Low Resistance of Senior Resident Females Toward Female Immigration in Bonobos (*Pan paniscus*) at Wamba, Democratic Republic of the Congo

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Abstract

Female aggression against outgroup conspecifics is an important aspect of intergroup relationships among female primates. Intense aggression from resident females toward immigrant females suggests that the costs of intrasexual competition outweigh the benefits of group living and has been reported in some species with female transfer. In bonobos (*Pan paniscus*), however, immigrant females are likely to integrate smoothly into an unfamiliar group through affiliative interactions with specific older females. We hypothesized that older resident females gain an indirect benefit from female immigration by increased mating opportunities for their philopatric sons. We examined the effects of 1) age and tenure and 2) the presence of adolescent or adult sons on the probability of aggression by resident females against immigrant females. We collected 73 instances of dyadic agonistic interactions between 14 female bonobos at Wamba, Democratic Republic of the Congo, for five different periods between November 2014 and June 2018, which included four immigrant females with a group tenure of <2.5 years. The female dominance hierarchy correlated with age and tenure, the slope of the hierarchy was weak but statistically significant, and the hierarchy was not linear. We found that the rate of aggression against immigrant females decreased with age in resident females but was unrelated to the presence of mature sons. Our findings suggest that the cost imposed by female immigration varies among resident females, and that social tolerance to immigrant females may be associated with low feeding competition rather than any future benefits.

Keywords Age difference · Dominance hierarchy · Female transfer · Intrasexual aggression · *Pan paniscus* · Social tolerance

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Introduction

Dispersal from a familiar group and immigration into another established group (Isbell and Van Vuren 1996) is one of the most important aspects of intergroup relationships. It contributes to gene flow between groups, and its pattern affects the genetic structure of local populations (Eriksson *et al.* 2006; Forcina *et al.* 2019). Changes in group size and composition associated with intergroup transfer could affect the reproductive success of individuals within the group (Gillespie and Chapman 2001; Robinson 1988; van Noordwijk and van Schaik 1999). For guenons (*Cercopithecus* spp.), female philopatry is the predominant pattern, but female transfer is a common feature in African apes and atelines (Moore 1984; Lee and Strier 2015). Philopatry can be advantageous for females in terms of cooperative defense of limited resources with familiar conspecifics, including kin (Cheney 1992; Wrangham 1980). In species with female transfer, resident females may try to prevent female immigration when the ecological and social costs of intrasexual competition outweigh the benefits of groping (Sterck *et al.* 1997; Watts 1991). Understanding the social relationships between resident and immigrant conspecifics may extend our knowledge of primate social structures.

Some level of intense aggression from resident females to new immigrant females settling into the group has been reported in several primate species with female transfer. For example, in chimpanzees (*Pan troglodytes*) and Geoffroy's spider monkeys (*Ateles geoffroyi*), resident females use aggression to repulse new immigrant females from their core areas (Kahlenberg *et al.* 2008b; Riveros *et al.* 2017), within which the quality of food resources affects their reproductive rates (Asensio *et al.* 2015; Emery Thompson *et al.* 2007). In mountain gorillas (*Gorilla beringei*), resident females may harass new immigrant females (Watts 1991, 1994) because of social competition for access to the silverback for protection of their offspring (Harcourt and Greenberg 2001). Immigrant female northern muriquis (*Brachyteles hypoxanthus*) are displaced from a food patch by resident females at a comparatively high frequency (Printes and Strier 1999). Such conflict between immigrant and resident females may result in disadvantages, such as nutritional sufficiency and social stress, for females in the process of integrating into unfamiliar groups (Printes and Strier 1999; Walker *et al.* 2018).

In bonobos (*Pan paniscus*), however, immigrant females are unlikely to experience spatial isolation and intensive aggression from resident females (Furuichi 1997; Idani 1991; Sakamaki *et al.* 2015). Female bonobos typically transfer from their natal group to other groups and remain in the new group after their first parturition (Kano 1992; Sakamaki *et al.* 2015). In bonobo society, unrelated females in a group aggregate and socialize with one another (Furuichi 2011; Moscovice *et al.* 2017; Yamamoto 2015). Abundant food resources including large patches of fruit-bearing trees and/or widely available terrestrial herbaceous vegetation may facilitate the high gregariousness of female bonobos (Badrian and Badrian 1984; White and Wrangham 1988). The relatively low costs of feeding competition may reduce the conflict between resident and immigrant females.

