Mating and Reproductive Success in Free-Ranging Stump-Tailed Macaques: Effectiveness of Male–Male Coalition Formation as a Reproductive Strategy

*Correspondence:
Aru Toyoda
aru.toyoda@gmail.com

†ORCID:
Aru Toyoda
orcid.org/0000-0003-1784-8553
Kazunari Matsudaira
orcid.org/0000-0003-2893-9928
Ikki Matsuda
orcid.org/0000-0002-0861-7801
Suchinda Malaivijitnond
orcid.org/0000-0003-0897-2632

Aru Toyoda[1]*†, Tamaki Maruhashi[2], Yoshi Kawamoto[3], Kazunari Matsudaira[4]†, Ikki Matsuda[1,5,6,7]† and Suchinda Malaivijitnond[8,9]†

[1] Chubu University Academy of Emerging Sciences, Kasugai, Japan, [2] Department of Human Cultures, Musashi University, Nerima, Japan, [3] Graduate School of Veterinary Medicine and Life Science, Nippon Veterinary and Life Science University, Musashino, Japan, [4] Graduate School of Asian and African Area Studies, Kyoto University, Kyoto, Japan, [5] Wildlife Research Center of Kyoto University, Kyoto, Japan, [6] Japan Monkey Centre, Inuyama, Japan, [7] Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia, [8] Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand, [9] National Primate Research Center of Thailand, Chulalongkorn University, Saraburi, Thailand

Male coalition-like formation, recently found in stump-tailed macaques (*Macaca arctoides*), occurs when several top-ranking males collaboratively guard females to prevent mating with other rival males and actively share secured mating opportunities with their allies. We lack a comprehensive understanding of the proximate mechanisms underlying such male coalitions, e.g., the effect of genetic relatedness. Such cooperative partner choice among males is particularly interesting in animals, such as *M. arctoides,* that live in matrilineal (female philopatry/male dispersal) society. Theoretically, in such a social system, females, and not males, are often related to each other by kinship. Thus, the occurrence of cooperative behavior between related females are generally common, but it would be rare between unrelated/non-kin males in such matrilineal society. Herein, for the first time, we report detailed copulatory behaviors, including mating and reproductive success, in relation to male coalition-like formation in free-ranging *M. arctoides* following direct behavioral observation and genetic analysis. We found that coalition-forming male–male alliances often occur among both individuals that are highly related and those that are less related. We identified two groups with different mating strategies, i.e., single-male monopoly and coalition-male monopoly groups. In both groups, nearly 80% of copulations were monopolized by a single male or by coalition males. However, the single-male monopoly strategy allows opportunistic/sneaky copulations by other males with a relatively high probability. Thus, the degree of reproductive success did not reflect mating success. In contrast, the males employing a coalition strategy successfully shared their mating and reproductive success, particularly in the largest group. Compared with single-male monopolized

groups, the coalition-male monopoly groups copulated with a considerably more number of females, suggesting that coalition males can effectively guard against opportunistic/sneaky copulation by rival males. We also found that coalition-forming male–male alliances often occur regardless of the degree of kinship/relatedness, indicating the complexity and flexibility inherent in the male social bond of *M. arctoides*.

INTRODUCTION

A fundamental problem in behavioral ecology is determining mechanisms that regulate differential reproduction among individuals, and intrasexual competition is considered one of the important factors closely associated with such mechanisms (Darwin, 1871). In theory, male–male competitions occur because males seek to maximize their reproductive success by mating with as many females as possible, and thus compete over access to mates in general (Emlen and Oring, 1977; Clutton-Brock, 1989). Male reproductive success has been studied in many animal taxa to understand differential reproduction (or reproductive skew) in males possibly caused by male–male competition (Clutton-Brock, 1988). Among primates that exhibit a stunning variation in both social structure and organization, male reproductive success has been historically difficult to measure, and consequently, male mating success is assumed to be a sufficiently reliable indicator to reflect male reproductive success, wherein success is often linked to dominance status (Robinson, 1982; Fedigan, 1983; Cowlishaw and Dunbar, 1991). With the development of genetic techniques, based on both observational and genetic data, this has been repeatedly tested in various primate species but has not yielded consistent results. Some studies show that mating and reproductive success are both closely related to male dominance status (e.g., Cowlishaw and Dunbar, 1991; de Ruiter and van Hooff, 1993; Wickings et al., 1993), although the skew in male reproductive success is often less pronounced than that predicted from observed mating success (e.g., Berard et al., 1993; Inoue et al., 1993; Constable et al., 2001; Young et al., 2013). Therefore, the variation in the relationship between mating and reproductive success is increasingly drawing attention.

In contrast, considering alternative male reproductive tactics to mitigate competition if males cannot achieve a high rank is equally important (Setchell et al., 2008). Coalition formation, defined as cooperation in an aggressive or competitive context, where one animal intervenes in an ongoing conflict between two parties to support one side (Harcourt and de Waal, 1992), is one of the notable alternative tactics in males to improve their dominance-based status, which improves their mating success (Noë and Sluijter, 1990). Coalition formation in males has been reported in various mammalian taxa, e.g., cetaceans (Diaz-Aguirre et al., 2018; Gerber et al., 2021) and carnivores (Packer et al., 1991; Caro and Collins, 2010), although it has most extensively been studied in primates (van Schaik et al., 2006). Nonetheless, at present, we lack a

comprehensive understanding of the proximate mechanisms underlying such cooperative coalition behaviors, i.e., who helps whom (Rodrigues and Kokko, 2016).

