

# **Female white-handed gibbons (*Hylobates lar*) lead group movements and have priority of access to food resources**

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## **Summary**

One of the disadvantages of group life is competition over food. How this conflict is solved is an interesting issue for sexually monomorphic species, with co-dominant sexes. Since female mammals, particularly primate females with long gestation and lactation periods, have higher reproductive costs, the question arises how this increased need translates into leadership among group members and, thus, priority of access to food resources. We investigated seven wild, pair-living and six multi-male groups of white-handed gibbons ( $N = 13$ ), in which females are expected to experience even increased rates of food competition. We examined leadership tendencies in the context of group movement, travel order, access to food resources and feeding priority (i.e., monopolizing/sharing a food patch). We found that females consistently led travel by maintaining their position at the front of groups and that traveling order amongst the entire group remained consistent between journeys. Lead females usually arrived first at food sources and tended to feed alone when food resources were limited. Female reproductive stage appeared to influence their motivation to lead, as cycling females led movements more frequently than pregnant and lactating females did. We conclude that, although appearing co-dominant, gibbon females assume a greater leadership role in coordinating group activities.

*Keywords:* feeding priority, gibbons, *Hylobates lar*, leadership, reproductive stages, travel progression.

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## Introduction

For many animals, forming groups is an advantageous strategy that allows individual members to gain better protection against predators, to out-compete groups of conspecifics over food resources and to improve breeding opportunities or information exchange (Wrangham, 1980; van Schaik, 1983; Tella et al., 1998; Meunier et al., 2006). Despite benefits associated with increased gregariousness, close spatial proximity commonly comes with costs in the form of increasing competition between individuals over limited resources. Thus, conflicts among group members may erupt at any time, for example over deciding where to search for food or which individual(s) is allowed to first access a food source. The outcome of such competition can directly affect group coordination (Biro et al., 2006). Although underlying mechanisms by which groups reach decisions and achieve coordination are generally poorly understood, two opposing processes have been suggested to explain decision making in non-human primates: (1) personal leadership and (2) distributed leadership (Leca et al., 2003; Conradt & Ropert, 2005).

The personal leadership hypothesis proposes that a single individual leads while the rest follows (unshared decision). Mountain gorillas, *Gorilla gorilla beringei*, are an example where dominant adult males usually impose their decisions on other group members by 'herding' them (Schaller, 1963). The distributed leadership hypothesis posits instead that all group members (equally shared decision, e.g., hamadryas baboons: Kummer, 1968), or only a subgroup of individuals (partially shared decision), make trade-offs to reach a collective decision (Leca et al., 2003; Conradt & Ropert, 2005). Sharing decisions, instead of accepting the decisions of a single leader, seems a more profitable strategy for gregarious individuals to both maintain group cohesion and the advantages of group life (Conradt & Ropert, 2007).

Although individual(s) at the front position of moving groups are not always the decision-makers (Boinski, 1993; Byrne, 2000), the travel directions of the lead individual(s) are likely to influence feeding and foraging opportunities (Boinski, 1991), as well as being important in territorial defense and/or encounters with predators (Rhine & Westlund, 1981). The leadership role may not be static, and may instead depend on individual motivation. Primate groups are usually comprised of individuals of different age, sex, and reproductive condition, with distinct nutritional needs, foraging tactics and susceptibility to predation. The conflicting requirements of individuals may

motivate them differently to take the leadership role in some but not in other circumstances (e.g., baboons: Muruthi et al., 1991; *Eulemur fulvus fulvus* and *Propithecus diadema edwardsi*: Erhart & Overdorff, 1999; zebras: Fischhoff et al., 2007). For example, female squirrel monkeys are usually extremely active in coordinating travel movements, but soon after giving birth, females no longer participate in leading groups, but instead take up position in the center of the troop (Boinski, 2000).

