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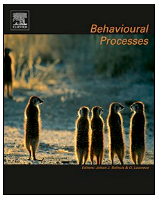

Behavioral responses to changes in group size and composition: a case study on grooming behavior of female Japanese macaques (*Macaca fuscata yakui*)

Yosuke Kurihara[a,*,1,2], Mari Nishikawa[a,2], Koji Mochida[b]

[a] *Primate Research Institute, Kyoto University, Inuyama, Japan*
[b] *Department of Biology, Keio University, Yokohama, Japan*

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ABSTRACT

Primates flexibly change their grooming behavior depending on group size and composition to maintain social relationships among group members. However, how drastic social changes influence their grooming behavior remains unclear. We observed the grooming behavior of adult female Japanese macaques in two groups temporarily formed as one-female groups from multi-female groups and compared their behaviors between the multi-female and one-female periods. Adult females more frequently performed grooming with both their relatives and unrelated juveniles during the one-female period when other adult females were unavailable as alternatives to their absent familiar partners. The increased grooming time and diversity of grooming partners might alleviate the short-term stress caused by the loss of grooming partners and reduce social instability or mitigate the long-term stress due to disadvantages in intergroup conflicts. Our study provides rare evidence on the flexibility in grooming behavior of primates and encourages accumulating case reports for understanding behavioral responses of primates to drastic social changes.

1. Introduction

In primates, grooming plays an important role in maintaining social relationships among group members, leading to fitness benefits of individuals (Silk et al., 2009; 2010a; 2010b) and social cohesion of groups (Dunbar, 1992; Henzi et al., 1997). Therefore, primates vary their grooming behavior in accordance with group size and composition. Primates increase their grooming time and partners with group size until ecological demands or cognitive constraints force them to compromise (Kudo and Dunbar, 2001; Lehmann et al., 2007). When primates lose their affiliative grooming partners owing to death, they compensate for the loss by finding new partners or by strengthening preexisting relationships with other individuals in groups (Engh et al., 2006; Silk et al., 2006). In such situations, alternative partners chosen tend to be similar to absent partners in terms of age, sex, and relatedness (Silk et al., 2006). Although previous studies demonstrated the flexibility in grooming behavior of primates, few studies have reported how drastic social changes influence their grooming behavior.

Here, we report on the grooming behavior of adult female Japanese macaques in one-female groups which were temporarily formed from multi-female groups. Typically, Japanese macaques form multi-male/multi-female, female philopatric groups (Yamagiwa and Hill, 1998). In their female-bonded nepotistic society, grooming among adult females is kin-biased, and it occurs more frequently compared to that between male-female and male-male dyads (Nakamichi and Yamada, 2010). Often, juveniles have grooming interactions with their mothers (Koyama, 1991), and most grooming is directed from mothers toward offsprings (Muroyama, 1995). As reported in other primates, adult females increased the number of grooming partners with group size (Nakamichi and Shizawa, 2003), and they compensated for the loss of their grooming partners by establishing grooming relationships with other adult females who had been affiliated with the dead partners (Nakamichi and Yamada, 2007). Additionally, adolescent females (5–7-years-old nulliparous females) without mothers and sisters performed grooming with unrelated adult females more frequently than those who had such close relatives (Yamada et al., 2005). Unlike previous studies, our subject females were not able to select other adult females as alternatives after the loss of grooming partners. Previous studies also reported one-female groups that were formed during the process of group extinction (Takahata, 1991; Takahata et al., 1994; Sugiura et al., 2002); however, how a single adult female performed grooming during the one-female period remains unclear. In the present study, we

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* Corresponding author at: Primate Research Institute, Kyoto University, Kanrin 41-2, Inuyama, Aichi, 484-8506 Japan.
E-mail address: kurihara.yosuke.35s@kyoto-u.jp (Y. Kurihara).

[1] Present address: Faculty of Agriculture, Shizuoka University, Nishifujidaira 1623-1, Tenryu, Hamamatsu, Shizuoka, 431-3532 Japan.