In primates, male–male coalitions are generally observed in the context of conflict/aggression and are widely found in nearly all major phyletic lines, with the exception of Malagasy prosimians. The frequency of observed coalitions differs across species and even within families or genera (Bissonnette et al., 2014). Although there is a trend that kinship contributes to driving the propensity for male–male coalitions (Silk, 1992, 2009), it would hardly explain such nepotism in female-philopatric–male-dispersal species common in non-human primates compared with male-philopatric species of some taxa, i.e., colobuses, apes, atelids, and lemurids (Pusey and Packer, 1986; Furuichi et al., 2015). Therefore, male–male coalitions, particularly in female-philopatric species, are interesting in the context of partner choice because males (possibly non-related males) are compelled to cooperate for the limited resource that cannot be shared. Male–male competition for females is universal in biological theory. In addition to the choice of partner in male–male coalitions, evaluating the effects of such coalitions on male reproductive success would provide critical implications for the evolutionary background of male–male coalition. Till date, in non-human primates, empirical studies demonstrating the link between male reproductive success and the participation of males in coalitions have been rare (but see Schulke et al., 2010).

The genus *Macaca* is the most widely distributed group of non-human primates in Asia (with the exception of the North African Barbary macaque), and their societies are characterized by profound unity and great diversity (Fa and Lindburg, 2005; Thierry, 2007). Of the 12 macaque species, male–male coalitions have been detected in 10 species, although the frequency of male–male coalitions varies across species (Bissonnette et al., 2014). Notably, of the species groups, the *Sinica-arctoides* lineage, including *Macaca assamensis*, *M. radiata*, *M. sinica*, *M. thibetana*, and *M. arctoides* (Delson, 1980; Jiang et al., 2016), is prominent in exhibiting pronounced male affiliations and frequent male–male coalition formation compared with other *Macaca* species groups (Bissonnette et al., 2014; Ostner and Schülke, 2014).

Similar to other macaques, *M. arctoides* (stump-tailed macaque) lives in multi-male–multi-female social groups and displays female philopatry and male dispersal (Thierry, 2011). Previous studies focusing on their social interactions have reported their tolerant or relaxed social hierarchy (de Waal and Ren, 1988; de Waal and Luttrell, 1989; Butovskaya, 1993). These social/individual characteristics are mainly based on

data from females in captivity living in a semi-free-ranging condition. A notable exception is a study by Richter et al. (2009) that investigated social interactions among males in a free-ranging population and suggested that *M. arctoides* males are less tolerant than predicted by previous captive studies, which have mostly focused on females. Conversely, although male–male coalition in *M. arctoides* is assumed (Bissonnette et al., 2014), a detailed description of male–male coalition has not been reported so far except in the authors' previous study (Toyoda et al., 2020b).

Coalition-like formations, recently found in free-ranging *M. arctoides*, have been interpreted as a cooperative behavior in which several top-ranking males collaboratively engage in guarding females against mating with other rival males, by possibly using a specific copulation call (Toyoda et al., 2020a), and actively share secured mating opportunities with allies (Toyoda et al., 2020b). In fact, in some male-philopatric primate species, such as muriquis and chimpanzees, males are tolerant to group males and share copulations with receptive females (Nishida, 1983; Watts, 1998; Strier et al., 2002), although little is known about such sharing copulations among males in female-philopatric species, i.e., coalition-like formation with the context found in *M. arctoides*. The rarity of such coalition in *M. arctoides* and intraspecific variations in the occurrence of such coalition is intriguing; male–male coalition-like formation has been observed in some groups but not in other groups living in the same habitat (Toyoda et al., 2020b). Therefore, *M. arctoides* males are promising models that could be particularly useful for evaluating how male–male coalitions contribute to reproductive success by comparing male reproductive success in groups that form male–male coalitions with those that do not.

Copulatory behaviors are one of the commonly studied themes in *M. arctoides*, e.g., male-specific copulatory calls at the time of ejaculation (Toyoda et al., 2020a) and harassment in relation to copulation (Gouzoules, 1974; Niemeyer and Chamove, 1983) have been described. A rarely observed copulatory pattern known as serial copulation (Estep et al., 1984; Fooden, 1990; Brereton, 1994) could be particularly important for understanding coalition-like formation in *M. arctoides* because it is always observed in this context (Toyoda et al., 2020b). During serial copulation, males copulate several times in a short interval, with repeated copulations involving ejaculation, although this species is a single-mount ejaculator (i.e., thrusting continues through a single uninterrupted mount until ejaculation is achieved). Here, in an attempt to understand the mating system in relation to the underlying mechanism of male–male coalitions, we first reported the copulatory behaviors, including specific copulation types, of *M. arctoides*. Second, through behavioral observations, we quantified the mating success of each male in multiple groups by comparing male–male coalition with non-coalition formations. Third, we quantified reproductive success based on genetic paternity tests and compared its extent between male–male coalitions and non-coalition formations. Lastly, we examined the relatedness among males, including the pairs that formed coalitions, and discussed the attributes that influence cooperative partner choice in male *M. arctoides*.

MATERIALS AND METHODS

Study Site and Animals

This study was conducted in a mixed landscape and forest fragments at the Khao Krapuk Khao Taomor Non-Hunting Area, Phetchaburi Province, Thailand (12°47′59″ N, 99°44′31″ E) from September 2015 to June 2017. The study area, covering ca. 4 km^2 of the ranging area of all groups, was mountainous and included secondary and bamboo forests, roads and human premises, such as temples, pineapple orchards and houses of local residents. Data on rainfall and temperatures were obtained from a nearby weather station of the Kaeng Krachan National Park (approximately 12 km from the nearest periphery and approximately 62 km from the center of the national park area from the study site), and the mean annual temperature and rainfall were approximately 27°C and 1,070 mm, respectively (Wijitkosum, 2012).

Five groups of *M. arctoides* were habituated to observers; all adults, most of the sub-adults and some juveniles were identified individually by their facial characteristics, scars or other remarkable physical traits (Toyoda et al., 2020a,b). The five study groups of *M. arctoides* included 391 individuals, i.e., Ting-Group: 120 individuals, including 30 and 33 adult males and females, respectively; Nadam-Group: 75 individuals, including 20 and 30 adult males and females, respectively; Third-Group: 79 individuals, including 23 and 23 adult males and females, respectively; Fourth-Group: 74 individuals, including 16 and 27 adult males and females, respectively; Wngklm-Group: 43 individuals, including 8 and 11 adult males and females, respectively [see 39 in details].

