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ORIGINAL ARTICLE

Leadership of old females in collective departures in wild bonobos (*Pan paniscus*) at Wamba

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Abstract

Group-living animals need to coordinate their activity in order to maintain gregariousness. Although individuals have their own nutritional, social, and reproductive needs, they have to reach consensus to decide where and when to travel. Collective movements are the outcome of one individual's departure, who is then followed by other group members. We investigated departure initiation in a group of bonobos at Wamba, DR Congo, to determine the distribution of leadership among group members. If three or more bonobos started moving more than 30 m, we assigned the individual who moved first as the one who initiated the movement. Two hundred and fifty-four departures were observed. First, we examined whether the frequency of initiation differed according to the following attributes of individuals: sex, age, stage in sexual swelling cycle, dominance, and affiliative relationship. We also examined whether one or more individual(s) initiate departure more or less frequently than expected by chance. A significant interaction between sex and age was found, indicating that the effect of age was greater among females than among males. Individuals who were more central to the grooming network initiated departures more frequently. The three oldest females initiated more often than expected. Old females may be followed because of coalitionary supports they often give to younger females, and of their greater knowledge about ranging area. Leadership in bonobos was not equally shared among group members, and old females were "key individuals" who helped to maintain cohesiveness in their fission-fusion society.

Significance statement

When group-living animals travel from one location to another, they must coordinate when and where to travel; otherwise, they might spread apart. Bonobos are one of our closest living relatives and have a fission-fusion social system. We investigated the initiation of group departure in wild bonobos to determine the distribution of leadership among group members. We found that the frequency of initiation was associated with the individual's age, affiliative relationships, and male dominance rank. The three oldest females initiated departures more frequently than expected, suggesting that these individuals were habitual initiators and took an important role to preserve cohesiveness. We discuss how this "old female leadership" may emerge in a male-philopatric society.

Introduction

Aggregating with conspecifics provides advantages, such as reducing predation risk, opportunities for social learning, and collectively protecting valuable resources (Fashing 2001; Childress and Lung 2003; Aplin et al. 2015). However, individuals need to synchronize their activities and maintain cohesiveness in order to benefit from these advantages, which may come at a cost to the nutritional, social, and reproductive needs of the individual (King and Sueur 2011; Sueur et al. 2013b). In particular, when the group travels from one

location to another, its members must coordinate when and where to travel; otherwise, they might fission (King and Sueur 2011). Some individuals might have to shorten their resting time when the group starts to travel, while others might have to wait until the group finishes feeding before they can depart. According to the costs and benefits of association, animals form various types of aggregations from cohesive groups, in which stable members always move together, to fission-fusion societies, in which either stable or flexible individuals aggregate when the benefits of aggregation exceed its costs (Aureli et al. 2008).

The process of decision-making during collective movement has gained much attention over the past several decades, being described in various animal species including insects, fish, birds, and mammals (Conradt and Roper 2005; Petit and Bon 2010). When individuals form a large group, such as a flock of birds or a school of fish, each individual follows a set of simple rules to synchronize the movement and maintain cohesiveness, for example, adjusting direction and speed to that of neighboring individuals (self-organizing system: Couzin and Krause 2003; Sumpter 2006). On the other hand, in species that form a stable and cohesive social group, wherein group members are able to communicate before or during travel, one or several individual(s) may lead the groups' movement while others follow; this is the concept of "leadership" (King 2010).

When all group members initiate departure or equally share the role of walking in the leading position, the leadership style is called "equally shared consensus" (Pyritz et al. 2011). In Tonkean macaques (Macaca tonkeana), all individuals, including immature ones, initiate departure at the same frequency (Sueur and Petit 2008; Bourjade and Sueur 2010). At the other extreme is the "unshared consensus" (Pyritz et al. 2011), when one individual always leads the group's movement. For example, in the mountain gorilla (Gorilla beringei beringei), the dominant silverback initiates all group movements (Schaller 1963; Watts 2000). The "partially shared consensus" style (Pyritz et al. 2011) is intermediate to the two extremes and is most commonly observed among mammals (Smith et al. 2015). In this style, leadership is distributed among group members, but unequally. Individuals with particular attributes are more often observed to initiate group departures or walk in the front position while traveling (King 2010; Smith et al. 2015).

