variations in the rank of each female.

To test the hypothesis that contest competition is greater with plant species that can be usurped, we aggregated the food site data into a single point for each plant species (Table 2). Our level of aggregation was chosen because we have only 1 set of nutritional measurements for each plant species, so we can examine differences among species but not the variance within each species. We examined the correlation between the average FSRT of each species versus the aggression rate while females were consuming it. To test whether gorillas spend more time at the sites of more valuable food species, we examined the correlation between average FSRT versus the average energy intake rate with each species. Hypothetically, food sites can have long residence times because the gorillas consume a lot of food at the site and/or because the gorillas consume the food slowly (e.g., if the food requires lengthy processing). To determine which of those 2 factors accounted for more of the variance in FSRT among species, we examined the correlations between the average FSRT of each species versus the average amount ingested per site (grams of total mass) and versus the average ingestion rate (total grams per minute). The average ingestion rate for each plant species equaled the total mass consumed at its food sites, divided by the total residence time of its food sites.

We used the coefficient of determination (R^2) from a univariate analysis of variance (Anova) to describe how much variance in the FSRT arose among species versus within each species. Each food site was a separate data point, and the predictor variable was the main food species consumed at the site. Otherwise, we preferred to maintain a consistent level of aggregation throughout the main hypotheses (1 data point per food species or per female). Such consistency helps to ensure that differences among the results will reflect the underlying data rather than the statistical methods.

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Table 2

Food sites as categorized by the main species consumed

Main species	N_{SITES}	kJ/site	kJ/min	FSRT
Basella alba	8	58.4	35.0	1.67
Carduus leptacanthus	19	93.2	41.0	2.27
Carduus nyassanus	640	186.3	59.0	3.16
Crassocephalum ducis-aprutii	4	11.3	13.9	0.81
Cyperus karisimbiensis	11	120.4	62.9	1.91
Dendrosenecio erici-rosenii	109	23.6	7.0	3.36
Discopodium penninervium	39	12.4	6.0	2.07
Droguetia iners	20	159.0	43.8	3.63
Echinops hoehnelii	11	104.7	49.6	2.11
Galium sp.	895	264.9	110.6	2.40
Helichrysum cf. formossissimum	28	52.5	25.3	2.07
Laportea alatipes	183	190.0	71.0	2.68
Lobelia giberroa	5	23.6	25.5	0.93
Lobelia stuhlmannii	59	258.3	138.1	1.87
Lobelia wollastonii	12	430.9	151.2	2.85
Pentarrhinum insipidum	11	29.1	18.8	1.55
Peucedanum kerstenii	6	10.1	9.2	1.10
Peucedanum linderi	377	158.7	55.0	2.88
Rubus runssorensis	369	417.3	165.5	2.52
Rumex ruwenzoriense	39	56.8	22.1	2.57
Senecio subsessilis	3	42.2	14.6	2.89
Vernonia adolfi-frederici	23	151.1	47.4	3.19
Yushania alpina	482	161.7	56.9	2.84

For each of the 23 main species, we report the number of food sites observed (N_{SITES}), as well as mean values for the energy intake per site (kJ/site), the energy intake rate (kJ/min), and the FSRT in minutes.

Proximate mechanisms of contest competition

To test the hypothesis that aggression is an important mechanism for contest competition while feeding, we ran a multivariate analysis with dominance rank and context (feeding vs. other behavior such as resting) as predictor variables. The model included 1 data point for each female in each context. The response variable was the aggression rate, which was calculated as the number of aggressive acts that the female performed in a context, divided by the number of focal hours that she was observed in that context. Aggressive acts included pig-grunting, screaming aggressively, chasing, lunging, excited displays, hitting, shoving, dragging, kicking, grabbing, or biting (Watts 1994).

To test the hypothesis that avoidance is an important mechanism for contest competition while feeding, we ran another multivariate analysis with dominance rank and context (feeding vs. other) as predictor variables. The model again included 1 data point for each adult female in each context. The response variable was average number of other adult females within 5 m of the focal female during her instantaneous scans in a context (Wright et al. 2014). Thus, we define avoidance as the tendency for an adult female to have a smaller number of other adult females within proximity of her, but this perspective does not determine who was avoiding whom. Results were similar for proximity within 2 m (not shown).