Theories and studies about the outcome of competitive situations within groups primarily focus on gregarious species, perhaps because individual relationships are more variable in larger groups and the potential for conflict and its resolutions appears, therefore, 'naturally' elevated. In contrast, within-group competition in pair-living species is usually neglected or considered unimportant (e.g., Sterck et al., 1997), although it has rarely been tested in monogamous primates.

Here, we were interested in group leadership in gibbons (family Hylobatiidae) as a reflection of potential conflict and competition between males and females. These smaller apes are sexually monomorphic, with males being only slightly larger than females (Plavcan & van Schaik, 1997) and possessing canine teeth of similar sizes (Frisch, 1963; Plavcan et al., 1995). Commonly, gibbons live in pairs suggesting that competition over access to food should be minimal. This together with sexual monomorphism suggests that aggressive interactions between the sexes will be rare, and that males and females will have the same dominance status (Carpenter, 1940; Smuts, 1987). In agreement with these theoretical expectations, overtly aggressive interactions between the sexes have not yet been reported in gibbons (Brockelman et al., 1998; Bartlett, 2007). Likewise, in this study aggressive inter-sexual exchange was rare and noticed only twice during more than 2000 hours of direct observation (C. Barelli, pers. obs.). Furthermore, gibbons are also known to sometimes live in seasonal environments with changing food availability (Savini et al., 2008). All in all, since female reproductive burdens may arise in seasonal environments, female' reproductive status may motivate gibbon females to lead groups more consistently in order to gain priority of access to food resources.

The aim of the present study was to examine if consistent sex-specific differences in leadership exist in a large population of wild white-handed gibbons (*Hylobates lar*). The study population resides in Khao Yai National Park, Thailand, and is composed of both pair-living and multimale groups

(Reichard, 2003; Barelli et al., 2007, 2008). Our null hypothesis was that no sex-specific asymmetry in leadership roles existed during (1) group travel, (2) arriving first at a food source and (3) feeding priority (monopolizing versus sharing a food patch).

If an asymmetry exists between the sexes, we expected one individual to lead group movements. Assuming that in stable social groups members possess individual recognition and social relationships (cf., Fischhoff et al., 2007), we predicted a habitual travel order among individuals of the same group. Moreover, due to the mammalian legacy of high female reproductive investment, and knowing that food limits female reproductive success, if an asymmetry between the sexes existed, it would most likely occur in the broader context of feeding. Specifically, upon examination of who entered a food source first, we predict females to arrive first more frequently during their more demanding reproductive stages (i.e., pregnancy, lactation). Additionally, looking at the proportions of visits in which adults fed together or separately, we expect females to have priority over males in cases of small food sources or if a source had little fruits.

## Methods

### *Study site and animals*

Behavioural data reported here come from approximately 2000 h of direct observations made between July 2003 and April 2005 of 13 habituated white-handed gibbon groups at Khao Yai National Park, situated in central Thailand (101°22'E, 14°26'N). Seven groups were pair-living while six comprised at least two adult males unrelated to the female and were considered multimale (see also Barelli et al., 2007, 2008). In multimale groups, we distinguished primary and secondary males by their singing and mating patterns, i.e., primary males engaged in duet singing and performed the majority of copulations with the group female (cf., Barelli et al., 2008). Study groups had up to three offspring except two groups, which did not have offspring during the time of data collection (Table 1).

Female reproductive status was assessed using previously validated measurements of fecal progesterone metabolites which enabled us to reliably determine whether a female was cycling, pregnant or in a state of lactational

**Table 1.** Social system, group composition and behavioural data collected during different reproductive stages of Khao Yai female gibbons.