Although the study macaques were free ranging, their ranging area was restricted between the north and south by large roads. Food provisioning by locals or visitors was occasionally observed along the road or around the temple ground. This population was geographically isolated from the other populations, i.e., Kaeng Krachan National Park, and no new immigrant males from other sites were observed during the study period (Toyoda et al., 2017; Toyoda and Malaivijitnond, 2018).

Behavioral Observation

Behavioral data on the five study groups were collected continuously by AT during the daily observation period from 09:00 to 17:00. The group that was first encountered each day was selected as the target group and followed for as long as possible. When the target group could not be followed further, e.g., when the group traveled along cliffs, we terminated the observation session and selected another group, which was subsequently chosen as the target group. We followed each target group alternately for 289 days, and the total observation times for the five aforementioned groups were 970.7 h throughout the study period. All copulations observed in the target group were recorded. Observation conditions were excellent, and the copulations of most group members were generally recorded when copulation occurred. Video cameras (JVC GZ-RX500 and Sony HDR-PJ675) were used to record the behavior in detail.
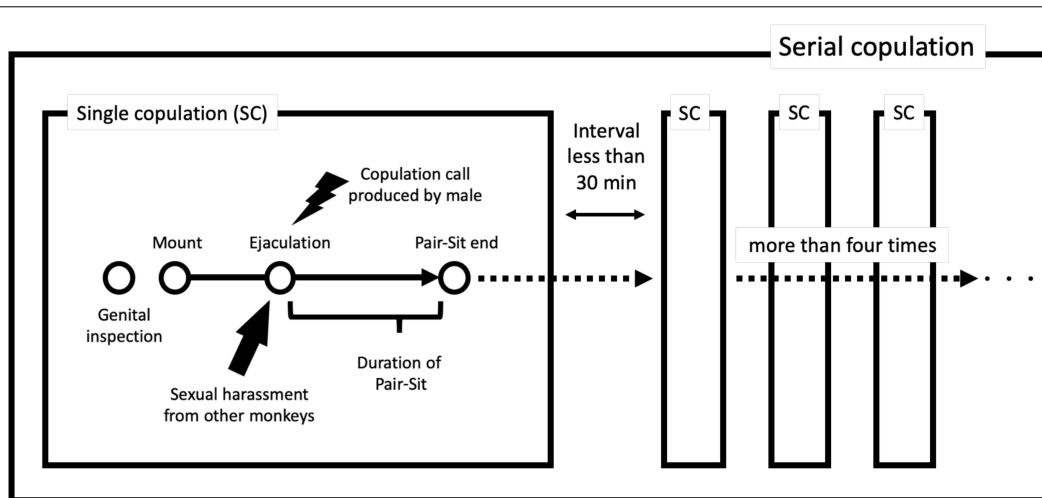
FIGURE 1 | Schematic diagram of the copulating sequence of *M. arctoides*. In most cases, mating begins with a genital inspection of the female by the male. Because *M. arctoides* is a single-mount ejaculator, copulation generally leads to ejaculation through thrusting in a single mount. When more than four instances of single copulations occur in succession within a 30-min interval, this continued copulation is classified as serial copulation.

In most cases, copulations began with a genital inspection of the female by the male (**Figure 1**), and male-specific copulation calls were often observed during the copulations (Toyoda et al., 2020a). The copulations observed in the study groups were divided into two categories: single and serial copulation types (**Figure 1**). The single copulation type was defined as a behavior in which a male mounted a female and thrust with intromission (Estep et al., 1984). The serial copulation type was defined as a sequence of single copulations that occurred more than four times with an interval of <30 min between each single copulation; the rationale for this definition is that 95% of the inter-copulation intervals were ≤30 min (Toyoda et al., 2020b) and the mean number of sequential serial copulations in three different previous studies was four (Brereton, 1994). In addition, the serial copulation type was subdivided into two sub-categories: male coalition mode and non-coalition mode. If multiple males were involved in the context of serial copulation with shared mating opportunities, previously known as coalition-like formation (Toyoda et al., 2020b), we defined this behavior as male coalition mode. Alternatively, the behavior was defined as non-coalition mode if only one male engaged in serial copulation (**Figure 2**).

DNA Sampling and Genotyping

As a DNA resource, buccal cells were non-invasively collected during the research period using a rope swab (Toyoda et al., 2021). A sterilized polyester rope was cut into 10-cm pieces, which were then soaked in a 20% sugar solution to bait individuals. Once used, rope swabs were immediately collected and quickly transferred to 3 mL lysis buffer containing 0.5% (w/v) sodium dodecyl sulfate, 100 mM ethylenediaminetetraacetic acid (pH 8.0), 100 mM Tris-HCl (pH 8.0) and 10 mM NaCl (Hayaishi and Kawamoto, 2006). Epithelial cells detached from the intestinal wall, collected from freshly dropped fecal samples, were also used as a DNA resource from group members when

buccal cells were unavailable. A sterile cotton bud, which was soaked in 2 mL lysis buffer, was used to swab the surface of the feces at least three times (Hayaishi and Kawamoto, 2006).

From the collected specimens, DNA was extracted following the procedure described in Kawamoto et al. (2013), and potential polymerase chain reaction (PCR) inhibitors were removed by adding 600 mg of hydrolyzed starch (Wako, Osaka, Japan) to 1.5 mL of lysis buffer per sample. Samples were then incubated at 36°C for 10 min and centrifuged at $1000 \times g$ for 15 min. Finally, 750 μL of each supernatant was processed using a commercially available DNA clean-up system (Wizard SV Gel and PCR Clean-Up System; Promega, Madison, WI, United States). The DNA was eluted into 50 μL pure water.