Nonetheless, immigrant female bonobos are usually subordinate to resident females (Furuichi 1997; Sakamaki *et al.* 2015; Surbeck and Hohmann 2013). Female dominance ranks in bonobos correlate with age and/or group tenure, as in other great apes (Foerster *et al.* 2016; Robbins *et al.* 2005). Older female bonobos are dominant over most males and play a central social role in the group (Furuichi 1989; Parish 1996;

Tokuyama and Furuichi 2016, 2017). Further, immigrant females may allocate more time and effort to establishing affiliative relationships with one specific older female than other resident females (Idani 1991). Affinity with older resident females occupying high dominance ranks might be important for immigrant females to access the central part of the new group for feeding and socializing (Idani 1991). However, it remains unclear whether older resident females are more tolerant of unfamiliar young females than younger resident females.

In bonobos, mothers have a strong influence on the reproductive success of their sons (Surbeck et al. 2019). Mothers can provide agonistic aid to their sons in male–male competition (Furuichi 1997; Surbeck et al. 2011) and maternal rank may correlate with the son's rank (Furuichi 1997; Ishizuka et al. 2018). Further, female immigration is beneficial for resident males because of the increased number of future reproductive partners (Kahlenberg et al. 2008a; Watts 1991). Resident females may also gain indirect reproductive advantages from immigrant females through their philopatric sons. We hypothesized that older female bonobos with mature sons are tolerant toward immigrant females because of a future benefit. If this is the case, older resident females and those with sons should be less aggressive to immigrant females than younger resident females and those without mature sons are. We therefore examined the effects of 1) age and tenure and 2) the presence of adolescent or adult sons on the rate of aggression by resident females against immigrant females.

Methods

Study Site and Group

KT conducted field observations at a long-term field site for bonobo research at Wamba, in the northern sector of Luo Scientific Reserve, Democratic Republic of the Congo (Kano 1992; Furuichi et al. 2012). Since 1974, researchers have conducted behavioral observations of wild bonobos using provisioning. The bonobos in one main study group, called E1, were all individually identified until 1986 (Furuichi 1989; Kano 1992). Field research was interrupted owing to a civil war between 1996 and 2002. However, continuous observations of the E1 group resumed without artificial provisioning in 2003. Researchers completed the reidentification of all bonobos in the E1 group in 2006 (Hashimoto et al. 2008). The E1 group ranges over primary, old, and young secondary forest, swamp, and agricultural field (Terada et al. 2015).

Study Subjects

The E1 group consisted of 31–43 individuals, including 8 or 9 adult males (≥15 yr old; Hashimoto 1997), 3–5 adolescent males (8 to <15 yr old), 9–12 adult females (parous, or ≥15 yr old), and 2–5 adolescent females (nulliparous, and 8 to <15 yr old). All these females had immigrated to the E1 group from other groups, and researchers estimated their year of birth based on their physical features (Table I; see also Sakamaki et al. 2015). We considered adolescent and adult male offspring of the females as mature sons, as previous studies have shown that male bonobos start to reproduce at 7 yr of age (Thompson-Handler 1990).

Table I Profile of female subjects in E1 group of bonobos at Wamba, DRC, in June 2018

ID	Estimated year of birth[a]	Estimated age (yr)[b]	Month and year of immigration	Tenure in E1 group (yr)	ID (birth year) of mature son(s)
Resident					
No	1971	47	Nov. 1983	34	
Ki	1974	44	Dec. 1984	33	NB (1988); KT (2004)
Hs	1981–85	35	Feb. 1996–Aug. 2003[c]	18	
Sl	1991–92	27	Feb. 1996–Aug. 2003[c]	18	SB (2004)
Yk	1981–85	35	Apr. 2004[d]	14	
Jk	1986–90	30	Apr. 2004[d]	14	JR (2001); JO (2006)
Nv	1994–95	23	Aug. 2007	11	
Fk	1998	20	Apr. 2008	10	
Ot	1997	21	June 2008	10	
Zn	2002	16	Oct. 2011	6	
Immigrant					
Pf	2003–05	14	Oct. 2013	4	
Ik	2007–08	10	Oct. 2014	3	
Sc	2008–09	9	Nov. 2015	2	
Db	2009	9	Aug. 2016	1	

[a] We estimated year of birth based on physical features and reproductive profiles (Sakamaki *et al.* 2015).

[b] We calculated age was from the midpoint of the estimated birth year.