	Social system	Group composition				Reproductive stage
		AF	AM	S	J <sup>a</sup>	
1	M–M	Andromeda <sup>b</sup>	2	1	1 (1999)	C
2	M–M	Daow	2	–	1 (2000)	C, P, L
3	M–M	Jenna	2	–	1 (1998)	P, L
4	M–M	Hima <sup>b</sup>	2	–	1 (1999)	C
5	M–M	Nasima	2	1	1 (2002)	C, P
6	M–M	Brenda	2	–	1 (2002)	C, L
7	P–L	Bridget	1	1	–	PR
8	P–L	Cassandra	1	1	2 (1999/2002 <sup>c</sup> )	L, C
9	P–L	Hannah	1	2	1 (2001)	L, C, P
10	P–L	Natasha	1	1	1 (1999)	C
11	P–L	Brit	1	2	1 (2002)	L, C
12	P–L	Sofi	1	1	1 (2002)	C
13	P–L	Wolga	1	1	1 (2001)	P, L

M–M, multimale; P–L, pair-living; AF, adult female; AM, adult male; S, subadult; J, juvenile; C, cycling; P, pregnant; L, lactating; PR, post reproductive.

<sup>a</sup> Juveniles' year of birth in parentheses.

<sup>b</sup> Offspring are not related to the adult female in the group.

<sup>c</sup> Second infant disappeared at approximately 1 year and 7 months of age, after a group male had changed.

acyclicity (Barelli et al., 2007; Barelli & Heistermann, 2008). Thirteen focal females were followed systematically during one or more reproductive conditions for approximately three months each. Data on female reproductive status were available for a total of ten cycling females, seven lactating females and five pregnant females, plus information on one potentially post reproductive female (Table 1). Three females (Brenda, Hima and Sofi) did not show regular hormone profiles. We considered them to be in a cycling stage and, therefore, added their data to the 'cycling female' data set, because they did not carry a nursing infant and back-counting from subsequent births indicated that they were not pregnant during the period of data collection.

#### *Leadership and travel order*

We distinguished five age-sex classes of subjects to provide information on group leadership: (1) adult female, (2) adult primary male, (3) adult sec-

ondary male, (4) subadult and (5) juvenile ( $2.5 \leq \text{age} \leq 7$  years; for age-class definitions see Reichard, 2003). For each focal female, data on occurrences of group movements were then sampled using interval scan sampling (Altmann, 1974) and, to avoid pseudo-replication, scans of travel sequences were recorded, whenever possible, every 10 min, which is an interval exceeding most travel events. The scan's starting minute was randomly chosen before each observational day and sequences were assigned by the observer whenever animals moved in line between food sources, or resting places. Only for scans in which the animal in the first position was known with certainty, was the sequence of the other subjects recorded. To determine whether females or primary males led their groups more often, the number of travels of each leader subject was then divided by the total travel events recorded and the proportions were tested using exact Wilcoxon tests (Siegel & Castellan, 1988; Mundry & Fisher, 1998). We conducted these tests separately for subjects in different reproductive stages.

Moreover, considering only sequences with at least three subjects participating, we investigated whether females or males were preferably following each other in immediate succession. For this we compared the number of cases a subject followed the leader with the corresponding expectation using an exact Binomial test (Siegel & Castellan, 1988; Mundry & Fisher, 1998). Expected values were calculated as follows: assuming the null-hypothesis that a subject chooses each available position after the leader with the same probability, it will be at the second position with probability  $1/2$  when three subjects travel,  $1/3$  when four subjects travel and so on. These probabilities, summed across all sequences and divided by the number of sequences, will then equal the expected proportion. We conducted this procedure for each female (and primary male) being the leader, separately for each group and reproductive stage.

To determine if group progression followed a preferred order, we standardized each subject's position in the travel sequence by dividing its position minus one by the number of subjects in the sequence minus one. This resulted in standardized positions, ranging from zero (first subject) to one (last subject). We then averaged the values for each combination of subjects and reproductive stages of the respective group's female. Based on this, we carried out two analyses: one included only groups in which juveniles were present and considered relative positions of the adult female, the primary male and the juvenile in the group; the second analysis included only groups

in which secondary males were present and compared the positions of adult female, primary and secondary males. We used the Friedman test to investigate these data. We correlated average positions of juveniles with their age using Spearman's rank correlation. To test whether older juveniles diverge more from the overall pattern of juveniles' moving in the intermediate position, we first calculated absolute differences between a juvenile's position and the median position of all juveniles and later correlated this with juvenile age.