Ten polymorphic loci (D8S1106, D19S582, D6S2793, D7S2004, D14S306, D18S537, D17S1290, D13S765, D11S2002, and D3S1768; refer to the details in the **Supplementary Material**), which exhibited sufficient variation and successful amplification, were amplified and used for genetic analysis (Toyoda and Malaivijitnond, 2018). These Loci were formulated in three combinations when we did multiplex PCR, avoiding overlap of fluorescent dyes and allele sizes; D8S1106, D19S582, and D6S2793 were in combination-A, D7S2004, D14S306, D18S537, and D17S1290 were in combination-B, and D13S765, D11S2002, and D3S1768 were in combination-C. The fragment analysis from sample collection to the PCR process conducted in Thailand was conducted using Macrogen, Inc. (Seoul, South Korea). The resulting fragment data were subsequently analyzed using GeneMapper software v. 4.1 (Applied Biosystems).

In total, 230 samples, including 224 buccal samples (95 adult males, 68 adult females and 50 infants) and 6 fecal samples (only infants) were successfully amplified and analyzed with observed heterozygosity, ranging from 0.431 to 0.794, as calculated by GenAlEx 6.3 (Peakall and Smouse, 2012). Each marker contained between 3 and 12 alleles (Toyoda and Malaivijitnond, 2018).
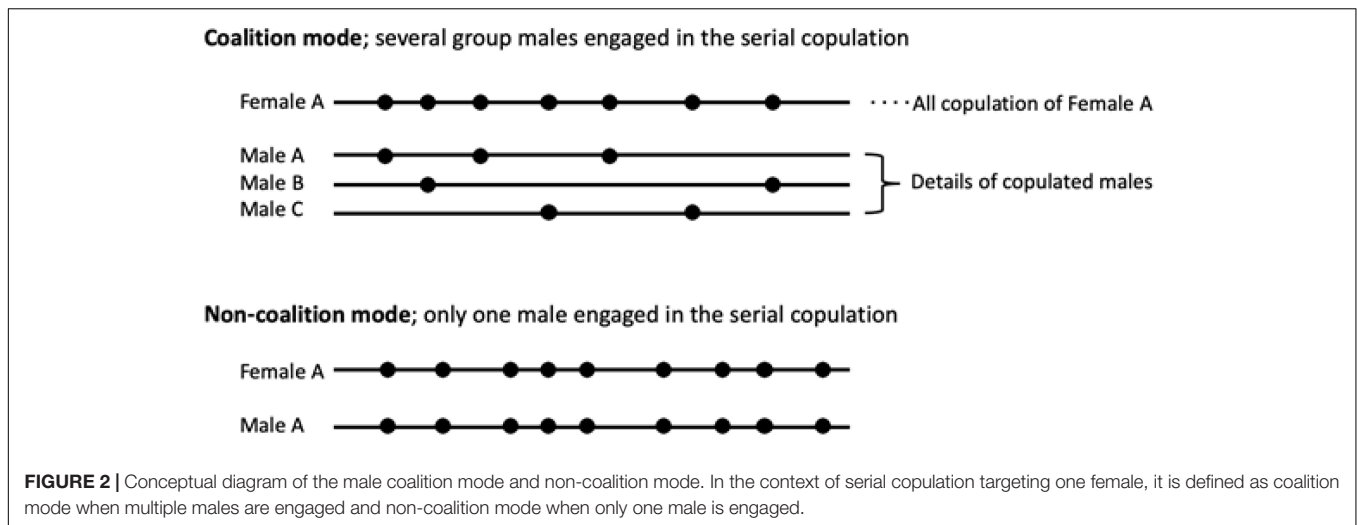
FIGURE 2 | Conceptual diagram of the male coalition mode and non-coalition mode. In the context of serial copulation targeting one female, it is defined as coalition mode when multiple males are engaged and non-coalition mode when only one male is engaged.

To ensure genotype consistency, PCR was performed at least twice based on the allelic dropout rates calculated by PEDANT 1.0 (Johnson and Haydon, 2007). Noted, however, if the results of the first and second tests were the same, we used those results, though if they differed, we conducted a third test and used the results of the one that confirmed reproducibility. The deviation from Hardy–Weinberg equilibrium was assessed using a χ^2-test with Bonferroni correction, and we confirmed that the tested loci did not deviate from the Hardy–Weinberg equilibrium (**Supplementary Table 1**).

Genetic Analysis

Parentage analysis was conducted using CERVUS 2.0 (Tristan Marshall, Edinburgh, United Kingdom) to evaluate the effects of copulation occupancy rate or coalition mode on reproductive success in males. The paternity of infants was tested using the males in each group and all males in the five study groups, and the results were compared based on allele mismatches and logarithm of the odds scores. Paternity was determined using maximum likelihood testing at confidence levels of >80% for relaxed confidence and >95% for rigorous confidence. Relatedness was estimated using the Queller and Goodnight estimator implemented in GenAlEx 6.3 to evaluate the structural kinship features in the population among males. The program estimated relatedness values by allele sharing of pairs and allele frequency among the population of this study site. Together with calculations conducted using GenAlEx, we also calculated maximum likelihood estimates of relatedness between each dyad of individuals (Wagner et al., 2006) using ML-RELATE (Kalinowski et al., 2006). Kin relationships between each dyad were also estimated using ML-RELATE by assignment to one of four kinship categories with the highest likelihood: parent–offspring (PO), full siblings (FS), half siblings (HS) and unrelated (U).