[c] Hs and Sl were identified after research resumed in 2003 (Hashimoto *et al.* 2008).

[d] Yk and Jk and their infants were identified in 2004 after research resumed. We assume that they come from adjacent groups that disappeared while research was interrupted (Hashimoto *et al.* 2008).

Females from other groups are often considered as immigrants until their first reproduction occurs, after which they are considered as residents (Kahlenberg *et al.* 2008a; Riveros *et al.* 2017). The median interval between immigration and first reproduction was 2.5 yr in female bonobos at Wamba (Sakamaki *et al.* 2015), and thus we classified female bonobos as immigrants if they had spent <2.5 yr in a group, and residents after 2.5 yr. The four immigrant females in this study (Pf, Ik, Sc, and Db) were well habituated at the beginning of the study because they came from adjacent study groups to the west of the E1 group, called PE and PW groups (Sakamaki *et al.* 2018; Tokuyama *et al.* 2019).

Data Collection

We observed E1 group for 2406 h during five periods: 1) November 2014–February 2015, 2) July–October 2015, 3) May–October 2016, 4) February–July 2017, and 5) February–June 2018. We followed bonobos from before they moved out of their night nests (usually around 06:00 h) until they made new night nests (usually around 17:00 h). Bonobos exhibit fission-fusion social dynamics where membership of the group is flexible and changes fluidly (Kuroda 1979; White 1988). We defined a party using the 1-h party method proposed by Hashimoto *et al.* (2001), determining party membership and size as

all the individuals observed within a 1-h segment (e.g., 06:00–07:00 h, 07:00–08:00 h, and so on). We recorded the individuals present from the beginning to the end of each 1-h segment. The 2278 1-h party segments included a mean of 6.9 ± 2.9 SD females.

KT recorded all observable agonistic interactions between females, including both contact aggression and directed displays (de Waal 1988; Furuichi 1997). We defined contact aggression as any physical attack, such as beating, pushing, pulling, kicking, and biting. We defined a directed display as charging, chasing, and branch dragging. When coalitionary aggression occurred, with two or more females chasing one common target (Harcourt and de Waal 1992; Tokuyama and Furuichi 2016), we distinguished the first actor from the accompanying actors and counted the event as an agonistic interaction between the first actor and her target, because of the difficulty in evaluating a power relationship between the accompanying actors and the target.

Data Analysis

We observed 73 dyadic agonistic interactions in 91 female–female dyads. To establish a dominance hierarchy, we calculated David's scores (David 1987) for each female ($N = 14$) based on dyadic dominance indices, in which the proportions of wins and losses were corrected for the chance occurrence of these interactions (de Vries 1998). We used a Spearman's rank correlation to examine the relationships between age and tenure and David's score. We converted David's scores into normalized David's scores (NDS), which varied between 0 and $N - 1$ (de Vries *et al.* 2006). Regressing the NDS ranks against the NDS values provides the steepness of the hierarchy, which varies between 0 and 1. We assessed the significance of this steepness through 10,000 randomizations of the observed matrix, using the steeptest function in the steepness package (de Vries *et al.* 2006) in R software (version 3.6.1, R Core Team 2019). We also calculated the h' index (de Vries 1995) as a modified version of Landau's linearity index (Landau 1951) to determine whether the female dominance hierarchy is linear or not. We compared the h' index was with the expected h' value generated in the 10,000 randomizations.

To examine the effect of age, tenure, and presence of mature sons of resident females on the probability of aggression against immigrant females, we used a generalized linear mixed model (GLMM) with a Poisson error structure and a log link function (Zuur *et al.* 2009), using the glmer function of the lme4 package in R (Bates *et al.* 2015). The response variable was the number of agonistic behaviors made by 10 resident females against 4 immigrant females (i.e., 40 resident–immigrant dyads). When immigrant females became resident females (i.e., when they had been in the group for >2.5 yr), we excluded them from analysis to standardize the number of resident females for each immigrant female. We controlled for differences in observation times between the 40 dyads by including the number of 1-h segments in which we observed each dyad together as an offset term in the model. The explanatory variables were the age (16–47 yr) and tenure (6–34 yr) of resident females, and the presence vs. absence of mature sons. Before running the model, we standardized the covariates age and tenure to a mean of zero and a standard deviation of one. We included immigrant's ID and resident's ID as a random variable to account for pseudo-replication.