#### *Order of arrival at food source*

As soon as a subject (adult females, primary and secondary males) reached a food source (cf., feeding tree), we recorded the time and order of arrival for the group. We compared proportions of initial food source entries by females or primary males using an exact Wilcoxon test (Siegel & Castellan, 1988; Mundry & Fisher, 1998), which we conducted separately for different female reproductive stages. Secondary males rarely first reached a food source or fed together with other adults and, thus, were not include in this analysis.

#### *Feeding priority*

We subdivided feeding visits at food sources into (1) visits in which the female exploited a food source while the male did not feed at all or only did so after the female had exited the food source ('female feeding priority'), (2) visits in which it was the other way around ('male feeding priority') and (3) visits in which male and female fed simultaneously ('co-feeding'). We then related these data to tree size and fruit load based on visual comparison of trees. Four categories of tree size were distinguished: 'huge' (i.e., fig trees: *Dipterocarpus* sp., approximately 35–45 m tall), 'big' (i.e., *Chorospondias* sp., approximately 20–25 m tall), 'medium' (i.e., cinnamon tree, *Cinnamomum* sp., approximately 10–15 m tall) and 'small' (i.e., rambutan trees, *Nephelium* sp., approximately 5–10 m tall).

To estimate the abundance of fruit we originally followed Savini et al. (2008) and measured abundance on a relative 0- to 4-point scale, with zero representing the absence of fruits and four the entire crown bearing fruits, which we later converted into only two qualitative classes. Fruit load was labeled as: 'few' (scores 1, 2: when the crown was almost empty or less than half of it carried fruits) or 'many' (scores 3, 4: when the crown was full or

more than half of it carried fruits). We then calculated the proportions of visits with female priority separately for each tree size and fruit load. We compared these data using a repeated measures design (ANOVA) with two within-subject factors (tree size and fruit load, both assumed to have fixed effects). Visual inspection of residuals plotted against predicted values did not indicate violations of the assumptions of homoscedasticity and normality of error variances of the data set. To correct for potential violations of the sphericity assumption we reported  $p$  values (but not degrees of freedom) based on the lower-bound correction (SPSS 15.0: Field, 2005) which is the most conservative correction applicable, leading to particularly large  $p$  values. However, this did not result in non significant  $p$  values, being significant using another or no correction.