Potential consequences of contest competition

To test the hypothesis that high-ranking females have greater energy intake rates, we combined the food site data into a single data point for each female. The average energy intake per minute equaled the sum of the energy content for all food units consumed (kJ), divided by the total feeding time observed (minutes). The average intake per food site equaled the sum of the energy content for all food units consumed, divided by the number of food sites observed. We examined the correlations between rank versus the average energy intake per minute and the average energy intake per food site.

Hypothetically, females can have high energy intake rates because they eat more quickly than other females and/or because they eat foods with higher energy concentrations. To determine which of those 2 factors accounted for more of the variance in energy intake rates among females, we examined the correlations between the average energy intake rate of each female versus their average ingestion rate (total grams per minute) and versus the average energy concentration of their foods (kJ per gram of total mass). The average ingestion rate of each female equaled the total (undried) mass that she consumed, divided by the total residence time from her food sites. The average energy concentration equaled the total energy intake of each female, divided by the total mass that she consumed.

To test the hypothesis that high-ranking females have lower energy expenditures for travel, we again combined the food site data into a single data point for each female. We excluded sites when the full distance was not observed and when the travel included behavior other than foraging (e.g., playing). To focus on travel that is most likely to differ among females, we also excluded sites immediately after the entire group was traveling simultaneously. We examined the correlation between rank and the proportion of time spent traveling between food sites. For each female, the proportion of time spent traveling equaled the total time spent traveling to reach food sites, divided by the combined time for traveling plus feeding at those sites. The travel time was estimated as the observed distance to reach the site, divided by an average walking speed of 0.5 m/s (Wright et al. 2014). We also compared the energy expenditure for travel with the average energy intake per site. The travel time was converted into an energy expenditure based on a conversion factor of 24.7 kJ/min (Wright et al. 2014).

To test the hypothesis that low-ranking females spend more time feeding than high-ranking females, we combined the feeding activity budget data into a single data point for each female. The predictor variable was the rank of the focal female, and the response variable was the proportion of scans that she was feeding versus other activities. Feeding refers to preparation and ingestion of food (which includes chewing), so unlike some studies, it does not include the time spent traveling while searching for food (Majolo et al. 2008).

Statistical analyses

When we combined the food site data into a single point for each food species, we used weighted least squares regressions for the analyses, and each data point was weighted according to the number of food sites observed (Chatterjee and Price 1991). Our results should be interpreted carefully to avoid the "ecological fallacy," which occurs when data that is aggregated at an ecological level (i.e., 1 data point for each species) are used to draw inferences about an individual level (Pollet et al. 2015). For example, when we used 1 data point for each food species to examine the relationship between average FSRT and the average amount of food ingested per site, the results can support conclusions about differences among food species, but those same conclusions do not necessarily apply to variations among sites within each food species.

When we combined data into one or more sets of values for each female, we ran a linear mixed model with a Gaussian error structure and an identity link. We included the group ID as a random effect variable, and a random slopes term for the potential interaction between rank and group ID. The size of each group remained

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relatively constant throughout the study (BWE = 6.8 ± 0.8 standard deviation [SD] weaned individuals, NTA = 9.3 ± 0.4, and PAB = 38.3 ± 0.6), so the random effect term can control for the potential influence of group size, and the random slopes term can control for any differences in steepness among the dominance hierarchies (de Vries et al. 2006). The analyses of aggression rates and avoidance involved multiple data points for each female, so we included female ID as another random effect variable in those models. To assess the statistical significance of each predictor variable, we conducted likelihood ratio tests by comparing the full model with a reduced model in which the predictor was excluded.

To check for normally distributed and homogeneous residuals in our models, we visually inspected the residuals plotted against fitted values and qq-plots. All models were fitted in R. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

RESULTS

Characteristics of food sites

When we combined the feeding sites into 1 data point for each female, the average FSRT was 2.7 ± 0.44 SD min. The average FSRT of each female had a significant statistical relationship with rank (coefficient = 0.7, $\chi^2 = 4.4$; degrees of freedom [df] = 1; $P = 0.037$), which suggests that high-ranking females may have greater access to food sites that can be usurped.