[2] These authors contributed equally to this work.

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examined the grooming behavior of the adult females before and after drastic changes in the size and composition of their respective groups by analyzing their grooming time and partners. Owing to possible correlations between grooming and other social behaviors (e.g., spatial proximity, aggression) (Ventura et al., 2006), we also provided data on proximity and aggression to discuss their relationship with grooming behavior.

2. Methods

2.1. Study site, groups, and subjects

We conducted this study in the western coastal forest of Yakushima Island, Japan (30 °N, 130 °E). Our study groups were the KwCE group and the E group whose members have been individually identified since 2010 and 2004, respectively. Relatives were defined as individuals with $r \geq 0.125$ (Koyama, 1991) based on demographic records. YK studied the KwCE group during January–August 2013. This group was a multi-female group during January–April 2013 and later became a one-female group during May–August 2013 (Fig. 1). The subject female, *Ema*, had two relatives (mother and son) and one relative (son) during the multi-female and one-female periods, respectively. *Ema* was ranked the lowest among the four adult females during the multi-female period. MN and KM intermittently studied the E group during February 2014–March 2016. This group was a multi-female group at least until August 2015 and later confirmed to have become a one-female group in March 2016 (Fig. 1). The subject female, *Kafka*, had one relative (nephew and daughter) during the multi-female and one-female periods, respectively. *Kafka* was ranked fourth among the five adult females during the multi-female period. Both females did not show mating behavior during the study periods.

2.2. Behavioral data collection

YK studied all adult females, including *Ema*, of the KwCE group via one-hour focal animal sampling during January–April 2013 (multi-female period; total observation time for *Ema*: 17.3 h) and studied the only adult female, *Ema*, via one-day focal animal sampling during May–August 2013 (one-female period; total observation time: 67.6 h). MN and KM studied the single adult female, *Kafka*, of the E group via one-day focal animal sampling in March 2014 (multi-female period; total observation time: 30.9 h) and March 2016 (one-female period; total observation time: 37.3 h). Throughout the study period, we recorded activities (feeding, traveling, resting, grooming, and others) and the identity of grooming partners of the focal animals via one-minute instantaneous recordings. We also recorded individuals in proximity with the focal animals and aggressive interactions involving them (Supplementary Material).

2.3. Data analysis

We compared activity budget, composition of grooming partners, and grooming diversity ratio (GDR) of each subject female between the multi-female and one-female periods. Activity budgets of *Ema* and *Kafka* were calculated as monthly and daily percentage of time spent for each activity in the total observation time, respectively. Grooming partners were categorized into nine types: unrelated adult females, adult/subadult males, mother, daughter, son, nephew, unrelated juvenile females, unrelated juvenile males, and unidentified. The composition of grooming partners was calculated as the percentage of grooming time with each individual in the total grooming time. The balance between grooming given and received was also calculated as (time of grooming given to individual i – time of grooming received from individual i) / (total grooming time with individual i). This value was 0 when grooming given to individual i was equal to that received from it. Grooming with individual i was defined as balanced when the value was between -0.5 and 0.5. GDR was calculated as follows (Nakamichi and Shizawa, 2003):

$$GDR = -\frac{\sum_i p_i \log p_i}{\log\,(n-1)}$$

Where, p_i was the percentage of grooming time with individual i in the total grooming time, and $n-1$ was the number of potential grooming partners (n: group size). GDR was 1 when the subject female distributed its grooming evenly across all group members and 0 when it performed grooming with only a specific partner. We also summarize data on proximity and aggression (Supplementary Material).