Statistical Analysis

We performed Fisher's exact tests to compare ratios of the numbers of infants sired from each male group (male

reproductive success) with the ratio derived from the number of counted copulations in each group male (male mating success). We analyzed the data for differences in the pair-wise relatedness of males (calculated by GenAlEx) among the study groups using a Kruskal–Wallis test. We also performed the Steel–Dwass test for multiple comparisons (Hsu, 1996) to compare the pair-wise relatedness of males among the study groups. Relatedness among males within groups was also compared using the asymptotic 2-sample permutation test. Apart from the analyses using the relatedness by GenAlEx, we statistically evaluated the categorical kinship, especially between the males observed coalition behaviors, by ML-RELATE; noted that the test was performed by repeating the test 1,000,000 times to obtain the p-value. First, we statistically examined whether a pair of the males judged as PO, FS, or HS, could be dismissed as unrelated (U). Second, we also examined whether a pair of the males judged as U, could be dismissed as HS. We used R 3.1.0 for statistical analyses (R-Core-Development-Team, 2021), and the significance level was set at 0.05.
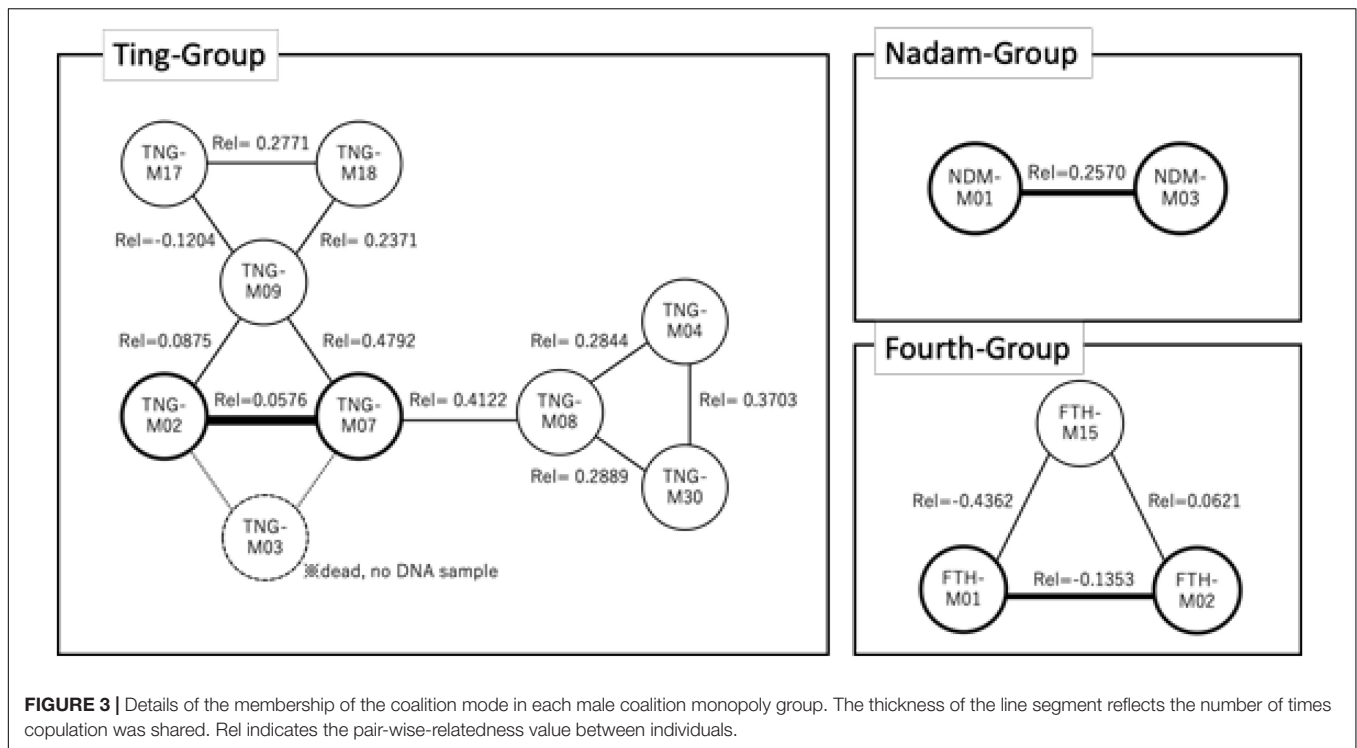
RESULTS

Copulatory Behaviors

Intra- and Inter-Group Copulations

During the 21 months of observation, 433 cases of copulation behaviors, i.e., 408 cases (94.2%) of intra-group copulation and 25 cases (5.7%) of inter-group copulation, were observed (**Table 1**). Inter-group copulations were rarely observed while encountering two groups, and it was generally observed that males approached females in another group. Of the 408 cases of intra-group copulations, 322 cases terminated in ejaculation (78.9%); notably, only 7 cases (8.1%) of interruption from other males were observed, although the reason for copulation without ejaculation was not apparent in most of these cases. Conversely, in 25 cases of inter-group copulations, only 7 cases (28.0%) were those of ejaculatory copulations, whereas 18 cases (72.0%) were terminated without ejaculation, i.e., the male stopped copulation

TABLE 1 | Mating success and reproductive success in each male of the study groups.

Group ID for mother–infant pairs	Male ID	Ejaculated copulation	Ejaculated copulation	No. of determined offspring	Note on extra-group paternity
		(Intra-group)	(Inter-group)		
Ting-Group	**TNG-M02**	36		1	
	TNG-M07	23	2	3	
	TNG-M08	24		1	
	TNG-M04	12			
	TNG-M17	7			
	TNG-M09	5		1	
	TNG-M18	2		5	
	TNG-M30	2			
	TNG-M19	2			
	TNG-M06	1		1	
	TNG-M10	1		2	
	TNG-M14		1		
	TNG-M31	1			
	TRD-M04			1	Male of Third-Group
	NDM-M01			1	Male of Nadam-Group
Fourth-Group	**FTH-M01**	42			
	FTH-M02	16			
	FTH-M15	10			
	FTH-M03	1			
	FTH-M06	1		1	
	FTH-M12	1			
	FTH-M04			1	
	TNG-M16			1	Male of Ting-Group
	TNG-M12			1	Male of Ting-Group
	TNG-M07			1	Male of Ting-Group
Third-Group	TRD-M01	68	1	4	
	TRD-M02	1	1		
	TRD-M03	2			
	TRD-M04	2			
	TRD-M05	1			
	TRD-M08	1			
	TRD-IM53	1			
	TRD-M06			1	
	TRD-M09			2	
	TRD-IM01			1	
	TNG-M07			1	Male of Ting-Group
	NDM-M02			1	Male of Nadam-Group
Wngklm-Group	WKM-M01	22			
	WKM-M02	5			
	WKM-M30	1			
	WKM-M03*			2	
	WKM-M32			1	
	TRD-M06			1	Male of Third-Group
	TRD-M09			1	Male of Third-Group

