

RESEARCH ARTICLE

Female Feeding Priority in Bonobos, *Pan paniscus*, and the Question of Female Dominance

FRANCES J. WHITE^{1*} AND KIMBERLEY D. WOOD²

¹Department Anthropology, University of Oregon, Eugene, Oregon

²Horizon Research, Inc., Chapel Hill, North Carolina

The question of whether bonobos show feeding priority and female dominance has been proposed and examined, both in the wild and in captive studies, with differing results. The relationship between female dominance and female feeding priority has been best studied in prosimian primates. These studies use established criteria of females consistently evoking submissive behavior from males in dyadic encounters for determining female dominance. Although the relationship is complex, female dominance in prosimians is associated with preferential access to food. Data from studies of wild habituated bonobos in the Lomako Forest, Democratic Republic of the Congo, are examined for evidence of both female feeding priority and female social dominance using similar criteria as used for prosimians. Bonobos showed evidence of female feeding priority in small, but not in large, food patches. Male–male competition for mating opportunities at the start of the food bout was related to some, but not all, differences in time spent feeding between the sexes. Female dominance similar to that seen in prosimians was not observed in these bonobos. Males were consistently dominant in dyadic interactions. Female feeding priority with male dyadic social dominance implies that male deference during feeding cannot be excluded as one explanation of interpretations of female dominance in bonobos. Additionally, dominance of male bonobos by females appears to require the presence of female coalition partners. As in other primates with female feeding priority, bonobo females express this trait where food is economically defensible. Unlike prosimians, however, bonobo female feeding priority may result from male deference and the importance of female coalitions in nondyadic interactions. *Am. J. Primatol.* 69:1–14, 2007. © 2007 Wiley-Liss, Inc.

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*Correspondence to: Frances J. White, Department of Anthropology, 1218 University of Oregon, Eugene, OR 97403. E-mail: fwhite@uoregon.edu

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INTRODUCTION

The question of whether bonobos should be considered as female dominant has been examined in both wild and captive studies without consensus [Furuichi, 1989; Hohmann & Fruth, 2002; Kano, 1992; Parish, 1994, 1996; Parish & de Waal, 2000; Stanford, 1998; White, 1996]. The question of what constitutes female dominance in bonobos, and the relevance of results from feeding versus nonfeeding contexts, has been especially contentious [Parish & de Waal, 2000]. It has been suggested [Kappeler, 1990; Pereira et al., 1990] that social dominance should be considered a separate phenomenon from feeding priority, defined as consistent priority of access to food but not necessarily other resources [Kappeler, 1990, 1992]. These authors suggest that female social dominance is achieved presumably through agonistic superiority and may result in female feeding priority, but female feeding priority may also be a result of male deference.

Defining dominance and determining rank hierarchies both within and between sexes has also long proved troublesome [Bernstein, 1981]. In general, consistent winners of agonistic conflicts are considered socially dominant, and a hierarchy is established using the outcomes of dyadic encounters [Drews, 1993]. By this definition, aggression alone is not sufficient to determine social dominance and coalitions do not affect individual social dominance rank. We follow this definition in this study and reserve the term “female social dominance” for species that fit these criteria.

Among anthropoid primates, female dominance has also been suggested in studies of patas monkeys (*Erythrocebus patas*) [Hall & Mayer, 1967; Kaplan & Zucker, 1980], talapoin (*Miopithecus talapoin*) [Dixon et al., 1973; Wolfheim, 1977], squirrel monkeys (*Saimiri*) [Baldwin, 1968; Baldwin & Baldwin, 1972; Boinski et al., 2002; Mitchell, 1990; Mitchell et al., 1991]. Claims of female dominance in patas monkeys, *Erythrocebus patas*, are based on studies of free-ranging animals [Hall & Mayer, 1967; Kaplan & Zucker, 1980]. In this species, females may attack males individually or in coalitions. Males do not show submission to females during these attacks, but rather stand their ground and fight. In contrast, female patas monkeys flee attacks by males. Thus, patas monkeys do not fall under Kappeler's [1990, 1992] definition of a species displaying female social dominance.