When we combined the feeding sites into 1 data point for each main food species ($N = 23$, Table 2), the average FSRT of each food species was not significantly correlated with the rate of aggression for that species (coefficient = −1.6, $R^2 = 2.3\%$, $F_{21,1} = 0.5$, $P = 0.48$). Thus, food species with longer average FSRT did not seem to elicit more aggression. The average FSRT of each food species was negatively correlated with the average energy intake rate, which suggests that females spent less time at the food sites of species that provide high energy intake rates (coefficient = −0.0045, $R^2 = 24.6\%$, $F_{21,1} = 6.9$, $P = 0.016$). The average FSRT of each food species was also negatively correlated with the average ingestion rate (coefficient = −0.0071, $R^2 = 20.8\%$, $F_{21,1} = 5.5$, $P = 0.029$), but it was not significantly correlated with the average amount of food ingested per site (coefficient = −0.0013, $R^2 = 3.5\%$, $F_{21,1} = 0.8$, $P = 0.39$). Thus, longer FSRT mainly occurred with species that the gorillas consumed more slowly (Figure 1).

When we treated each food site as a separate data point, the R^2 value from a univariate Anova indicated that only 2% of the variance in the FSRT arose among species, with the remaining variance occurring within species ($F_{3330,22} = 3.1$, $P < 0.001$). Due to the low R^2 value for differences among species, we ran post hoc tests to evaluate other potential sources of variance in the FSRT. We ran 6 separate univariate Anova, which all used 1 data point for each food site. Each test examined a different category variable: the female ID, the group ID, the month of the year, the hour of the day, the habitat type (bamboo, subalpine/alpine, and Hagenia), and the reproductive status of the female (cycling, gestating, or lactating). The R^2 values were low for each category variable: 2.6% for female ID, 0.4% for group ID, 0.7% for the month of the year, 0.3% for the hour of the day, 0.1% for the type of habitat, and <0.1% for reproductive status. Thus, we did not identify any major sources of variance in the FSRT.

Potential mechanisms of contest competition

A total of 162 aggressive acts were observed during 821 focal hours, which represents an average aggression rate of 0.20 acts per focal hour. The rate was 0.28 aggressive acts per focal hour during 326 focal hours while feeding, which significantly higher than 0.14 acts per focal hour during other activities (coefficient = 5.3, $\chi^2 = 8.5$; df = 1; $P = 0.0035$). These results suggest that aggression could be a proximate mechanism for contest competition while feeding. The aggression rate had a positive significant relationship with rank, which indicates that high-ranking females were aggressive more frequently than low-ranking females (coefficient = 7.2, $\chi^2 = 6.7$; df = 1; $P = 0.0094$).

Adult females had an average of 1.3 ± 1.3 other adult females within 5 m of proximity. The average number of other adult females within 5 m was 0.95 ± 0.34 while feeding, which is significantly less than 1.6 ± 0.45 during other activities (coefficient = −0.71, $\chi^2 = 53.0$; df = 1; $P < 0.001$). Thus, the adult females were less densely spaced while feeding than during other activities. The number of other adult females within 5 m did not have a significant relationship with dominance rank, however, so we

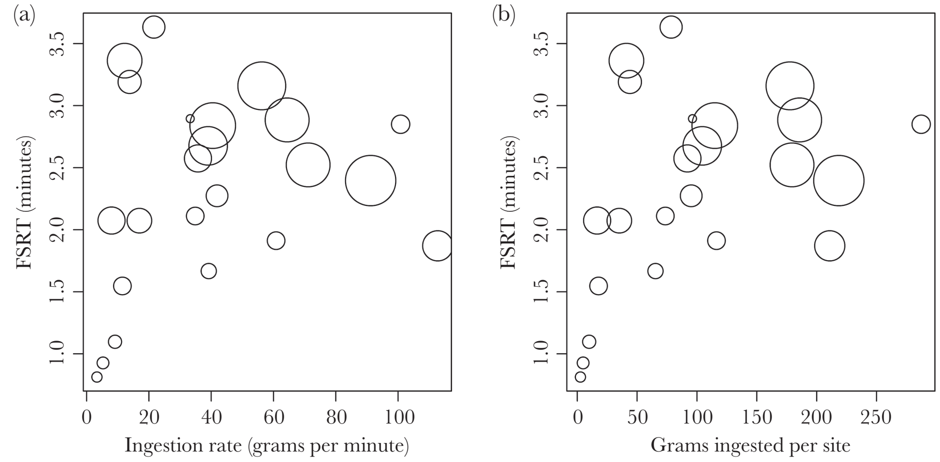

Figure 1
FSRT versus the ingestion rates (total grams per minute) (a) and the amount consumed per food site (grams) (b). Each data point represents one of the main species listed in Table 2. The size of each point reflects the number of sites that were observed for the species.