*In the Ting-Group and Fourth-Group, male coalition mode was observed; males involved in the coalition mode are marked in bold face. *WKM-M03 repeatedly migrated/immigrated between the Third- and Wngklm-Group, and thus the group ID of this individual was not reliable.*

FIGURE 3 | Details of the membership of the coalition mode in each male coalition monopoly group. The thickness of the line segment reflects the number of times copulation was shared. Rel indicates the pair-wise-relatedness value between individuals.

spontaneously possibly because of the appearance of other group members, but no direct interference from other males was observed. Female partner choice was not clear based on direct observations (but see the discussion); when copulation began, females often attempted to flee, screamed or resisted. The males, however, often forced copulation. Of the 347 mating cases for which it was possible to record whether or not the females resisted, 134 (38.6%) copulations were recorded as forced.

Single and Serial Copulation Types
In total, 26 cases of serial copulation, including 213 single copulation cases observed (49.2% of all observed single copulation cases), were recorded in the 5 study groups, i.e., 9, 4, 5, 6, and 2 cases of serial copulation type, such as 64 (38.1% of all single observed copulation cases), 21 (48.8%), 65 (55.8%), 48 (49.0%), and 15 (38.5%) single copulation cases were observed in the Ting-Group, Nadam-Group, Third-Group, Fourth-Group and Wngklm-Group, respectively. Both copulation types were observed in intra-group copulations, but only single copulations were observed in inter-group copulations.
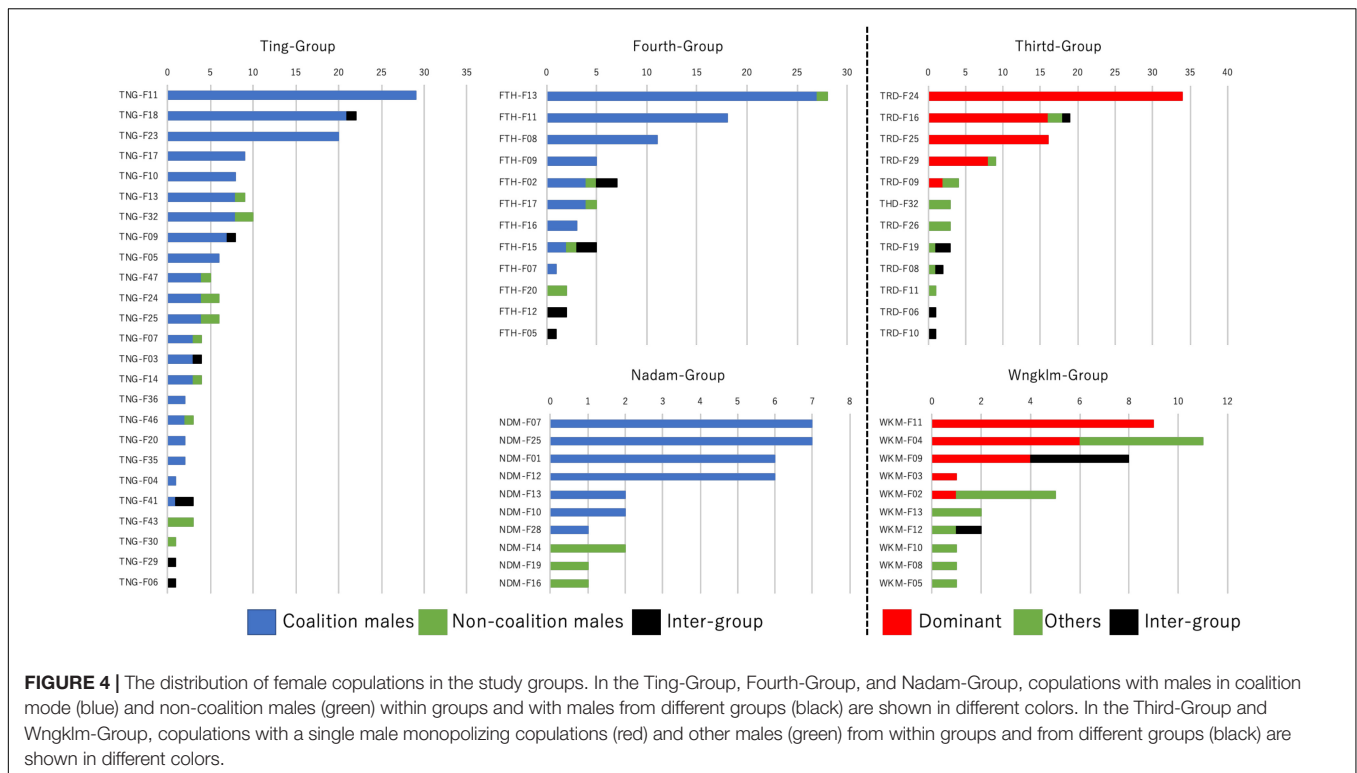
Coalition and Non-coalition Modes
Coalition mode forming male–male alliances (**Figure 3**) was only observed in three study groups (Ting-Group, Nadam-Group and Fourth-Group) during the serial copulation time. In the Ting-Group, males with four different combination patterns on coalition membership were observed, i.e., coalition01: TNG-M02, TNG-M03, TNG-M07, and TNG-M09; coalition02: TNG-M09, TNG-M17, and TNG-M18; coalition03: TNG-M07 and TNG-M08; and coalition04: TNG-M04, TNG-M08, and TNG-M30. In contrast, males with two fixed members in the Nadam-Group,

i.e., NDM-M01 and NDM-M03, and three fixed members in the Fourth-Group, i.e., FTH-M01, FTH-M02, and FTH-M15, were observed. However, this coalition mode was never observed in the Third-Group and Wngklm-Group, and a single male performed all serial copulations observed in these two groups.