The best evidence that female talapoin, *Miopithecus talapoin*, are dominant to males comes from captive studies. Aggressive threats, stares, and attacks, by ranking individuals in small groups (one to two males, three to four females), resulted in stable hierarchies with females outranking males in most groups [Dixon et al., 1973]. When animals were ranked based on avoidance behaviors, females were avoided by males more often than the reverse; however, all females avoided a male on at least one occasion, and results differed by season [Wolfheim, 1977]. These results are difficult to interpret since no information is given on coalition formation. We conclude it has yet to be demonstrated that this species fits our criteria for female social dominance.

Early studies of Central American squirrel monkeys (*Saimiri oerstedii*) found that males often fled during the birth season when coalitions of females chased them away from infants [Baldwin, 1968; Baldwin & Baldwin, 1972]. Because these interactions did not occur in dyads, Kappeler [1993] did not consider them to demonstrate female dominance. Comparisons of *Saimiri oerstedii* to the South American species, *S. boliviensis*, and found striking differences in nearly every aspect of social behavior [Mitchell, 1990; Mitchell et al., 1991]. In *S. sciureus*,

males win dyadic conflicts over resources during the mating season, whereas females win all conflicts during the birth season. Although this female superiority does not occur year-round, it is a clear and consistent phenomenon during this part of the year. Thus, this study population of *Saimiri sciureus* represents the best example of female social dominance, as defined by Kappeler [1993], in a monkey species. This comparison also demonstrated the ecological basis of this trait as the female dominant South American squirrel monkey, *Saimiri boliviensis*, feeds in economically defensible patches whereas its nonfemale dominant congener, *Saimiri oerstedii*, feeds in much smaller patches that are not worth defending [Mitchell et al., 1991]. Further comparisons of *Saimiri* species have extended this ecological link between female dominance and female feeding priority. *Saimiri sciureus* in Suriname feed in small, dense feeding patches that can be monopolized by one female, thus making female coalitions unstable [Boinski et al., 2002].

Problems of definition, combined with the lack of differentiation between social dominance and feeding priority, and the inclusion of interactions involving coalitions of females, have made comparisons among species difficult. Part of the confusion of whether bonobos are female dominant may be based on definitions of social dominance that include coalitions. Studies of feeding in captivity have found that females form coalitions to dominate males and control access to resources [Parish, 1994; Vervaecke et al., 1992]. Studies of provisioned wild bonobos have also found that while individual females do not out-rank males, coalitions of females can elicit submissive behavior from males [Furuichi, 1989] and females show feeding priority in mixed parties [Furuichi, 1989, 1997; Kano, 1992], which may be related to lower infant mortality at this site [Furuichi et al., 1998]. In this study, we examine data from wild bonobos for evidence of female social dominance using the dyadic-based definitions used in studies of Malagasy prosimians.

The question of female dominance often involves questions of sex differences in feeding, especially whether females show feeding priority. Following Clutton-Brock's [1977] important study detailing sex differences in primate feeding, field studies have identified the energetic demands of reproduction on females as an important factor related to females feeding differently from males (for example; Cords, 1986; Gautier-Hion, 1980; Wright, 1984). Sex differences in feeding can be divided into two different elements: having preferential access to food sources and needing to feed for longer. If the amount of high-quality food in a food source is limited and depleted during feeding, having first access to that food and feeding most while high-quality items are available are important advantages. In contrast, individuals who only have access to poorer quality foods may need to feed for longer to compensate. Although female feeding priority is often an important aspect of female dominance, social dominance does not always result in feeding priority [Gerald, 2002]. In this study, we focus on whether females have priority of access to the food sources and feed more at the start of the bout when presumably most high-quality food is still available.