In some species, females lead group movements more frequently than do males. Such "female leadership" is commonly explained by the females' relatively high motivation to find food at the next destination, since they typically require more energy than males for reproduction (e.g., Boinski 1991; Erhart and Overdorff 1999; Fischhoff et al. 2007; Barelli et al. 2008). Moreover, in the plains zebra (Equus quagga), pregnant or lactating females are more likely than others to travel in front of the group, possibly because these females have markedly high nutritional needs (Fischhoff et al. 2007; also see Furrer et al. 2012), although some studies failed to detect similar results (Stueckle and Zinner 2008; Barelli et al. 2008; Belle et al. 2013). In addition, females displaying sexual signals attract males (Nunn 1999), who may then follow them. Female sexual attractiveness may influence collective group movement and partly explain female leadership.

Experience is also an important factor (King et al. 2009). In an experimental study using homing pigeons (Columba livia domestica), individuals who had more experience flying the route led the flock more frequently than did less experienced individuals (Flack et al. 2012; but see also Flack et al. 2013). Also, McComb et al. (2011) found that groups of African elephants (Loxodonta africana) that were led by older matriarchs were able to make better decisions when faced with dangerous situations. Older individuals might have more knowledge of their range and be better equipped to lead group members to better feeding or safer resting places (McComb et al. 2001, 2011; Brent et al. 2015).

Social relationships within the group, both agonistic and affiliative, affect the distribution of leadership (King et al. 2009). In species with a steep dominance hierarchy and intolerant social relationships, higher-ranking individuals often lead group movements (e.g., Squires and Daws 1975; Peterson et al. 2002; Sueur and Petit 2008; King et al. 2009; Bonnani et al. 2010; Flack et al. 2013). On the other hand, leadership is more likely to be distributed equally in species with a weakly linear or non-linear dominance hierarchy and tolerant social relationships (Squires and Daws 1975; Sueur and Petit 2008; Fernández et al. 2013). In species that engage in affiliative interactions, such as grooming and greeting other group members, individuals with strong social affiliations tend to be followed more often (King et al. 2008, 2009; Sueur et al. 2013a). For example, in Tibetan macaques (Macaca thibetana), individuals with higher eigenvector centrality in the proximity network, and those who spent more time grooming, successfully initiated departures more frequently than did asocial individuals (Wang et al. 2016).

In species characterized by fission-fusion grouping, leadership by a specific individual(s) is perhaps unlikely because the membership of subgroups varies from time to time (Fischhoff et al. 2007). Nonetheless, recent empirical studies revealed that consistent leadership can also be exhibited by certain individuals living in fission-fusion societies (Lewis et al. 2011; Smith et al. 2015). This might be because associating with these individuals benefits followers, and such benefits surpass the cost of association. Bottlenose dolphins (Tursiops truncatus) encountered abundant food resources more frequently when they were led by habitual leaders than when they were led by other individuals (Lewis et al. 2013). Similarly, subordinate spotted hyenas (Crocuta crocuta) follow the movement of dominant females, expecting long-term benefits in the form of increased social and feeding tolerance

gained from frequent association with dominants (Smith et al. 2008, 2015). However, information on leadership patterns in fission-fusion societies is still scarce.

Bonobos (*Pan paniscus*) are, evolutionarily, one of our closest living relatives, and live in male-philopatric, multi-male/multi-female social groups of stable membership (Kano 1982; Eriksson et al. 2006; Sakamaki et al. 2015). They mainly feed on ripe fruit (Kano and Mulavwa 1984; White 1998) and have a fission-fusion association pattern in which a group splits into temporary subgroups ("parties"; Kano 1982). Although bonobos were reputed to be egalitarian (de Waal 1997), some studies have shown that male bonobos have a linear, steep dominance relationship (Stevens et al. 2007; Surbeck et al. 2011). However, researchers agree that bonobos are highly tolerant, as dominants and subordinates engage in close relationships, with low levels of violence and high levels of tolerance around contested resources, especially among females (Kano 1992; Parish 1994; Furuichi 1997; Vervaecke et al. 2000; Hare et al. 2007).