To check the assumption of the full model, we calculated variance inflation factors (VIFs, Quinn and Keough 2002), using the vif function in the car package (Fox and Weisberg 2018). The VIF values of the explanatory variables of the age, tenure, and

presence of mature sons were 15.7, 13.8, and 1.65, respectively, and thus collinearity between age and tenure was a considerable issue (Zuur *et al.* 2010). We reran two GLMMs that considered the explanatory variables of the age and tenure, separately, in addition to son presence. The age model (Aikake's information criterion [AIC] = 73.64) was slightly better than the tenure model (AIC = 75.35), so we interpreted the results of the age model. Collinearity was not an issue in the age model (largest VIF = 1.44). We tested the model with a Poisson error structure for overdispersion (Faraway 2006), which was not an issue (dispersion parameter = 1.08, χ^2 = 37.8, df = 35, P = 0.342). Finally, we compared the age model and null model that consisted only of the random variables using the anova function in R (Dobson and Bernett 2008).

Ethical Note

This study was approved by the Research Centre for Ecology and Forestry and the Ministry of Scientific Research of the Democratic Republic of the Congo. This study conformed to the Guidelines for Field Research established by the Ethics Committee of the Primate Research Institute, Kyoto University, Japan. The authors declare that they have no conflict of interest.

Data Availability The data set of dyadic agonistic interactions used in this study is available upon request.
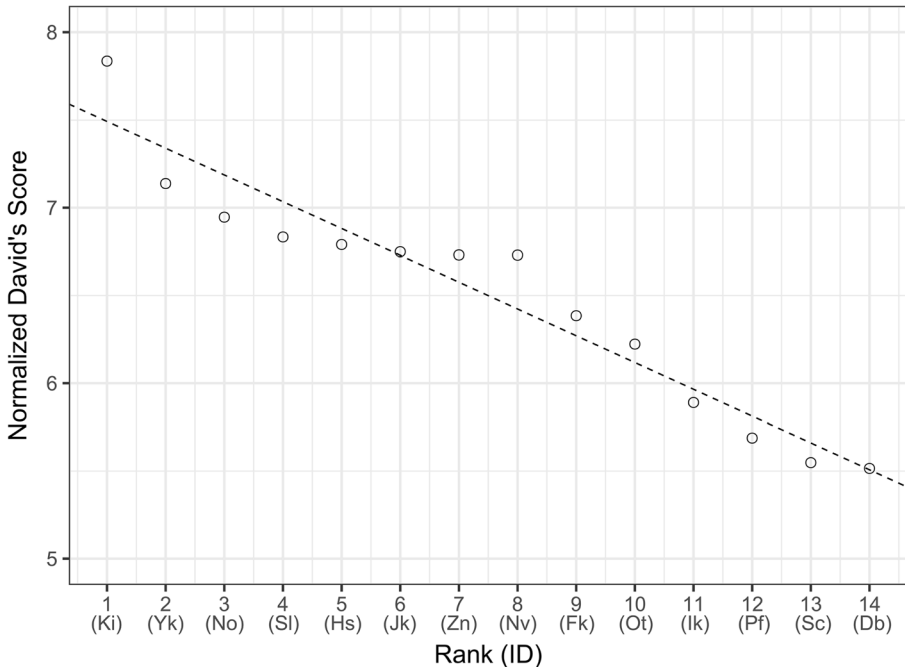

Fig. 1 Normalized David's scores plotted against the rank of 14 female bonobos, Ki–Db, ranked from 1 (highest) to 14 (lowest). Data are for bonobos at Wamba, DRC, between November 2014 and June 2018. We fitted the regression line from the normalized David's scores, with a slope of –0.153 and an intercept of 7.645.

Results

Females' David's scores based on dyadic dominance indices were significantly correlated with their age ($N = 14$, $r_s = 0.931$, $P < 0.001$) and tenure ($N = 14$, $r_s = 0.925$, $P < 0.001$). The slope of the linear regression of the ranks against the normalized David's scores was $R^2 = -0.153$ (Fig. 1). This observed steepness was significantly greater than a randomly generated steepness (one-tailed $P < 0.001$). The linearity index h' of 0.276 was not significantly different from the expected h' value of 0.200 (one-tailed $P = 0.257$).

We observed 17 instances of aggression initiated by resident females against immigrant females, which occurred in 12 of the 40 resident–immigrant dyads. The full model, testing the effects of the age of resident females and the presence of mature sons on the probability of aggression, while controlling for the number of the 1-h party segments in which each dyad was observed together, was significantly different from the null model ($\chi^2 = 8.28$, df $= 2$, $P = 0.020$). Age had a significant negative effect on the probability of aggression, but the effect of the presence of mature sons was nonsignificant (Fig. 2; Table II).