Female feeding priority is a phenomenon known mostly from Malagasy prosimians that results in females having preferential access over males to food sources [Jolly, 1984; Kappeler, 1990; Pereira et al., 1990; Richard, 1987]. Studies of sex-based feeding priority have used a variety of criteria to determine if a species or study group show female feeding priority. Criteria include sex differences in winning fights or displacements over food or in feeding contexts [Jolly, 1966; Pochron et al., 2003], having first access to feeding and drinking sites [Budnitz & Dainis, 1975], length of feeding bout, percentages of feeding time, and

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differences in plant parts eaten [Hemingway, 1999; Morland, 1991; Overdorff, 1991; Pollock, 1977; Richard, 1978; Sauther, 1992, 1993].

Females can also gain preferential feeding success over males by initiating and leading group movements [Boinski, 1991] and thus gain first access to food, as has been observed in two species of Malagasy prosimians [Erhart & Overdorff, 1998]. Additionally, in a third species, in a group where the dominant female leads group movements, she arrived first at food patches and subsequently experienced a higher food intake [Overdorff et al., 2005]. There was, however, variation in both female dominance and female leading depending on group composition. Female feeding priority can, therefore, encompass several phenomena, including arriving first at food patches, feeding first or longer, and having greater feeding time on preferred foods, and can be dependent on group composition.

As is important for the perspective of this study to determine female feeding priority separate from female dominance, only criteria that measure feeding success without reliance on female aggression are relevant for this study. Female feeding priority is, therefore, defined here as females having first access to food patches, having longer feeding bouts, and higher feeding success than males. The question of whether female bonobos lead group movements to feeding patches, however, is complicated by the fission-fusion social organization of this species. We can, therefore, only address this aspect of female feeding priority by examining whether females in cohesive parties that are traveling together lead the entry into a food patch and exclude cases in which fission or fusion events are associated with feeding bouts. Additionally, it was expected that expression of female feeding priority may be dependent on party composition and on whether preferred foods were limited by the size of the patches available, so these variables were included in this study. If female feeding priority results from a male reproductive strategy of deference, we would expect to see an association between female feeding priority, male deference, and male mating success.

The relationship between female dominance and female feeding priority in Malagasy prosimians is complex [Hemingway, 1999; Kappeler, 1993; Pereira & Kappeler, 1997; Radespiel & Zimmermann, 2001; Wright, 1999]. As summarized by Hemingway [1999] and Radespiel & Zimmermann [2001], female feeding priority, sex differences in feeding, and female dominance may be associated but do not invariably co-occur in different species or study populations. Similarly, the hypothesis that female dominance and associated female feeding priority can be related to the high energy demands and relatively inefficient reproductive physiology of these primates in the highly seasonal environments of Madagascar [Jolly, 1984; Richard, 1987; Richard & Nicoll, 1987; Young et al., 1990] has also proved more complex. Studies showing that lemur do not have high energetic stress during reproduction [Kappeler, 1996; Tilden & Oftedal, 1995, 1997] have lead to further hypotheses for the evolution and potential association of these traits. These hypotheses include: 1) the proposal that female dominance originated as paternal investment in monogamous ancestral lemur [Jolly, 1998]; 2) that female dominance and associated feeding priority allows females to build fat storage during times of abundant food [Pereira et al., 1999]; and 3) that female dominance is part of a complex of energy frugality traits that maximize the use of scarce resources [Wright, 1999]. All of these hypotheses incorporate some aspect of female preferential access to food, either with or without female agonistic dominance over males.