Bonobo society is unique among male-philopatric societies, in that female-female pairs associate as frequently as, if not more than, male-male or (non-related) male-female pairs (Kuroda 1979; White 1988, 1998; Kano 1992; Furuichi 2009, 2011; Hohmann and Fruth 2002). Females frequently form coalitions, which might be important for preventing male harassment (Kano 1992; Parish 1996; White and Wood 2007; Furuichi 2011; Tokuyama and Furuichi 2016). Such coalitions have a unidirectional relationship, in which older females support younger ones, making associations with older females potentially very beneficial for younger ones (Tokuyama and Furuichi 2016). Possibly because of this benefit, young female bonobos actively keep close association and interact with older females (Furuichi 1989; Idani 1991). This leads to the prediction that cohesiveness of female bonobos in their fission-fusion society may be maintained by the motivation of younger females to follow older ones. Anecdotal observations also suggest that old females play an important role in bonobos' party movement. Before traveling, bonobos typically descend from tall fruiting trees and take a short break (Furuichi 2011). During this time, some of the males climb down and perform branch-dragging behavior, but the entire party does not move until the old females climb down and initiate movement in a direction of their own choice (Furuichi 2011). However, this observation has yet to be tested in a systematic study.

The goal of this study was to examine the distribution of leadership during group travel in wild bonobos. Here, we focused on determining which factors affect the direction and timing of departure (i.e., initiation; Pryitz 2011) during group movement, recognizing that individuals who initiate departure do not necessarily continue to walk in the leading position (Pryitz 2011; Belle et al. 2013). Drawing on past studies, we propose the following predictions, which are not mutually exclusive:

- Because animals with high nutritional needs may determine the timing of departure, females will initiate departures more frequently than males.
- Because maximally tumescent females may attract sexually mature males and provoke collective departures, females initiate departure more frequently when they are with maximal swelling, compared to when they are with non-maximal swelling.
- Because of the benefits of following a knowledgeable, experienced individual, older individuals will initiate departures more frequently than younger ones. In addition, because younger females may benefit from agonistic support by older females against male harassment, the age effect will be larger among females than among males.
- Because of the tolerant social relationships in bonobos, dominance does not affect the frequency of initiation, and none of the group members will initiate departures more or less frequently than expected.
- Because of the affiliative relationships in the group, individuals with a higher value of eigenvector centrality in grooming networks will initiate departures more often than individuals with smaller values.

Methods

Study site and subjects

Observations were conducted on the "PE group" of wild bonobos in the Wamba, Luo Scientific Reserve, Democratic Republic of the Congo, where long-term research has been conducted since 1973 (Kano 1992; Tokuyama and Furuichi 2016).

At the time of this study, PE group consisted of 26–27 individuals. All individuals were already identified and habituated before the beginning of the study period. Our study subjects were individuals older than 8 years, excluding one female who emigrated during the study period (15 individuals: nine females and six males; Table 1). Data from females who temporarily visited this group were not analyzed. We estimated each subject's age based on physical features. The kin relationships among study subjects were unknown, except for Ic, the known mother of IR.

Behavioral observation

NT observed bonobos for 1698 h, with the help of two local assistants, from August to November 2012, August 2013 to January 2014, July to September 2014, and January to June 2015. We recorded 1-h party size, i.e., all individuals seen within 1 h (1-h party method: Hashimoto et al. 2001; Mulavwa et al. 2008). We continuously recorded "general

Table 1 Study subjects with estimated age, dependent offspring, social dominance, value of eigenvector centrality coefficient in the grooming network, number of attendance in collective departures, and number of initiation of collective departures