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got mixed results regarding whether avoidance was an important mechanism for contest competition in this study (coefficient = 0.1, $\chi^2 = 0.5$; df = 1; $P = 0.47$).

Potential consequences of contest competition

When we combined the feeding sites into 1 data point for each female, the average energy intake rate was 79.5 ± 13.7 kJ/min. Rank did not have a significant relationship with average energy intake rate (coefficient = −4.9, $\chi^2 = 0.5$; df = 1; $P = 0.48$) or the energy intake per site (coefficient = 35.1, $\chi^2 = 1.4$; df = 1; $P = 0.24$). Variance in the average energy intake rate among females arose mainly from differences in their ingestion rates (coefficient = 1.5, $\chi^2 = 6.7$; df = 1; $P = 0.010$), rather than the energy concentration of their foods (coefficient = 80.5, $\chi^2 = 1.8$; df = 1; $P = 0.18$). Thus, the greater potential for contest competition might be for foods that can be consumed quickly, rather than foods that have high energy concentrations (Figure 2).

The average distance traveled to reach a food site was 4.5 ± 0.76 m, which corresponds to an estimated travel time of 0.15 ± 0.025 min between feeding sites. The average time spent traveling to a food site equaled 5% of the combined time for travel plus feeding. Rank did not have a significant relationship with the proportion of time that females spent traveling (coefficient = −0.020, $\chi^2 = 3.1$; df = 1; $P = 0.081$). The estimated travel time per food site corresponds to an energy expenditure of 3.7 ± 0.63 kJ/site, which represents only 1.6% of the average energy intake per site (228.7 ± 62.5 kJ). Thus, the energy expenditure for traveling among food sites was relatively small in comparison with the energy gained by feeding at those sites.

Females were observed feeding during an average of 40.0 ± 6.9% of their focal scans. The proportion of scans spent feeding did not have a significant relationship with rank, so we found no support for the hypothesis that low-ranking females spend more time feeding to compensate for lower foraging efficiency (coefficient = −0.05, $\chi^2 = 0.8$; df = 1; $P = 0.37$).

DISCUSSION

Comprehensive studies of contest competition should ideally examine its potential causes based on food characteristics, its proximate mechanisms of aggression and avoidance, as well as its ultimate consequences for energy balances and reproductive success (Koenig and Borries 2009; Koenig et al. 2013). This study of female mountain gorillas in the Virunga Massif found mixed results from those 3 perspectives. The average FSRT of each female was significantly correlated with dominance rank, which suggests that high-ranking females may have greater access to foods that are easier to usurp. Aggression rates were also positively correlated with rank, and both aggression and avoidance were significantly higher while feeding than during other activities. Contrary to predictions for contest competition, however, high-ranking females did not have significantly higher energy intake rates or lower expenditure for travel, so our results do not explain why high-ranking females had significantly higher reproductive success in earlier studies (Robbins et al. 2007a, 2007b, 2011a). This study provides some contrasts with mountain gorillas in the nearby Bwindi Impenetrable National Park (Wright et al. 2014), but results from the 2 populations are collectively consistent with theoretical expectations for species with relatively weak dominance relationships (Watts 1994; Sterck et al. 1997; Snaith and Chapman 2007).

Characteristics of food sites

The significant correlation between the average FSRT and the dominance rank of female mountain gorillas is similar to studies of yellow baboons and vervet monkeys, where longer feeding bouts have been reported for high-ranking females (Post et al. 1980; Isbell et al. 1999). Long FSRT mainly arose with plant species that the mountain gorillas ingested more slowly, however, so the benefits for high-ranking females remain unclear (see below).