Discussion

We found that older resident female bonobos were less aggressive toward immigrant females than younger resident females were. In contrast to our prediction, however, resident females with mature sons did not differ from those without mature sons in the rate of aggression against immigrant females. Our results do not support the hypothesis
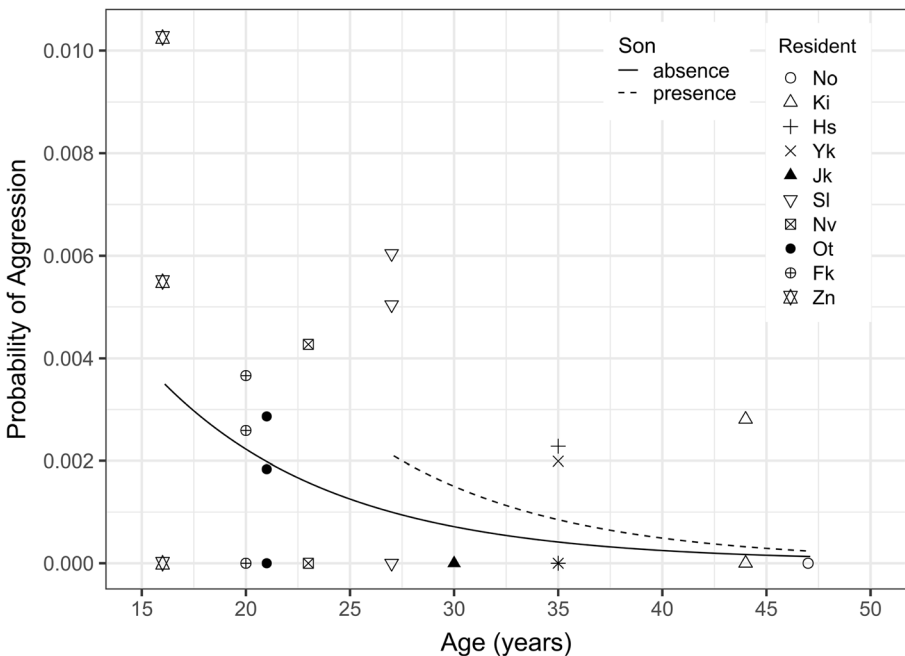

Fig. 2 Probability of aggression by 10 resident females against immigrant females (rate of aggression per time the females were observed together) plotted against resident age in bonobos at Wamba, DRC, between November 2014 and June 2018.

Table II Effects of age and presence of a mature son on the probability of aggression by resident females against immigrant females in bonobos at Wamba, DRC, between November 2014 and June 2018

	Estimate	SE	Z	P
Intercept	−7.419	0.483	−15.37	< 0.001
Age	−1.057	0.410	−2.58	0.010
Son presence (0 = No; 1 = Yes)	0.774	0.606	1.28	0.202

that older female bonobos tolerate female immigration to receive an indirect benefit through their philopatric sons. This study implies that the high tolerance of older resident females is not necessarily associated with the potential future reproductive advantage they accrue if their sons breed with the new females.

Older resident female bonobos occupied higher ranks than young immigrant females, which were positioned at the bottom of dominance hierarchy. Most female aggression was by older females against younger females (73 of 79 instances). The female dominance hierarchy we observed was significantly but weakly steep but not significantly linear. Our results are consistent with previous studies of bonobos (Furuichi 1997; Sakamaki *et al.* 2015; Stevens *et al.* 2007; Surbeck and Hohmann 2013). Similar age-related female–female agonistic relationships are seen in chimpanzees (Foerster *et al.* 2016) and mountain gorillas (Robbins *et al.* 2005), but evidence for agonistic dominance hierarchy is weak in female western lowland gorillas (*Gorilla gorilla*: Stokes 2004). The rarity of aggressive challenges to the older, dominant females, appears to be common among female African great apes and contrasts with the pattern found in many primate species with female philopatry. In many cercopithecines, for example, daughters inherit their mother's rank (Berman 2017). In other cases, female dominance ranks gradually decline with age after sexual maturation (e.g., hanuman langurs, *Semnopithecus entellus*: Borries *et al.* 1991).