ID (abbreviation)	Sex	Estimated age in 2012	Dependent offspring (born year)	Dominance rank	Eigenvector centrality coefficient in grooming network	The number of attendance in departures	The number of initiation of departures
Bokuta (Bk)	F	49	–		0.056	101	46
Kabo (Kb)	F	39	2006, 2012		0.26	176	73
Hide (Hd)	F	35	2006, 2011		0.24	147	38
Maluta (Mt)	F	27	2006, 2012		0.41	97	5
Pao (Po)	F	21	2009, 2013		0.26	144	25
Ichi (Ic)	F	21	2007, 2012, 2015		0.37	106	13
Saku (Sk)	F	17	2009, 2013		0.10	90	4
Marie (Mr)	F	12	2014		0.24	111	2
Nara (Nr)	F	11	2014		0.24	69	2
Gai (GI)	M	39		5	0.20	67	6
Malusu (ML)	M	30		3	0.23	90	5
Snare (SN)	M	21		1	0.31	102	17
Turkey (TK)	M	20		2	0.33	128	13
Daniel (DN)	M	17		4	0.21	66	4
Ikura (IR)	M	8		6	0.15	54	1

activity"—the activity in which the majority of the party members were engaging (i.e., resting, feeding, and traveling).

We also recorded grooming interactions by instantaneous scan sampling (Altmann 1974); at 5-min intervals and for all visible individuals, we recorded whether they were grooming with any other individuals. 5403 ± 1491 scan samples per subject individual (average $\pm$ SD) were collected. The grooming index was calculated as follows: number of scans a pair was seen to be grooming, divided by the number of scans the pair was found in the same scan. The eigenvector centrality coefficient for each individual was calculated from the grooming index, using UCINET software (Table 1). To assess the dominance relationships, we recorded all observed dyadic aggressive interactions. The firmness of each female's sexual swelling was scored daily (see Ryu et al. 2015 for details). It was not possible to record data blind because our study involved wild animals in the field.

For each departure, the individual who started to move first was defined as the initiator. We recorded the identity of the initiator and other subjects who followed them. Each follower had to join the departure <1 min after the previous follower moved. Collective departures were defined as occurring when at least three individuals moved in the same direction for more than 30 m horizontally, without stopping, and after engaging in an activity (other than traveling) for at least 5 min. These parameters were defined during a pilot study conducted 2 months prior to this study period (Pyritz et al. 2010). For this study, we used the departures in which the initiator-follower relationship was clear. For example, when two animals started moving simultaneously and other individuals

joined the movement, we discarded the data because we could not determine who the initiator was. We also excluded cases where the initiator did not move with followers for more than 30 m, i.e., when other individuals continued traveling even though the initiator stopped before having traveled 30 m.

For each individual, we calculated the frequency of being an initiator through an "Initiation Index." The Initiation Index of an individual (A) was calculated as follows:

$$\text{Initiation Index (A)} = \frac{\text{the number of observed departures that (A) initiated}}{\text{the number of observed departures that (A) participated in.}}$$

In this study, we refrained from recording cases in which one or two individuals left the party, because such individuals often leave the party quietly and it is difficult to observe them in dense vegetation. Branch-dragging, considered to be a pre-departure behavior in bonobos (Ingmanson 1996), was not analyzed in this study because branch-dragging was suggested not to be associated with the timing and direction of departures (Furuichi 2011). Also, branch-dragging is used as a displaying behavior by males (Kano 1992), and it is difficult to distinguish between these two forms of the behavior.

Data analysis

We used two approaches: attribute-based analysis and individual-based analysis. All statistical analyses were conducted using R version 3.2.3 (R development Core team 2008), with a 95% confidence level. Probabilities between 5 and 10% are reported as trends.

The attribute-based analysis

We examined whether the frequency of initiation differed according to the attributes of individuals: sex, age, stage of sexual swelling, dominance, and affiliative relationships. We did not assess the reproductive status of females, because their sexual swellings also come into maximal tumescence during pregnancy and lactation (Furuichi 1987; Douglas et al. 2016), which makes the status (pregnant, lactating, or cycling) of each female difficult to determine. We ran a generalized linear model (GLM) to examine the effect of age, sex, and sociality on the Initiation Index. Initiation Index for each individual was used as a predictor using the "c-bind" function and binomial error distribution. We used estimated age (in 2012), sex, value of eigenvector centrality in the grooming network, and interaction of age and sex as fixed factors.