## Results

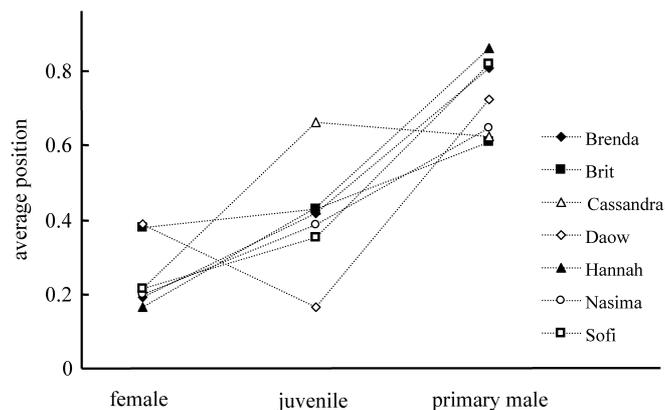
### *Leadership and travel order*

In total, the leader of the group movement was identified for 3180 events (average sequences per group = 245, range = 58–435). Although each subject class was observed to sometimes occupying the first position during travel (juveniles 12%, subadults 9% and secondary males 1%), most sequences (78%) were led by adult females (55%) and primary males (23%). Thus, our further analyses were restricted to these two subjects' classes. Overall, adult females led group movement proportionately significantly more often than primary males did (females: mean  $\pm$  SD =  $0.55 \pm 0.15$ , males: mean  $\pm$  SD =  $0.23 \pm 0.15$ , Wilcoxon test:  $T^+ = 75$ ,  $N = 12$  (1 tie),  $p = 0.002$ ) and this applied to both the pair-living and group-living situation (pair-living females: mean  $\pm$  SD =  $0.54 \pm 0.17$ , males: mean  $\pm$  SD =  $0.25 \pm 0.14$ , Wilcoxon test, pair-living groups:  $T^+ = 26$ ,  $N = 7$ ,  $p = 0.047$ ; multimale living females: mean  $\pm$  SD =  $0.56 \pm 0.12$ , males: mean  $\pm$  SD =  $0.20 \pm 0.17$ ,  $T^+ = 15$ ,  $N = 5$  (1 tie),  $p = 0.063$ ). With regard to the proportion of travel events led by the female, there was no significant difference between pair-living and multimale groups (Mann–Whitney  $U$ -test, cycling females:  $U = 11$ ,  $N_{\text{pair-living}} = 5$ ,  $N_{\text{multimale}} = 5$ ,  $p = 0.841$ ). Testing the influence of female reproductive stage on leadership revealed that only cycling females occupied significantly more often the lead position compared to primary males (cycling females: mean  $\pm$  SD =  $0.60 \pm 0.09$ , males: mean  $\pm$  SD =  $0.20 \pm 0.15$ ,

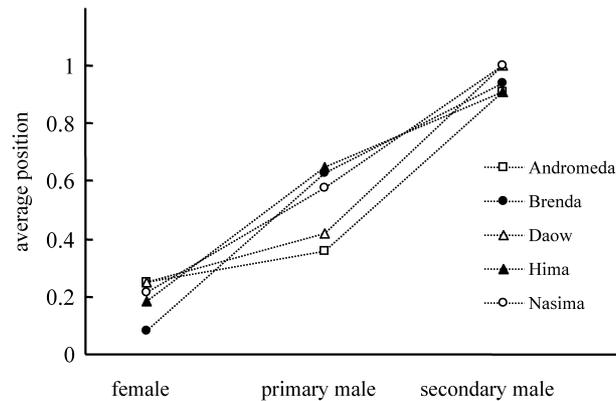
Wilcoxon test:  $T^+ = 55$ ,  $N = 10$ ,  $p = 0.002$ ), while the difference for pregnant and lactating females was not significant (lactating females: mean  $\pm$  SD =  $0.59 \pm 0.21$ , males: mean  $\pm$  SD =  $0.34 \pm 0.20$ ,  $T^+ = 19.5$ ,  $N = 7$ ,  $p = 0.406$ ; pregnant females: mean  $\pm$  SD =  $0.47 \pm 0.21$ , males: mean  $\pm$  SD =  $0.23 \pm 0.15$ ,  $T^+ = 13$ ,  $N = 5$ ,  $p = 0.188$ ).

When females led the travel, we analyzed whether primary males responded by immediately following the leading female by taking the second position depending on her reproductive stage. We found that in eight of nine groups with a cycling female, primary males followed less frequently immediately than expected by chance (Binomial test:  $p = 0.019$ ), and in five of these groups males did not significantly maintain this position (Binomial tests: all  $p < 0.001$ ). Likewise in the five groups with pregnant females, three out of five primary males did not significantly follow the females immediately (Binomial tests: all  $p < 0.01$ ).

With respect to travel order in both pair-living and multimale groups which comprised juveniles, cycling adult females led the group more frequently, whereas adult primary males were mainly found in the last position and juveniles between them (Friedman test, cycling stage:  $F = 10.29$ ,  $N = 7$ ,  $p = 0.004$ , Figure 1; pregnant stage:  $F = 2.80$ ,  $N = 5$ ,  $p = 0.367$ ). No correlation between juveniles' age and position in the sequence was found ( $r_s = 0.11$ ,  $N = 7$ ,  $p = 0.84$ ). Upon examining however, the absolute



**Figure 1.** Average position in travel sequences of subjects in groups which comprised a juvenile. Position within a travel order was standardized such that it ranged from zero (first position) to one (last position) and then averaged across all travel records and within subjects. Note that juveniles of females Cassandra and Daow were the oldest individuals in this age class in the sample.