MATERIALS AND METHODS

Data were taken during 428 hr of observation between 1983 and 1995 on nonprovisioned *Pan paniscus* in the Lomako Forest, central Democratic Republic of the Congo. The study site is located at 0° 51'N, 21° 5'E and consists of approximately 40 km² of mapped trails. The study area includes a mosaic of forest types, but is principally evergreen, polyspecific rain forest, with some areas of secondary growth, slope, and swamp forest [White, 1992]. The study animals were members of two communities and a splinter-group (data for 1983–1985 only). Communities varied in size over the study period but at maximal size consisted of (not including infants): 1) Bakumba community—eight adult males, one subadult male, four juvenile males, 14 adult females, five adolescent females, four juvenile females; 2) Eyengo community—five adult males, three subadult male, one juvenile males, nine adult females, two adolescent females, one juvenile female; and 3) the splinter group—five adult males, one adult female, and four adolescent females. By 1991, the female members of the splinter group were members of the Bakumba community.

To determine social dominance, all occurrences of dyadic agonistic interactions were scored in any context according to aggressive (A), submissive (S), or no signals (0) given by each participant. The outcome of decided interactions was used to construct a partial dominance hierarchy for the two communities and the splinter group. The frequency of decided interactions won by each sex was compared to an expected distribution based on equal chance of winning by either sex using a G test of goodness-of-fit with Williams correction [Sokal & Rohlf, 1995].

Feeding priority was established by recording the order of progression of individuals in a cohesive party into a food patch and the order and duration of feeding during the first third of a bout. The first third of the feeding bout was selected to compare bouts of differing lengths. We are assuming that the beginning of the bout is the time when the most preferred food items are taken. Although food intake rates were not collected during this study, Malenky [1990] found that bonobo feeding rates at this site are determined primarily by fruit structure and pulp content. Malenky [1990] also found that feeding rates measured in a large *Ficus* tree remained constant during the feeding bout and decline just prior to the party leaving the food patch.

Food patches were defined as discrete areas within which individuals were able to collect food continuously [White & Wrangham, 1988]. Following White and Wrangham [1988], visual estimates of radius were used to define patches as either small and food-limiting (less than 10 m) or large (greater than or equal to 10 m). Feeding bouts were defined as the time from the first individual's entry to the last individual's exit from a food patch.

In order to allow for comparison of parties of different sizes and compositions, the first three males and first three females observed moving into each feeding patch were identified, and the number of 2-min time points each of these individuals spent feeding during the first third of the bout was recorded. For cases in which there were less than three individuals of either sex present, the number of feeding time points for all individuals of that sex present was used. Food patches were fruit and trees with new leaves. Feeding on terrestrial herbaceous vegetation (THV) was not included as this is a dispersed food that does not occur in patches; bonobos disperse and usually feed singling on this type of food. Bouts were excluded from analysis if another party joined during the first third, or if the party did not contain at least one male and one female. The feeding

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time was then averaged separately for each sex and for each patch to calculate a mean proportion of time points during the first third of the feeding bout that was spent feeding by males and females. Mating was recorded when observed. All females were observed mating. Estrus females were rarely observed and mate at lower frequencies than nonestrus females [White et al., 1998], and so were not excluded from the analysis.

The frequency with which each sex led a party into a feeding patch was compared with the sex ratio of observed feeding parties using a goodness-of-fit test. G tests of independence were used to compare mating frequency, the sex of the first individual into a patch, and the frequency of not feeding to feeding in males and females. A one-way analysis of variance (ANOVA) was then used to compare this transformed proportion between males and females. To better fit assumptions of the ANOVA, the proportion of time spent feeding during the first third of the bout was arcsine transformed [Sokal & Rohlf, 1995]. A nonparametric Spearman correlation was used to examine the relationship between the number of males and females present and the mean proportion of time spent feeding.

RESULTS

A total of 55 agonistic interactions were observed of which 49 could be scored for aggressive or submissive signals from both participants. Most interactions ($n = 42$) were decided. Decided agonistic interactions in which both participants could be identified and matched to community membership were used to construct individual dominance rankings separately for the two communities and the splinter group (Bakumba community: $n = 15$, Eyengo community: $n = 12$, splinter group: $n = 11$) (Table I). Although there were not enough agonistic interactions to allow definitive determination of all relative rankings, the results were consistent with adult and subadult males outranking females. Most agonistic interactions were decided and there were 16 decided interactions between a male and a female of which the male won 13 (Fig. 1).