3. Results

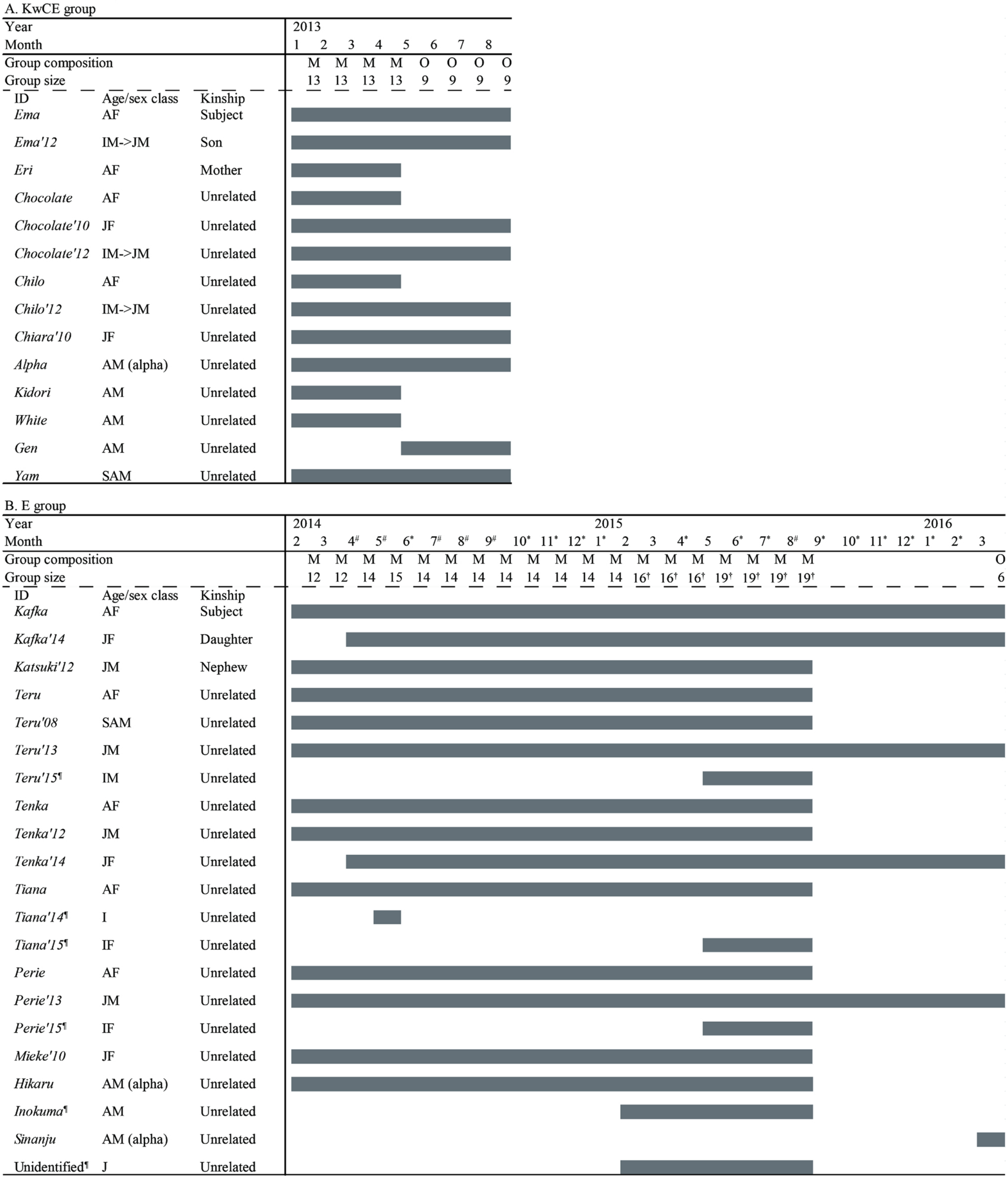
Ema and *Kafka* increased grooming time during the one-female period at the expense of feeding and resting times, respectively (Table 1). The GDRs of *Ema* and *Kafka* for overall grooming and those of *Kafka* for grooming given and received increased during the one-female period, although those of *Ema* for grooming given and received did not. During the multi-female period, *Ema* mainly had grooming interactions with her mother (balanced), her son (biased towards giving), and one of the adult males (biased towards receiving). She had the fourth-most frequent grooming interactions with one adult female (balanced), but rarely performed grooming with other females. She was not observed performing grooming with unrelated juveniles and adult males, except for *White*. During the one-female period, she mainly performed grooming with her son (biased towards giving) and unrelated juvenile females (balanced). During the multi-female period, *Kafka* mainly had grooming interactions with her nephew (biased towards giving), unrelated adult females (except for *Teru*) (balanced), and a subadult male (balanced). She rarely performed grooming with an adult male. During the one-female period, she mainly performed grooming with her daughter (biased towards giving) and unrelated juvenile males (balanced).