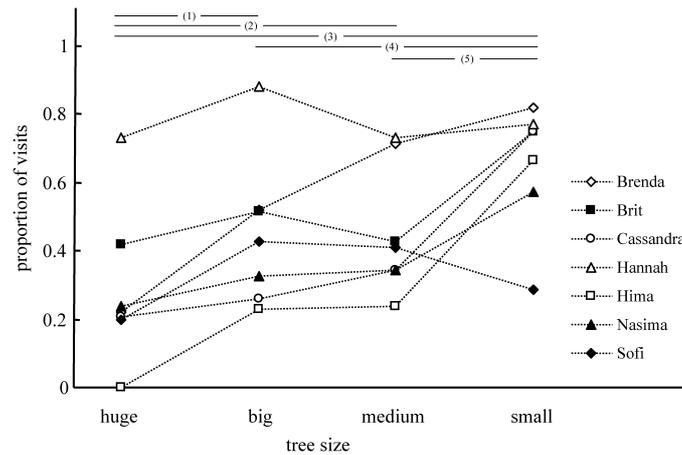


**Figure 2.** Average position in travel sequences of subjects in multimale groups. Position within a travel order was standardized such that it ranged from zero (first position) to one (last position) and then averaged across all travel records and within subjects.

differences of each juveniles' position and the median across all of them, a significant correlation with juvenile age was revealed ( $r_s = 0.82$ ,  $N = 7$ ,  $p = 0.034$ ). With respect to multimale groups, females were once again found to lead the group, with primary males mostly taking an intermediate position, followed by the secondary males ( $F = 10$ ,  $N = 5$ ,  $p = 0.001$ ; Figure 2).

#### *Order of arrival at food source and feeding priority*

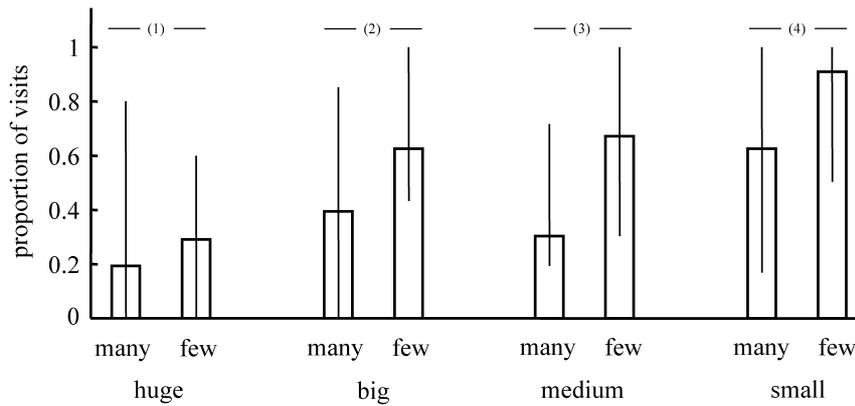
In the 1394 arrivals at food sources recorded, adult females first entered the source significantly more often than primary males (females: mean  $\pm$  SD =  $0.90 \pm 0.08$ , males: mean  $\pm$  SD =  $0.10 \pm 0.08$ , Wilcoxon test:  $T^+ = 55$ ,  $N = 10$ ,  $p = 0.002$ ; no data available for females Andromeda, Bridget and Natasha). Disregarding reproductive stage and separating the sample into pair-living and multimale group living females, females still tended to arrive at the food sources before the males (pair-living females: mean  $\pm$  SD =  $0.90 \pm 0.06$ , males: mean  $\pm$  SD =  $0.10 \pm 0.06$ , Wilcoxon test:  $T^+ = 15$ ,  $N = 5$ ,  $p = 0.063$ ; multimale living females: mean  $\pm$  SD =  $0.90 \pm 0.10$ , males: mean  $\pm$  SD =  $0.10 \pm 0.10$ ,  $T^+ = 15$ ,  $N = 5$ ,  $p = 0.063$ ). Comparable results were obtained when the analyses were conducted separately according to female reproductive stage (cycling females: mean  $\pm$  SD =  $0.91 \pm 0.07$ , males: mean  $\pm$  SD =  $0.09 \pm 0.07$ , Wilcoxon test, cycling stage:  $T^+ = 36$ ,  $N = 8$ ,  $p = 0.008$ ; pregnant females: mean  $\pm$  SD =