The effect of dominance status on the Initiation Index was examined only in males because the dominance hierarchy among females was not significantly linear (calculated by ADAGIO, Douglas et al. 2017; h' = 0.39, ns), probably because of the small number of dyadic agonistic interactions (see Supplemental Table 1). The male dominance hierarchy was determined using the outcome of dyadic male-male aggression. From August 2012 to March 2015, the dominance hierarchy among males was stable and the alpha-male was SN. However, after multiple individuals severely attacked SN on March 5, 2015, his dominance status dropped to the rank of third or fourth (NT and T. Sakamaki, personal observation). Because of this drastic change in dominance hierarchy, we only used data for initiation of departures and agonistic interactions observed *before* March 4, 2015, to examine whether dominance status affected the male Initiation Index. Data obtained after March 4, 2015, were not used for this analysis. The dominance hierarchy between August 2012 and March 4, 2015, was significantly linear (ADAGIO, h' = 1.0, $p < 0.01$) and was not significantly correlated with age (Pearson's product-moment correlation test, $r = -0.32$, df = 4, $p = 0.53$). We tested the effect of dominance rank on the Initiation Index using Pearson's product-moment correlation test.

We calculated two Initiation Index values for each female—with and without maximal sexual swelling—and compared these by paired t test to examine whether the stage of a female's sexual swelling affected their Initiation Index.

Individual-based analysis

To determine whether specific individual(s) initiated departures more or less often than expected, we compared the number of times each individual initiated a departure with the expected number, based on 1000 randomized iterations for each individual (randomization protocol: Manly 2006; see also Lewis et al. 2011). For all departures in which an individual participated, we randomized the order of individuals and counted the number of departures in which the individual was in the first position, repeating this procedure 1000 times for each individual. Then, we compared the observed number to the distribution of the expected number of departures for which the individual was the initiator. We considered that an individual initiated departures more often than expected if the observed number was greater than 97.5% of the randomization distribution, and less than expected if the observed number was less than 2.5% ($p < 0.05$ for a two-tailed test).

Results

Parties were composed of 9.8 ± 3.2 individuals (mean ± SD, 6.0 females and 3.8 males) during the observation period. We observed 254 successful departures. Departures contained 6.1 ± 0.2 individuals (mean ± SE, 4.1 females and 2.0 males). Of the 255 successful departures, 208 (82.0%) were initiated by females and 46 (18.0%) by males. All individuals were observed to initiate departures at least once (Table 1).

Sex, age, and sociality of the individual

Interaction between age and sex showed a significant effect on the Initiation Index (GLM, Table 2). This was due to the fact that older females were more likely to initiate movement than younger females, while initiation of movement by males was little influenced by age (Fig. 1). Eigenvector centrality coefficients in the grooming network were positively correlated with the Initiation Index (GLM, Table 2).

Social rank among males

Among males, dominant individuals tended to have a higher Initiation Index than subordinates (Pearson's product-moment correlation test, $r = -0.76$, df = 4, $p = 0.08$).

Stages of sexual swelling among females

Departure initiation frequency for females did not vary according to the firmness of sexual swellings (paired t test, $t = 1.82$, df = 8, $p = 0.11$). Nor did the number of male or female followers significantly increase when the initiator was maximally swollen (female initiator with maximal swelling ($n = 115$) vs. female initiator with non-maximal swelling ($n = 93$): 1.88 male followers vs. 1.93 male followers; Wilcoxon rank sum test, $W = 5783$, $p = 0.31$; 4.16 female followers vs. 4.23 female followers, Wilcoxon rank sum test, $W = 5699$, $p = 0.49$).

Table 2 The effect of age, sex, and the value of eigenvector centrality on the Initiation Index. Overall, the model was statistically significant ($p < 0.01$)

	Estimates	SE	z	p
Intercept	−4.46	0.48	−9.25	
Age	0.075	0.0093	8.13	
Sex	1.36	0.55	2.47	
Centrality in grooming network	1.91	0.90	2.12	0.034
Sex × age	−0.067	0.021	−3.23	<0.01

Individual-based differences in initiation

Three females (Bk, Kb, and Hd) initiated departures more frequently, and three males (ML, GI, and IR) and four females (Mt, Sk, Mr. and Nr) did so less frequently than expected by chance (Fig. 2). The three who initiated departures more frequently than expected were the oldest individuals among females in this study group.