Even during the multi-female period, *Ema* and *Kafka* were in proximity with individuals with whom they mainly performed grooming during the one-female period as frequently as other individuals. In the one-female period, *Ema* tended to be in proximity with her son and unrelated juvenile females more frequently than with adult males (Supplementary Material). While aggressive interactions involving *Kafka* rarely occurred throughout the study period, *Ema* increased aggression given to unrelated juvenile females during the one-female period (Supplementary Material).

4. Discussion

After *Ema* and *Kafka* experienced drastic social changes, they increased the grooming time and diversity of grooming partners during the one-female period. A trade-off between feeding and grooming times has been reported (Agetsuma and Nakagawa, 1998). However, in the present study, the increase in grooming time was not necessarily caused by the decrease in feeding time, suggesting that it did not solely result from relaxed constraints on foraging time due to the decline in group size. In the short term, increased grooming effort could alleviate the stress caused by the loss of grooming partners (Engh et al., 2006) and stabilize their social relationships with group members (Sueur et al., 2011). Additionally, it might mitigate the long-term stress due to disadvantages in intergroup conflicts because of the small group sizes (Pride, 2005; Markham et al., 2015).

When *Ema* and *Kafka* lost their respective grooming partners, they frequently had grooming interactions with their relatives and unrelated juveniles. This result suggests that adult females continue kin-biased grooming but devote little grooming effort to adult males even under unusual social conditions, consistently with the general pattern of Japanese macaques (Nakamichi and Yamada, 2010). The biased



A. KwCE group

Year	2013							
Month	1	2	3	4	5	6	7	8
Group composition	M	M	M	M	O	O	O	O
Group size	13	13	13	13	9	9	9	9

ID	Age/sex class	Kinship
Ema	AF	Subject
Ema'12	IM->JM	Son
Eri	AF	Mother
Chocolate	AF	Unrelated
Chocolate'10	JF	Unrelated
Chocolate'12	IM->JM	Unrelated
Chilo	AF	Unrelated
Chilo'12	IM->JM	Unrelated
Chiara'10	JF	Unrelated
Alpha	AM (alpha)	Unrelated
Kidori	AM	Unrelated
White	AM	Unrelated
Gen	AM	Unrelated
Yam	SAM	Unrelated

B. E group

Year	2014											2015												2016		
Month	2	3	4#	5#	6*	7#	8#	9#	10*	11*	12*	1*	2	3	4*	5	6*	7*	8#	9*	10*	11*	12*	1*	2*	3
Group composition	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M							O
Group size	12	12	14	15	14	14	14	14	14	14	14	14	16†	16†	16†	19†	19†	19†	19†							6

ID	Age/sex class	Kinship
Kafka	AF	Subject
Kafka'14	JF	Daughter
Katsuki'12	JM	Nephew
Teru	AF	Unrelated
Teru'08	SAM	Unrelated
Teru'13	JM	Unrelated
Teru'15¶	IM	Unrelated
Tenka	AF	Unrelated
Tenka'12	JM	Unrelated
Tenka'14	JF	Unrelated
Tiana	AF	Unrelated
Tiana'14¶	I	Unrelated
Tiana'15¶	IF	Unrelated
Perie	AF	Unrelated
Perie'13	JM	Unrelated
Perie'15¶	IF	Unrelated
Mieke'10	JF	Unrelated
Hikaru	AM (alpha)	Unrelated
Inokuma¶	AM	Unrelated
Sinanju	AM (alpha)	Unrelated
Unidentified¶	J	Unrelated