**Figure 3.** Proportions of visits during which cycling females exploited the food sources alone in relation to food source size: huge, big, medium and small. (1):  $T^+ = 28$ ,  $N = 7$ ,  $p = 0.016$ ; (2):  $T^+ = 21$ ,  $N = 6$  (1 tie),  $p = 0.031$ ; (3):  $T^+ = 28$ ,  $N = 7$ ,  $p = 0.016$ ; (4):  $T^+ = 25$ ,  $N = 7$ ,  $p = 0.068$ ; (5):  $T^+ = 25$ ,  $N = 7$ ,  $p = 0.078$ .

$0.90 \pm 0.07$ , males: mean  $\pm$  SD =  $0.10 \pm 0.07$ ; pregnant stage:  $T^+ = 15$ ,  $N = 5$ ,  $p = 0.063$ ). Sample size for lactating females was too small to test for significant differences, but the available data on three females indicated similar proportions of first entry into food sources compared to the other two reproductive stages (85% of times first entry of lactating females compared to 90% in cycling and pregnant females).

With respect to cycling females, small food sources were more often exploited by females alone than were larger sources (repeated measures ANOVA:  $F_{3,12} = 62.5$ ,  $p < 0.001$ ; Figure 3). In fact, in six out of seven groups, when a food source was small, the female fed alone more frequently than both subjects fed together, whereas in huge food sources this was true for only one group. For big and medium size trees findings were intermediate. Comparing trees with few and many fruits revealed that females were more frequently feeding alone in trees that provided few fruits than in trees with many fruits (ANOVA:  $F_{1,1} = 15.1$ ,  $p < 0.02$ ; Figure 4). The interaction between tree size and fruit load was not significant (ANOVA:  $F_{3,12} = 0.83$ ,  $p > 0.42$ ), suggesting that female priority in accessing trees with ‘few’ fruits was not influenced by the size of trees and nor was female priority in accessing small trees influenced by the amount of fruits available.



**Figure 4.** Median (min and max) of proportions of total visits ( $N = 688$ ) performed by cycling females alone, separated by tree size category (huge, big, medium and small) and fruit load (many and few fruits). (1):  $T^+ = 12$ ,  $N = 6$ ,  $p = 0.84$ ; (2):  $T^+ = 27$ ,  $N = 7$ ,  $p = 0.03$ ; (3):  $T^+ = 28$ ,  $N = 7$ ,  $p = 0.02$ ; (4):  $T^+ = 17$ ,  $N = 6$ ,  $p = 0.22$ .

## Discussion

Based on the results of this study, gibbon females assume a greater leadership role in coordinating group movement than males. As predicted for sexually monomorphic species, clear inter-sexual dominance does not exist in gibbons and, thus, no personal leadership, in terms of a single dominant individual leading the entire group, was found. However, although each class of subjects (e.g., adults, subadults and juveniles) could assume the front position during movements, only adult females succeeded in doing so more frequently than other group members. They lead travel movements by consistently maintaining the front position and, presumably as a direct consequence, they arrived first at food sources more often than males. Moreover, when food sources were limited, small in size or scarce in fruit, females fed more often alone than together with males. Assuming reproductive females have higher energetic costs than males, taking leadership in terms of coordination of group movements, access to food sources and monopolization of food resources might be optimal strategies to be adopted by species where both sexes are similar in body mass and weaponry (Jolly, 1984; Young et al., 1990).

Adult individuals led more frequently the travels than subadult and juveniles, a finding which is not unexpected given that young animals possibly do not have the energy to lead group movements for prolonged time (e.g., may not be able to maintain the average speed needed for leading a group).