Discussion

We examined the initiation of departures in wild bonobos, who have a fission-fusion grouping pattern and are considered to be one of the most tolerant primate species. Species with high levels of social tolerance tend to have equally shared consensus leadership (Sueur and Petit 2008; Petit and Bon 2010; Fernández et al. 2013). We found that all individuals initiated departures at least once. However, both our attribute-based and individual-based analyses showed that the frequency of initiation was greatly skewed, suggesting that wild bonobos in this study exhibited a rather strong "partially shared consensus" leadership (Pyritz et al. 2011).

We found that age had a greater effect among females than among males. In previous studies, the tendency for older individuals to lead group movements more often than younger individuals was detected mostly among females. For example,
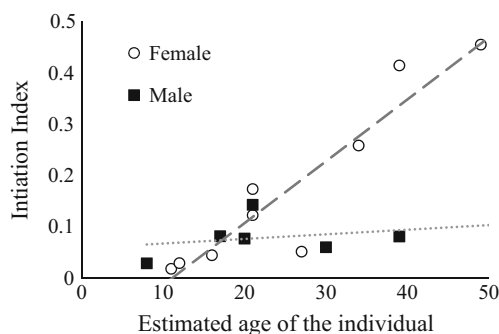

Fig. 1 The effect of age and sex on Initiation Index. *White dots* represent independent females. *Black squares* represent independent males

such tendency was observed in African elephants (*Loxodonta africana*; McComb et al. 2001) and in giraffes (*Giraffa camelopardalis*; Berry and Bercovitch 2015), both of which have grouping patterns in which females aggregate while males do not often associate with other individuals. Killer whale females live more than 30 years after menopause (ca. 35 years old), whereas most males die before reaching 35 years, and these post-menopausal females tend to be in the lead position during group movement (Brent et al. 2015). Post-menopausal females are observed in the lead position more frequently in times of food scarcity, suggesting that younger killer whales may rely on the greater knowledge of post-menopausal females to find prey (Brent et al. 2015). In our study, the effect of age on Initiation Index was also greater among females than among males. This tendency might reflect differences in reproductive strategies between the sexes; the reproductive success of females depends on feeding efficiency, while that of males depends on mating opportunities (Trivers 1972).

The other possible explanation as to why the effect of age was stronger among females might be that younger females follow older ones because of the benefits they get from coalitions (Tokuyama and Furuichi 2016). Despite living in a male-philopatric society, female bonobos are more cohesive and centralized in the party than males (White 1988, 1998; Kano 1992; Parish and de Waal 2000; Hohmann and Fruth 2002; Furuichi 2009, 2011). They form coalitions more frequently than do males (Stevens et al. 2006; Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016). Furthermore, older females actively give agonistic support to younger females when the latter are harassed by males (Tokuyama and Furuichi 2016). The benefit of coalitionary support might contribute to the greater effect of age on the Initiation Index among females compared to males.

Among males, dominant ones tended to have higher initiation indices, although this was not found to be statistically significant. In all captive and wild bonobo groups, some females clearly possess higher social ranks than males (Furuichi 1997, 2011; Vervaecke et al. 2000; Surbeck and Hohmann 2013). We could not determine a linear dominance hierarchy containing both males and females in this study, because the number and combinations of dyadic inter-sex aggression were too few. However, the three oldest females, who initiated departures more frequently than expected, won 84% of inter-sex dyadic agonistic interactions during the study period (Tokuyama and Furuichi 2016), suggesting that these females were apparently dominant over the males in the study group. This dominance structure might have contributed to the distribution of the initiation of departures in this group of bonobos.

Prolonged maximal sexual swelling periods are a conspicuous aspect in bonobos (Furuichi 1987; Kano 1992). Although female chimpanzees exhibit maximal sexual swelling only when they are fertile, female bonobos do so and