Nonetheless, agonistic relationships of resident females toward immigrant females differ considerably the *Pan* species. This study indicates that older resident females have a lower rate of aggression against immigrant females than younger resident females. The pattern is not known in other species with female transfer. Female chimpanzees living in higher-quality core areas are more aggressive toward immigrant females than other resident females are (Kahlenberg *et al.* 2008b), suggesting that aggression against newcomers might be associated with the quality of core areas. Immigrant female chimpanzees also tend to be subordinate to natal adolescent females of a similar age (Kahlenberg *et al.* 2008b). Maternal presence appears to help nondispersing daughters in their initial rank acquisition, which can be subsequently more advantageous for their reproduction in chimpanzees than immigrant females (Foerster *et al.* 2016; Walker *et al.* 2018). Our study group did not include natal females (nondispersing females) for comparison with these findings for chimpanzees.

The hostility of resident females to immigrant females may depend on the immediate costs imposed by female immigration, such as feeding competition (e.g., Kahlenberg *et al.* 2008b; Printes and Strier 1999; Riveros *et al.* 2017). In this study, older female bonobos may suffer little competition from immigrant females. Although female bonobos aggregate with each other, higher-ranking females experience better feeding efficiency than lower-ranking females (Nurmi *et al.* 2018). Given the age-related female dominance hierarchy, younger females may suffer more from female immigration than older females

do. In addition, aggression can be exchanged or escalated more often among closer-ranking females than those that are very different in rank (e.g., Barrett *et al.* 2002; Vogel *et al.* 2007), as individuals generally avoid fighting with clearly dominant opponents (Parker 1974). We therefore suggest that younger resident female bonobos may need to use aggression to dominate younger immigrant females, whereas older resident female bonobos may not need to do so.

In Lui Kotale bonobos, agonistic interactions are seen more often among female dyads with relatively shorter coresidence in the same group than between longer-term coresidents (Moscovice *et al.* 2017). Our results partially match this pattern in that aggression occurred more often between resident and immigrant females than among older resident females with similar tenure. As female dominance ranks become established in the group, the rate of female aggression may decrease. The pattern also applies to other species with female transfer. For example, in Geoffroy's spider monkeys, the rate of female aggression against immigrant females decreases sharply 6 mo after they arrive in the new group (Riveros *et al.* 2017). In northern muriquis, immigrant females were often targeted only during the season in which they joined the group (Printes and Strier 1999). Established dominance relationships may reduce agonistic interactions for access to food resources (Parker 1974). Further studies examining patterns of female–female agonistic interactions based on social dynamics are required to extend our knowledge about generational relationships in species with female transfer.

We provide an example of tolerance in resident females, particularly older females, toward immigrant females in bonobos. Immigrant females might benefit from the tolerance and dominance of older resident females (Idani 1991), which play a central role in the group (Parish 1996; Tokuyama and Furuichi 2017), such as their readiness to permit cofeeding in a given food patch (Parish 1994; Yamamoto 2015) and the availability of coalitional defense against male harassment (Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016). However, given the small sample size of immigrant females and limited social dynamics in this study, caution should be taken when drawing conclusions from our results. For example, nulliparous female bonobos tend to make repeated visits to other groups, for temporary periods ranging from a few days to several months (Kano 1992; Sakamaki *et al.* 2015). However, no such temporary visitors appeared in E1 group during this study. Conflict and affinity with resident females may be one of the factors affecting whether immigrant females remain in a new group or leave.

Abundant food resources facilitate intergroup associations with less female aggression (Kinnaird 1992; Sakamaki *et al.* 2018). Females may benefit from affiliative intergroup relationships, such as intensified defense against predators or sharing valuable food resources without risk of injuries (Grueter *et al.* 2012). So far, however, the benefit of tolerance of resident females for immigrant females has been not examined in species with female transfer. The increase in females in the group as mating partners for philopatric males is a conceivable potential benefit for their mothers. However, we did not find that female aggression against immigrant females was affected by the presence of mature sons in bonobos, perhaps because such a future benefit is too uncertain.

In summary, we showed that the rate of female aggression against immigrant females decreased with age in resident females but was unrelated to the presence of mature sons in bonobos. Our findings suggest that the costs of intrasexual competition imposed by female immigration on resident females vary within the group and between species. Further studies of social interactions between resident and immigrant females are required in primates with

female transfer, to better understand the socioecological factors enhancing social tolerance among female primates.

Author Contributions   KT conducted fieldwork and data analysis. KT and TF wrote the manuscript.

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