Fig. 1. Group size and composition of (A) KwCE group and (B) E group. Group composition was either multi-female (M) or one-female (O). The IDs of offspring are a combination of the mothers' name and year of birth (e.g., *Ema'12* was *Ema*'s offspring born in 2012). Age-sex class during the period of behavioral data collection is shown, except individuals who were absent from the group during such period. The members of the two groups were categorized into the following seven types: AF, adult female (> 5 years old); AM, adult male (> 9 years old); SAM, subadult male (6–9 years old); JM/JF, juvenile male/female (1–5 years old); IM/IF, infant male/female (< 1-year-old). Note that infants were reclassified as juveniles on March of the following year of their birth. ¶These individuals were absent from the group during the period of behavioral data collection. We have shown the age-sex class of such individuals during the period when they were in the group. *The members of the E group in months when we did not observe the group was estimated from the data before and after such months. #Y. Shima, personal communication. †Minimum group size is shown here since the number of unidentified individuals was not confirmed.

grooming could prevent adult females from spending long time grooming with adult males. In the present study, *Ema* and *Kafka* gave grooming to adult males more than what they received (Table 1), as with Tsukahara (1990). In contrast, balanced grooming could enable adult females to spend long time grooming with unrelated juveniles, although it was limited to > 1-year-old juveniles. *Ema* and *Kafka*

Table 1
Comparison of Grooming Time, Number of Grooming Partners, Grooming Diversity Ratio, Composition of Grooming Partners, and Balance between Grooming Given and Received between the Multi-female and One-female Periods.

Ema			Multi-female	One-female	*Kafka*			Multi-female	One-female
Activity budget	Groom		20.0% ± 16.4%	37.5% ± 6.2%	Activity budget	Groom		14.1% ± 8.5%	30.8% ± 4.3%
	Feed		43.9% ± 12.8%	13.6% ± 2.4%		Feed		31.2% ± 4.0%	27.7% ± 4.5%
	Travel		21.4% ± 5.3%	23.0% ± 4.4%		Travel		21.9% ± 5.1%	18.6% ± 8.0%
	Rest		14.6% ± 1.1%	25.8% ± 4.9%		Rest		32.7% ± 1.5%	22.7% ± 3.3%
	Other		0.0% ± 0.0%	0.2% ± 0.1%		Other		0.1% ± 0.1%	0.2% ± 0.1%
Number of grooming partners[a]	Overall grooming		6 (46%)	8 (89%–100%)	Number of grooming partners[a]	Overall grooming		9 (75%)[b]	6 (100%)
	Grooming given		6 (46%)	8 (89%–100%)		Grooming given		9 (75%)[b]	6 (100%)
	Grooming received		5 (38%)	4 (44%–50%)		Grooming received		6 (50%)	6 (100%)
Grooming diversity ratio	Overall grooming		0.60	0.65	Grooming diversity ratio	Overall grooming		0.58	0.78
	Grooming given		0.59	0.60		Grooming given		0.46	0.73
	Grooming received		0.44	0.33		Grooming received		0.62	0.74
Composition of grooming partners	Unrelated adult female	*Chocolate*	3.7%	–	Composition of grooming partners	Unrelated adult female	*Teru*	1.0%	–
		Chilo	10.0%	–			*Tenka*	13.0%	–
	Adult/subadult male	*Alpha* (alpha male)	0.0%	7.0%			*Tiana*	8.2%	–
		Kidori	0.0%	–			*Perie*	6.5%	–
		White	22.0%	–		Adult/subadult male	*Hikaru* (alpha male)	1.0%	–
		Gen	–	1.2%			*Sinanju* (alpha male)	–	8.3%
		Yam	3.3%	6.2%			*Teru'08*	11.3%	–
	Mother	*Eri*	38.9%	–		Daughter	*Kafka'14*	–	30.8%
	Son	*Ema'12*	22.4%	41.4%		Nephew	*Katsuki'12*	55.8%	–
	Unrelated juvenile female	*Chocolate'10*	0.0%	35.7%		Unrelated juvenile female	*Mieke'10*	1.7%	–
		Chiara'10	0.0%	8.4%			*Tenka'14*	–	9.2%
	Unrelated juvenile male	*Chocolate'12*	0.0%	0.1%		Unrelated juvenile male	*Tenka'12*	0.0%	–
		Chilo'12	0.0%	0.1%			*Teru'13*	0.0%	2.7%
							Perie'13	0.0%	44.0%
						Unidentified	Unidentified	1.4%	5.0%
Balance between grooming given and received	Unrelated adult female	*Chocolate*	0.56	–	Balance between grooming given and received	Unrelated adult female	*Teru*	1	–
		Chilo	0.42[*]	–			*Tenka*	0.21[*]	–
	Adult/subadult male	*Alpha* (alpha male)	NA	1			*Tiana*	−0.33[*]	–
		Kidori	NA	–			*Perie*	0.37[*]	–
		White	−0.55	–		Adult/subadult male	*Hikaru* (alpha male)	1	–
		Gen	–	1			*Sinanju* (alpha male)	–	0.57
		Yam	−0.25[*]	0.61			*Teru'08*	−0.09[*]	–
	Mother	*Eri*	−0.29[*]	–		Daughter	*Kafka'14*	–	0.60
	Son	*Ema'12*	1	1		Nephew	*Katsuki'12*	0.99	–
	Unrelated juvenile female	*Chocolate'10*	NA	−0.19[*]		Unrelated juvenile female	*Mieke'10*	0.2[*]	–
		Chiara'10	NA	−0.37[*]			*Tenka'14*	–	−0.49[*]
	Unrelated juvenile male	*Chocolate'12*	NA	1		Unrelated juvenile male	*Tenka'12*	NA	–
		Chilo'12	NA	1			*Teru'13*	NA	−0.33[*]
							Perie'13	NA	0.02[*]
						Unidentified	Unidentified	NA	NA