Fig. 2 Initiation Index of each individual (see Table 1 for IDs and abbreviations). *One asterisk* means that the individual initiated departures more frequently than expected. *Two asterisks arranged in tandem* mean that the individual initiated departures less frequently than expected
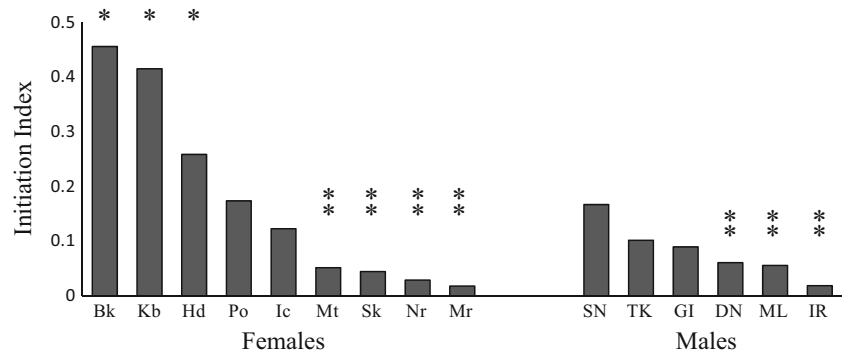
copulate even during non-ovulatory periods (Furuichi 1987; Reichert et al. 2002; Douglas et al. 2016). Although we predicted that the movements of females with maximal swelling may attract males and provoke collective departures, females with maximal swelling did not initiate departures more frequently compared to those without maximal swelling. Also, the number of male and female followers did not significantly increase when the initiator was a female with maximal swelling. Further studies that include hormonal analyses are needed to investigate whether females initiate departures more frequently when they are in the peri-ovulatory period than when they are not. Such studies may help understand whether male bonobos are able to discriminate when females are ovulating in their prolonged maximal swelling period.

Eigenvector centrality coefficient in grooming networks was positively correlated with the Initiation Index. Social grooming is an important social tool in non-human primates for constructing and maintaining social bonds. Higher centrality in grooming networks suggests that the individual is more strongly connected with other group members. Departures by such individuals might elicit a reaction from followers more efficiently than departures by individuals with fewer connections (King et al. 2008; Sueur et al. 2013a; Wang et al. 2016). However, it is worth noting that the oldest female, Bk, who had the highest Initiation Index in the group, also had the lowest eigenvector centrality coefficient value in the grooming network.

Three females initiated departures more frequently than expected in the individual-based analysis. Although leadership by a restricted set of individuals is considered less likely in a fission-fusion society (Fischhoff et al. 2007), recent studies, including this one, are revealing that the relationship of habitual leaders and followers *does* emerge in fission-fusion societies. About 20% of individuals consistently acted as leaders of group movements in bottlenose dolphins, another dynamic fission-fusion grouping species (Lewis et al. 2011, 2013). The spotted hyena also exhibits a flexible fission-fusion society, and individuals usually follow the movement of the most dominant female in the subgroup (Smith et al. 2015). Individuals may be motivated to associate with a specific individual(s), for example, to benefit from experienced

individuals (this study; Lewis et al. 2013), to engage in tolerant relationships by frequent associations (Smith et al. 2015), or to obtain coalitionary support (this study; Tokuyama and Furuichi 2016).

Although equally shared consensus leadership has the lowest consensus cost to group members (Conradt and Roper 2003, 2007), it seems the distribution of individuals in leadership roles is skewed in all group-living great apes. Although there is no systematic study, it has been reported that mountain gorillas have personal leadership, wherein the dominant silverback leads group movements (Schaller 1963; Watts 2000), and also that dominant male chimpanzees coordinate group movements (Boesch and Boesch-Achermann 2000). In bonobos, we found that the leadership of group departures was partially shared and that old females most frequently dictated the timing of departures.

Human societies exhibit skewed leadership when groups engage in consensus on decision-making. Great variations exist in the strength and type of leadership, from despotic to democratic and female-led to male-led (Vugt 2006). Great apes are known to exhibit rather diverse and flexible social patterns within species. Feeding habits and social organization vary among subspecies of gorillas (Yamagiwa et al. 2003). Food availability, patterns of fission-fusion dynamics, strength of social bonding, and dominance steepness are different between groups of chimpanzees and bonobos (Boesch et al. 2002; Lehmann and Boesch 2008; Kaburu and Newton-fisher 2015). A comparison of the leadership distribution among (sub-) species, and even among groups of great apes with different social patterns, might give us important insights into the emergence and evolution of various types of leadership roles in humans.

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