Mating Success
In the Third-Group and Wngklm-Group, a single male mostly occupied the copulation opportunities (**Table 1**). The male in the Third-Group (TRD-M01) and Wngklm-Group (WKM-M01) successfully occupied 89.5 and 78.6% of the ejaculated copulations within groups, respectively, indicated as a "single-male monopoly group." In contrast, several males in coalition modes occupied the copulation opportunities in the other three groups, indicated as a "male coalition monopoly group." Males in coalition mode occupied 89.3, 79.1, and 87.2% of the ejaculated copulations in the Ting-, Nadam-, and Fourth-Groups, respectively.

Copulation distribution among females showed marked variation similar to that in the males in that copulation was not distributed evenly (**Figure 4**). Generally, the females were seldom to copulate with other males within the groups where mating opportunity was monopolized by a single male or male coalition (top of each graph). Likewise, such a tendency was found for copulations with other group males. Notably, males forming coalitions in male coalition monopoly groups could successfully copulate with a larger number of females within the groups, i.e., the Ting-Group (84.0% of the overall number of females in the group), Nadam-Group (70.0%) and Fourth-Group (75.0%), compared with the single male monopolizing copulation

FIGURE 4 | The distribution of female copulations in the study groups. In the Ting-Group, Fourth-Group, and Nadam-Group, copulations with males in coalition mode (blue) and non-coalition males (green) within groups and with males from different groups (black) are shown in different colors. In the Third-Group and Wngklm-Group, copulations with a single male monopolizing copulations (red) and other males (green) from within groups and from different groups (black) are shown in different colors.

opportunities in each of the single-male monopoly groups, i.e., the Third-Group (41.6%) and Wngklm-Group (50.0%).

Reproductive Success and Pair-Wise Relatedness in Males
Paternity Determination With a Comparison of Reproductive Success
DNA samples were collected from 48 mother–infant pairs within the possible 115 mother–infant pairs during the study period. The coverage rate of potential paternity candidacy was 91.7% (Toyoda and Malaivijitnond, 2018). We set a confidence level to guarantee the accurate judgment of the father candidate estimated using Cervus; however, we did not achieve this confidence level in six pairs. Because only two samples for mother–infant pairs were available in the Nadam-Group, we excluded this group from paternity determination. Consequently, we successfully determined the paternity of 36 mother–infant pairs with >80% confidence levels.

In the Third-Group, paternity was determined in 10 out of 13 tested infants. A single male (TRD-M01) who monopolized the copulations sired only four infants, although the male was the most successful in mating among all group males (**Table 1**). Additionally, the results of paternity determination showed that the degree of reproductive success did not reflect mating success in the Third-Group (Fisher's exact test, $P = 0.02$). Of the 18 tested infants in the Ting-Group (male coalition monopoly group), paternity was determined for 16 infants. The six males in coalition mode sired six infants. We found that the degree of reproductive success reflected mating success in the Ting-Group ($P = 0.27$),

suggesting that males involved in the coalition mode fairly shared their copulation opportunities.

It should be noted that the statistical evaluation of the difference between the mating and reproductive success in other groups (Wngklm-Group and Fourth-Group) was not performed because of the small sample size of infants for paternity determination. Nonetheless, although the sample size was not sufficient for statistical evaluation, in the single-male monopoly group, i.e., Wngklm-Group, the male (WKM-M01) that mostly occupied copulations, was surprisingly excluded as a paternal candidate for all tested infants; paternity was determined in five out of nine infants. The male (WKM-M03) that sired two infants was the most reproductive in the Wngklm-Group, although copulation by this male was not observed. In the Fourth-Group (male coalition monopoly group), the males who were involved in the coalition mode were excluded as paternal candidates for all tested infants for which paternity was determined; paternity was determined in five out of seven infants. Conversely, one infant was sired by each of the two males (FTH-M04 and FTH-M06), and they were the most reproductive in the Fourth-Group.

Although inter-group copulations were rarely observed, extra-group paternity was confirmed in the study groups, i.e., in 25.0–30.1% of all confirmed infants (**Table 1**). The reason for the variation in the percentages was that one male (WKM-M03) repeatedly migrated/immigrated between Third- and Wngklm-Group during the study period. More specifically, the extra-group paternity of the two infants in the Third-Group, two in the Ting-Group, two in the Wngklm-Group and three in the Fourth-Group was determined. Several infants with extra-group paternity tended to be related to a number of adult males in each