Feeding bout length was highly variable, with the first third ranging from 2 to 120 min (mean = 24.6 min, standard error [SE] = 3.4). Feeding minutes were recorded for 112 males and 167 females. Males were more likely than females to not feed during the first third of the bout (25 for males, seven for females; $G = 21.371$, $P < 0.05$). Males fed less than females in 50% of all feeding bouts, the same as females in 39%, and females fed less than males in 8%. Of the 66 feeding bouts recorded, in 12% some of the males did not enter the food tree, in 6% some males arrived at the food tree after the start of the bout, and in 5% some males left the food tree before the first third was finished. The same was not true for females, as all females entered the food tree at the start of the bout and remained either in or near the food tree for the duration of the feeding bout. The amount of time spent feeding during the first third of the feeding bout differed significantly by sex ($F = 13.140$, $n = 64$ patches, $P < 0.001$). This difference varied with food patch size (Fig. 2): in small patches, females fed more than males ($F = 7.214$, $n = 21$ patches, $P < 0.02$); however, there was no significant difference in the amount of feeding in large patches ($F = 2.619$, $n = 32$ patches, $P = 0.11$).

Of the 66 food patches into which first entry by a cohesive party was observed, the order of entry was recorded for 37 patches. The first animal to feed was recorded for 28 of these patches. Seven feeding parties were led by males, and the remaining 30 were led by females. Given an average sex ratio of one male to 1.96 females for these 37 patches, males led in significantly less frequently than expected ($G = 3.992$, $P = 0.0457$). The sex that led the party into the patch was

TABLE I. Decided Agonistic Interactions Among Adults and Subadults in Bakumba Community (Before Arrival of Splinter Group), Eyengo Community, and Splinter Group for Identified Individuals

Winner	Loser											
	M1	M2	M3	M4	F1	F2	F3	F4	F5	F6	F7	F8
Bakumba community												
M1	xxx		2					2				
M2		xxx	1	4	1						1	
M3			xxx									1
M4				xxx								
F1					xxx					1		
F2						xxx	1		1			
F3							xxx					
F4								xxx				
F5									xxx			
F6										xxx		
F7											xxx	
F8												xxx
Eyengo community												
	M1	M2	M3	M4	M5	M6	M7	M8	F1	F2	F3	F4
M1	xxx	1	2	1								
M2		xxx										
M3			xxx									
M4				xxx						2		
M5					xxx	1				1		
M6						xxx						
M7							xxx	1		1	1	
M8								xxx				
F1									xxx			1
F2										xxx		
F3											xxx	
F4												xxx
Splinter group												
	M1	M2	F1	F2	F3	F4						
M1	xxx		1		1	2						
M2		xxx				1						
F1			xxx		4	1						
F2				xxx		1						
F3					xxx							
F4						xxx						

always the first to feed. Only adults and higher-ranking older adolescent females, and not subordinate subadult males and adolescent females, led into food patches. The radius of the food patch was recorded for 32 of these patches. Which sex led into the food patch was dependent on the size of the patch (Table II: $G = 7.134$, $P < 0.01$). Females led into all 12 of the small patches, whereas males led into seven of the 20 large food patches with females leading the other 13 times.