The average FSRT of each species was not significantly correlated with aggression rates while females consumed it, so we did not find evidence of greater contest competition for species that are easier to usurp. In contrast, measures such as FSRT have been positively related to the frequency of agonism in several other primates (Post et al. 1980; Janson 1990; Pruetz and Isbell 2000; Chancellor and Isbell 2008; Gemmill and Gould 2008; Chancellor and Isbell 2009; Verderane et al. 2013). In our study, only 2% of the variance in FSRT arose among plant species, with the remaining variance occurring within species. Other differences within plant species (e.g., variability in ripeness) have been reported for both folivorous and frugivorous primates, which may contribute to contest competition within groups (Koenig et al. 1998; Koenig 2000; Murray

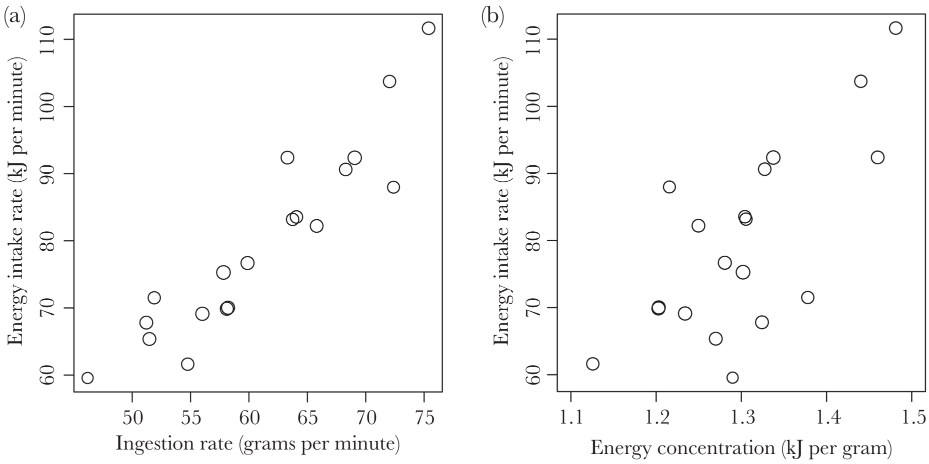

Figure 2
Energy intake rates (kJ per minute) versus the ingestion rates (total grams per minute) (a) and energy concentrations (kJ per gram) (b). Each data point combines all of the food sites for one of the females in the study. The size of each point reflects the number of sites that were observed for the female.

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et al. 2007; Snaith and Chapman 2007). Further study is needed to more fully quantify the sources of variance within plant species consumed by mountain gorillas and other herbivores (Rothman et al. 2009).

Proximate mechanisms of contest competition

Aggression rates were significantly higher when feeding than during other activities, which has been considered evidence for within-group contest competition over food (Stewart and Harcourt 1987; Watts 1994; Robbins 2008; Wright and Robbins 2014). High-ranking females had significantly higher aggression rates than low-ranking females, a finding that is consistent with studies of several other species (van Noordwijk and van Schaik 1987; Cote 2000; Creel 2005; Vogel 2005; Foerster et al. 2011). Nonetheless, mixed results have emerged from studies of such correlations among gorillas (Watts 1994; Scott and Lockard 2006; Robbins 2008; Wright and Robbins 2014). If fighting can be costly, then contest competition may not lead to high levels of aggression among individuals who are familiar with each other, because subordinates may avoid encounters that they are likely to lose (Koenig and Borries 2009; Wheeler et al. 2013). Higher rates of aggression can be expected when those relationships are in flux, and lower rates may occur when the relationships are well-established (Parker 1974; Koenig 2002). Interventions by the dominant male can further reduce aggression among female mountain gorillas (Harcourt and Stewart 1989; Watts 1994, 1997).

Adult females were in proximity with significantly fewer other adult females while feeding than during other activities, which could reflect efforts to avoid contest competition while feeding (Harcourt 1979). A reduction in proximity while feeding could also help to reduce scramble competition by increasing group spread (Barton and Whiten 1993; Pazol and Cords 2005; Saj and Sicotte 2007; Grueter et al. 2009). The number of individuals in proximity was not significantly correlated with rank, in contrast with a recent study of Bwindi mountain gorillas that found that higher-ranking females had fewer individuals in close proximity while feeding (Wright and Robbins 2014). Avoidance has also been considered an important aspect of contest competition in several other species (van Schaik and van Noordwijk 1988; Janson 1990; Thouless 1990; Fournier and Festa-Bianchet 1995; Saito 1996; Hall and Fedigan 1997; Murray et al. 2007; Hirsch 2011). Regardless, dominance relationships in both gorilla populations are still relatively weak, as indicated by the high proportion of aggression by lower-ranking females toward high-ranking females (22% at Bwindi vs. 30% in this study).