Interestingly, females led more frequently group movements than males irrespective of social organization (pair-living versus multimale), but not of their reproductive stage. In fact, only cycling females led travel movements statistically more often than males, while pregnant and lactating females did not differ from males in proportions of leadership. Due to the highest energetic costs faced by pregnant and lactating females, we would have predicted opposite results. However, considering the new findings on gibbons' socio-sexual strategies and the active role females play in mating activity (Barelli et al., 2007, 2008), one plausible explanation of cycling females traveling in the front position might relate to non-ecological factors. Females who lead the travels might actively make decisions in terms of exploring their own territory and meeting neighbouring groups, which may likely enhance their chance to meet with other potential mates. Whereas the lack of statistical significance obtained from pregnant females might be due to the small sample size tested (only five females), the findings that lactating females lead less often than males can be interpreted as a response to possible risks infants may encounter if females consistently traveled in the front position, as also found in other primate species (e.g., squirrel monkeys: Boinski, 2000). In fact, although animals at the vanguard of the group are most likely to encounter food sources first (Boinski, 1991; Erhart & Overdorff, 1999; Fischhoff et al., 2007), they are also more likely to encounter predators (Rhine, 1975; Rhine & Westlund, 1981) or neighbouring groups which might be risky for females carrying small infants. An alternative, but not mutually exclusive explanation would be that lactating females do not often lead the group because they adjust to the cruising speed of their young. Whether leadership of travel by female gibbons is merely a result of physical restraints as a function of female reproductive condition or more influenced by socio-ecological contexts is difficult to test since both factors cannot be easily disentangled. However, although speculative, females may still maintain a leading role in terms of deciding where to go and, thus, have priority of accessing food resources, as supported by our data.

Another interesting finding regarding group movements concerns the travel order each group member exhibits during travel progressions. Our results show that across groups each subject class consistently maintained a certain position. Females usually led the travel, followed by young juveniles and these by primary males, whereas in multimale groups secondary males were observed mostly in the last travel position. These findings are

in line with the assumption that males might benefit their offspring by both (1) deferring the vanguard position to females to let them reach feeding sites first and (2) directly protecting the juveniles from imminent danger. As reported in yellow baboons, weaned juveniles are more likely to be attacked than other group members, and by occupying intermediate positions during travel, they might gain protection from adults (Rhine et al., 1981). The two juveniles which did not follow this pattern were both the eldest juveniles in our data set, which perhaps reflected the transitional stage of older juveniles in becoming subadult individuals, which commonly explore the territory and travel more independently from the adults. However, more data are necessary to fully understand the effect of age on travel order in gibbons.

When we examined the proportions of visits to food sources in which males and females could feed, we found a relationship between feeding priority, tree size and fruit load. When exploiting limited resources, females shared less frequently the same food source with males, which were commonly observed to rest and wait on a neighboring tree until the female left the food tree. However, both animals fed together when food sources were huge or smaller but full of fruits. Because gibbons are considered fruit specialists (Vellayan, 1981; Chivers, 1984), showing preference for ripe fruits, which are not abundant year-round (Savini et al., 2008), we expected competition over preferred food. As found in a few other primate species (e.g., *Indri indri*: Pollock, 1977, 1979; ring-tailed lemurs: Pereira et al., 1990; bonobos: White & Wood, 2007), our data, however, suggest that females and males try to reduce feeding competition whilst, and at the same time, may benefit from enhancing their reproductive success. For example, as already suggested in other primate species, males who have mated with a female may benefit indirectly from deferring access to food resource to females in order to enable successful weaning/survival of 'their' infants (e.g., lemurs: Pollock, 1979; Hrdy, 1981; Sauther, 1993).

In conclusion, the sex-specific asymmetry in leading group movements and maintaining a travel order, accessing and monopolizing food resources, indicate that gibbon females play an active role, although, further studies on the initiation of group movements and vocalizations used in this context will better elucidate the role of females in the decision-making process.

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