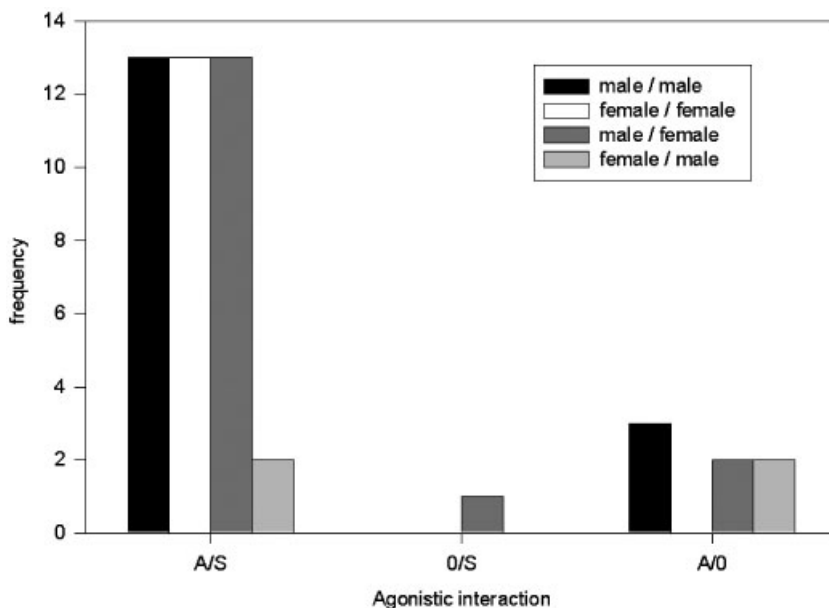


Fig. 1. Frequency of dyadic agonistic interactions (from 427 hr 51 min of observation). A denotes an aggressive signal, S denotes a submissive signal, and 0 denotes no signal. Decided interactions are A/S and O/S interactions. The winning sex is on the left of the pairs in the key. A/0 interactions are undecided.

Mating occurred in 32% of all feeding bouts. Mating was observed in nine of the 37 patches in which the order of entry into the food patch was observed. Mating occurred in 71% of food patches into which males led but in only 13% of patches where females led ($G = 9.118$, $P < 0.05$). On two occasions, male aggression against females was followed by matings, as consistent with sexual coercion [Smuts & Smuts, 1993].

The proportion of time spent feeding by males decreased with the number of males present. This was not true for females. There was a significant nonparametric correlation between the mean amount of feeding by males and the number of males present (correlation coefficient = -0.255 , $n = 62$, $P < 0.05$) but not with the number of females present (correlation coefficient = -0.086 , $n = 62$, $P = 0.51$). There was no significant correlation between mean amount of feeding by females and either the number of males present (correlation coefficient = -0.157 , $n = 62$, $P = 0.22$) or the number of females present (correlation coefficient = -0.216 , $n = 62$, $P = 0.09$).

DISCUSSION

Using consistent definitions of any behavioral term is important in comparative primate studies, especially those interested in the evolutionary significance of traits. The question of whether bonobos are female dominant has been strongly proposed by some [Parish & de Waal, 2000], but was not supported in other reviews of bonobo behavior [Stanford, 1998]. Studies of captive groups of bonobos have reported female dominance [Parish, 1994, 1996], whereas field studies have been more equivocal [Furuichi, 1989; Hohmann & Fruth, 2002;