Potential consequences of contest competition

Contrary to predictions for contest competition, dominance rank was not significantly correlated with energy intake rates or the proportion of time spent traveling, so we did not find significant benefits from the longer FSRT of high-ranking females. In contrast, rank was significantly correlated with energy intake rates and energy expenditures for Bwindi mountain gorillas (Wright et al. 2014). In addition, many other studies have revealed a link between female dominance and foraging superiority, which can be expressed as higher food and energy intake rates, higher foraging efficiency, and/or higher frequency of winning contests over food (Janson 1985b; Barton and Whiten 1993; Range and Noe 2002; Wittig and Boesch 2003; Vogel 2005; Murray et al. 2006). Those studies have been interpreted as evidence of contest competition in which high-ranking females had improved access to resources (Koenig 2000; Schülke and Ostner 2012).

Our results are consistent with concurrent findings that the rank of these same female mountain gorillas was not significantly correlated with levels of urinary C-peptide, which is considered a marker of energy balances (Grueter et al. 2014). Taken at face value, these results collectively suggest that differences in energy balances do not explain why high-ranking females had significantly higher reproductive success in earlier studies of this population (Robbins et al. 2007a, 2007b, 2011a). It is difficult to show that aggression and avoidance have absolutely zero impact on energy balances, so our results may merely indicate that the consequences of contest competition were too weak to be detected in this study. Our results suggest a stronger possibility for low-ranking females to have higher travel expenditures ($P = 0.081$) rather than lower energy intake rates ($P = 0.48$). Travel expenditures could be especially important if mountain gorillas are limited by gut passage time, but the impact on energy balances seems minimal (Steudel 2000; Isbell 2004). Thus, our energy results highlight the need for alternative hypotheses to explain the significant rank-related differences in aggression and reproductive success.

One alternative hypothesis is that rank and reproductive success may both covary with the mother's physical condition, even if those variables are not strongly related to contest competition (Pusey et al. 2005; Robbins et al. 2007a). For example, healthier females might be more efficient at converting energy into reproductive success, and they might be more likely to win interactions against weaker females, even if those interactions have minimal impact on foraging efficiency (Robbins et al. 2007a). Variability in physical condition among females could be due to factors such as genetics, maternal effects, and environmental influences (Kruuk et al. 2000; Teplitsky et al. 2009). If so, then our results illustrate that researchers cannot merely use data on reproductive success to conclude whether contest competition is occurring, because they need to look at foraging efficiency too (Koenig and Borries 2009; Koenig et al. 2013).

Another alternative explanation for our results is that digestive constraints could cause females to compete for foods that optimize their digestive rates, rather than their energy intake rates (Verlinden and Wiley 1989; Jeschke and Tollrian 2005; Whelan and Brown 2005). In addition, high-ranking females might gain preferred access to foods with key nutrients such as sodium that were not reflected in our energy calculations (Rothman et al. 2006; Wright and Robbins 2014). Females also compete for proximity to the dominant male, and the stress from such competition could affect reproductive success (Watts 1994). Thus, several alternative causes for contest competition could still explain why rank is correlated with aggression and reproductive success but not with energy intake or expenditures.

Variance in average energy intake rates among females in this study arose mainly from differences in their ingestion rates ($P = 0.010$), rather than the energy concentration of their foods ($P = 0.184$), which resembles results from 2 populations of Hanuman langurs (Schülke et al. 2006). Differences in ingestion rates can reflect differences in body size if individuals with larger hands and mouths can eat more quickly (Shipley et al. 1994). If larger individuals are also more likely to win interactions than smaller individuals, then such scenarios might also lead to correlations between rank and energy intake rates, even if those interactions have minimal impact on foraging efficiency. The link between ingestion rates and body size has been discounted by studies of other primates, but it further illustrates the potential complexities

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of assessing contest competition, especially when dominance relationships are weak (Janson 1985b; Barton and Whiten 1993; Vogel 2005; Wright et al. 2014). In light of their weak dominance relationships and the apparent abundance of food throughout their habitat, it seems likely that any rank-related foraging differences among female mountain gorillas are currently small. Nonetheless, due to the increasing population and changes in food abundance, it remains important to continue monitoring the potential for feeding competition in this critically endangered species (Robbins et al. 2011b; Grueter et al. 2013).

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