-The partner was absent from the group.

[a] Values in parentheses represent the proportion of observed grooming partners in potential grooming partners (group size - 1).

[b] Unidentified partners were counted as one individual (e.g., The total number of partners for Kafka in the multi-female period was "at least" nine).

[*] Grooming was defined as balanced when the value was between −0.5 to 0.5.

tended to give grooming to 1-year-old juveniles more than what they received, agreeing with previous findings (Nakamichi, 1989; Muroyama, 1995). These observations suggest that > 1-year-old juveniles can play important roles as alternative grooming partners for adult females. Additionally, for *Ema*, increased grooming with unrelated juvenile females could be as a result of frequent proximity with them (Clark, 2011) and increased aggression toward them (e.g., reconciliation, Kutsukake and Castles, 2001). Conversely, *Ema* and *Kafka* could be valuable grooming partners for most juveniles who had lost their mothers according to Yamada et al. (2005). Orphaned juveniles would compensate for the loss of their mothers by performing grooming with *Ema* and *Kafka*, which increased grooming between unrelated juveniles and *Ema* and *Kafka*.

In summary, adult female Japanese macaques during the one-female period (1) increased the grooming time and diversity of grooming partners and (2) not only maintained kin-biased grooming but also compensated for the loss of their grooming partners by having grooming relationships with unrelated juveniles. Most studies on social relationships in primates have focused on adults (Nakamichi and Yamada, 2010); however, investigating grooming networks with juveniles might assist in evaluating their roles as grooming partners, as also recommended in Fedurek and Lehmann (2017). Our results should be interpreted with caution owing to limited data availability (e.g., the number of subject animals and observation time). Nevertheless, our study provides rare evidence on the flexibility in grooming behavior of primates. Investigating behavioral responses to drastic social changes is necessary for understanding social relationships of primates but difficult through hypothesis-driven studies owing to their infrequency and unpredictability (Nakamichi and Yamada, 2010; Kutsukake, 2011). Therefore, accumulating case reports should encourage future systematic studies and could be clues to better understand the society of primates.

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