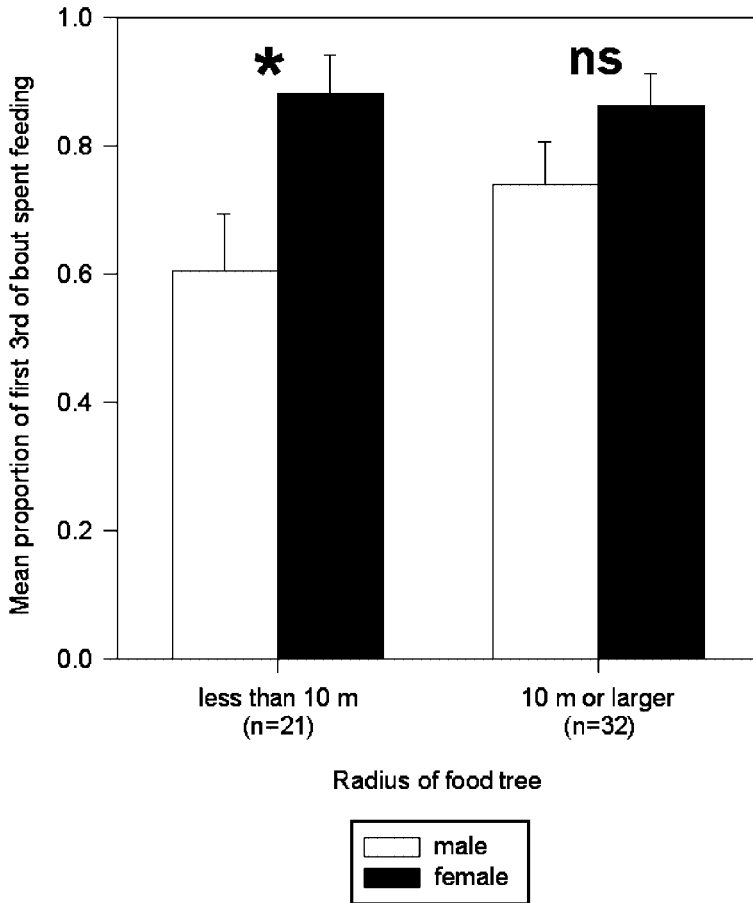


Fig. 2. Feeding success during the first third of the feeding bout for males and females in small and large food patches (mean and SE).

TABLE II. Order of Entry into Food Patches

	Small food patches								Large food patches								
	Radius (m)								Radius (m)								
	3	3.5	5	6	7	8	9	Total	10	11	12	14	15	17	20	21	Total
Female led	1	1	2	1	3	2	2	12	1	0	4	1	2	0	1	4	13
Male led	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	3	7
Totals	1	1	2	1	3	2	2	12	1	1	5	1	2	1	2	7	32

Kano, 1992; White, 1996]. The debate has also included considerations of whether female feeding priority is a separate issue or an integral part of female dominance.

Female social dominance is defined by Kappeler [1990, 1992] as females consistently evoking submissive behaviors from males in dyadic encounters and is found in a number of, but not all, Malagasy prosimians. Additionally, although feeding priority may be present in some Malagasy prosimians, this trait does not necessarily correspond to sex differences in feeding [Hemingway, 1999]. As summarized by Radespiel & Zimmermann [2001], unambiguous female dominance has been found in five species, moderate female dominance in two, feeding priority in four, and no female dominance in two species of Malagasy prosimians. Although there is consistency among Malagasy prosimian studies, expansion of studies into comparisons of the evolution of female feeding priority and female dominance to other primates has been complicated by the use of different criteria in different studies.

In this study, we found that bonobo females were not socially dominant to males by Kappeler [1993] definition. All adult and subadult male bonobos outranked all females, male aggression against females was relatively common and included evidence of sexual coercion, and male submission to female aggression was rare. Despite this lack of female social dominance, there is evidence from both captivity and the wild that female bonobos can control resources. In a captive study, females fed more and co-fed more at an artificial termite-fishing site at the exclusion of the single male in the group [Parish, 1994]. Furthermore, control and sharing of meat and fruit has been observed in the wild [Badrian & Badrian, 1984; Badrian & Malenky, 1984; Hohmann & Fruth, 1993; Kuroda, 1984; White, 1994]. Unlike common chimpanzees, individual bonobo females are not subject to sharing with either males or females under pressure, but can retain control of even highly prized food items like meat [White, 1994]. This study also demonstrated female feeding priority in the wild: females entered and fed in food patches before males more than expected, and females fed more than males at the start of the feeding bout.

If female feeding priority is not related to female social dominance, can it be related to male behavioral strategies such as deference? Males may feed less at the start of a feeding bout because of male–male competition that results in exclusion of males from patches or loss of feeding time to aggressive evictions of other males. Dominant males did reduce the feeding of other males: in four cases of males not entering or leaving a bout early, one or more males were aggressively evicted or excluded by other males. Feeding differences between the sexes may therefore be influenced by male–male competition.

This exclusion of males may be related to control of access to females for mating opportunities [Hohmann & Fruth, 2003]. Many matings took place at the start of a feeding bout and matings were most frequent when males were the leaders into large food patches. Males were often observed to arrive at a food patch just ahead of a party of females. The dominant male would then evict other males and control the main access route into the food tree, and females would mate with this dominant male as they entered the tree to feed. Therefore, the start of feeding bouts in large patches are important mating opportunities for males. Males may also leave food patches early in order to search for more female parties and more mating opportunities. In general, lone males leave and join parties more frequently than lone females [White, 1988].

However, not all sex differences in feeding can be attributed to male–male competition for mating opportunities. Mating did not occur in most patches and males fed less than females even when there were no matings (males fed less than females in 57% of patches with no mating, same as females in 40%). When not feeding during the first third of a feeding bout, males usually rested either in or

out of the feeding tree. The difference in feeding may reflect male strategies to increase reproductive success through increased access to females. Males could influence female mate choice by allowing them to feed first. Females would then choose males based on this deference. This may be similar to the sex-for-food phenomenon that has been observed in provisioned and captive groups [de Waal, 1987; Kuroda, 1984] where sharing or transfer of provisioned food from males to females was associated with mating.

The ecological basis of female feeding priority in bonobos is related to feeding competition: in large patches, there was no significant difference between bonobo female and male feeding. Both males and females lead parties into large patches. In contrast, in small patches where food is limited, females enter the food patch first and feed more than males at the start of the bout. The positive correlation between sex difference in feeding and monopolizability of food patches can be extended to captive studies, where food sources are highly monopolizable and females feed more than males [Parish, 1994].

Economically defendable resource distribution, therefore, appears to be a necessary criterion for the evolution of female feeding priority in many species of primates. It is not, however, sufficient to cause female feeding priority to evolve. Many species feed in economically defendable food patches but show neither female social dominance nor female feeding priority. The resource distribution may render a resource defendable, but an additional factor is needed to determine which individuals will be selected to defend it.

In Malagasy prosimians, the importance of female nutritional stress, particularly during reproduction, has been suggested to be this additional selective pressure for female feeding priority. Similarly, female squirrel monkeys, as one of the smallest anthropoids that does not twin, become highly stressed during reproduction [Mitchell, 1990]. Although these stresses may provide the selective advantage to female feeding priority, it can only evolve in those species in which the ecological basis of economically defendable resources makes this strategy viable.

In contrast, bonobos do not fit an argument that female feeding priority has evolved in response to nutritional stress. This species experiences less nutritional stress due to seasonality than its congeneric chimpanzee, *Pan troglodytes*, in which males dominate food resources. Feeding priority in bonobos may therefore have evolved for different reasons.

There is evidence in bonobos that female feeding priority may be the results of both male deference, as discussed above, and the importance of female coalitions in nondyadic interactions. Although not included in the definition of female dominance examined here, the ability to form female coalitions to dominate males may be an important factor in gaining female feeding priority through male deference. Female coalitions are more likely as the number of females present increases. In bonobos, males appear deferent only in feeding contexts but are socially dominant in other contexts, and feeding parties are larger than nonfeeding parties (mean feeding party size = 7.8, SE = 0.08; mean nonfeeding party size = 6.6, SE = 0.07; Mann-Whitney $U = 193.3$; $P < 0.001$). As a fission-fusion species, female bonobos will not always be with their coalition partners. It is interesting, in this regard, that coalitions are common in captivity where females are consistently with the same partners. Furthermore, bonobo communities are made up of unrelated females [Gerloff et al., 1999] so that coalitions may only form when there is potential for individual benefit, such as during shared food defense. In a female-resident species, in contrast, female coalitions may be kin-selected in all contexts. Therefore, unlike ring-tailed lemurs

and South American squirrel monkeys, the threat of female coalition formation in bonobos is more variable. This variation may prevent female social dominance in bonobos as compared to the other two species and yet allow for female feeding priority in some contexts in this species.

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