FIGURE 5 | Violin plot showing the average relatedness between males in the five study groups. Different colors indicate the group types, i.e., male coalition monopoly or single-male monopoly groups.
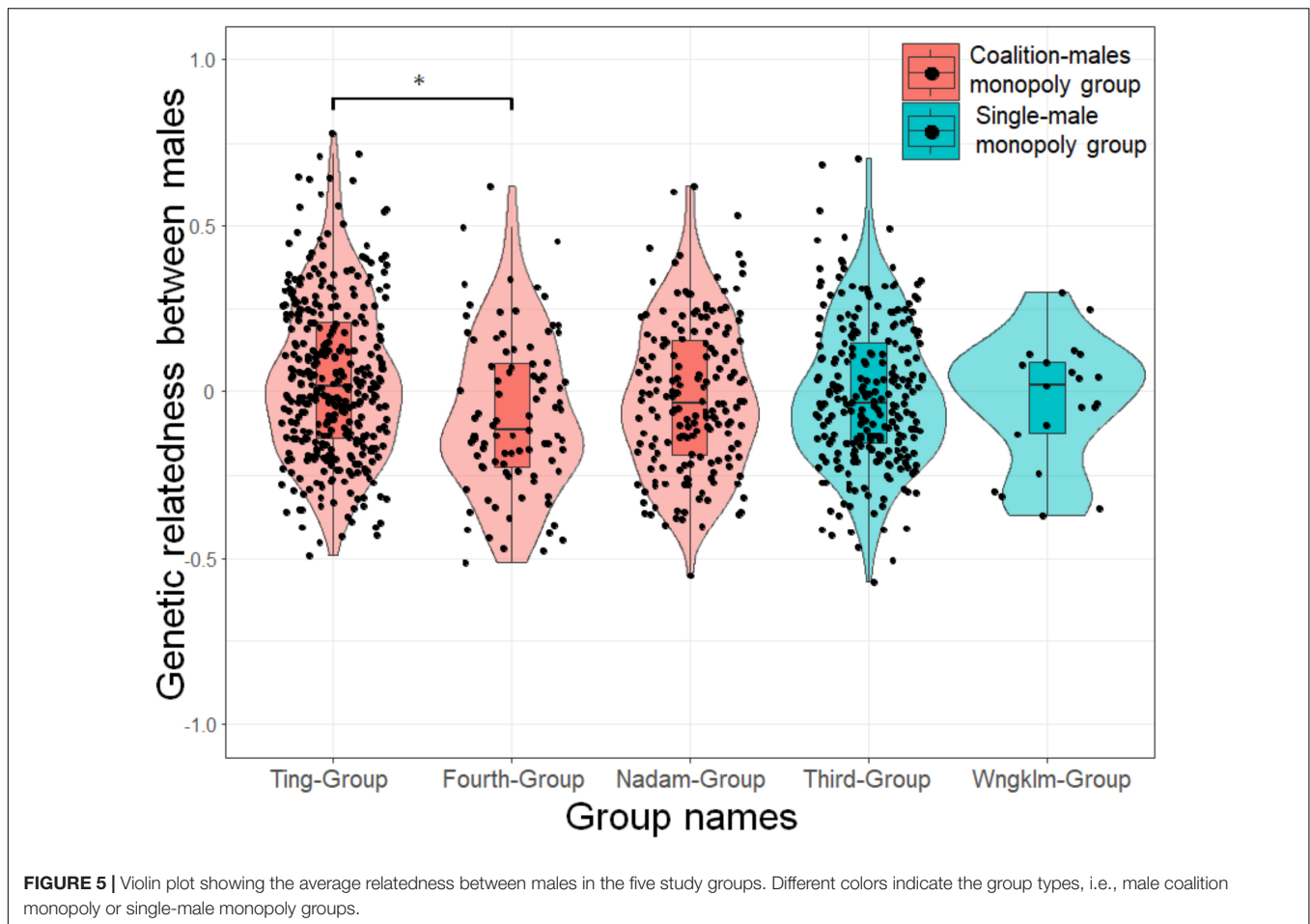
group. More infants with extra-group paternity were detected in the groups with fewer males, i.e., the number of infants with extra-group paternity accounted for 12.5% in the Ting-Group (30 males), 20.0% in the Third-Group (23 males), 60% in the Fourth-Group (16 males) and 40–80% in the Wngklm-Group (8 males) from all confirmed infants in each group.

Male–Male Relatedness

In the results of GenAlEx analysis, there was a significant difference in the pair-wise relatedness of males within study groups across the five study groups (Kruskal–Wallis test: $\chi^2 = 15.147$, $P = 0.004$; **Figure 5**). The Steel–Dwass test for multiple comparisons showed that pair-wise relatedness of males within the Ting-Group was significantly higher than that of males within the Fourth-Group ($t = 3.49$, $P = 0.0043$). Both Ting-Group and Fourth-Group were male coalition monopoly groups, indicating that the overall structure of higher genetic relatedness among males was not always the driving force for male–male coalitions.

Conversely, males tended to choose genetically closer males as coalition partners within the groups (**Figure 6**). In the Ting-Group, the relatedness among the male coalition was significantly higher than that among the other non-coalition males (asymptotic 2-sample permutation test,

$p < 0.05$; **Figure 6**). Nonetheless, the coalitions were not always formed among the highly related males in the Ting-Group because relatedness fluctuated from 0.06 (TNG-M02 and TNG-M07) to 0.48 (TNG-M07 and TNG-M09) among the males forming the coalitions (**Figure 3**). In the other two groups, statistical comparisons of pair-wise relatedness were impossible because of the small number of males participating in the coalitions; however, the coalitions were not formed in the most closely related male combinations within the groups similar to that of the Ting-Group.

Among the males forming the coalition, there were several male-male pairs categorized into PO, FS, and HS, especially in the Ting group (see the details in **Supplementary Table 3**). It was confirmed that a pair of the males judged as PO and FS could be dismissed as unrelated (U), though the pairs judged as HS could not be dismissed. In addition, all pairs of males judged as U could be dismissed as HS. Thus, The assigned kinship by ML-RELATE supported the results based on the relatedness. In the Ting-Group, among the 10 dyads of male pairs involved in the male coalition, 6 dyads were assigned as related, i.e., PO, FS, or HS. The other 4 dyads were assigned as unrelated. Note that only 3 of the 10 cases were statistically singinicant probably due to the small number of microsatellite markers used in this study. The

FIGURE 6 | Violin plot showing the average relatedness between the males in coalition mode and other males in each male coalition monopoly groups. Note that conducting the asymptotic 2-sample permutation test was possible only in the Ting-Group and not in the Nadam-Group and Fourth-Group because of their small sample size.
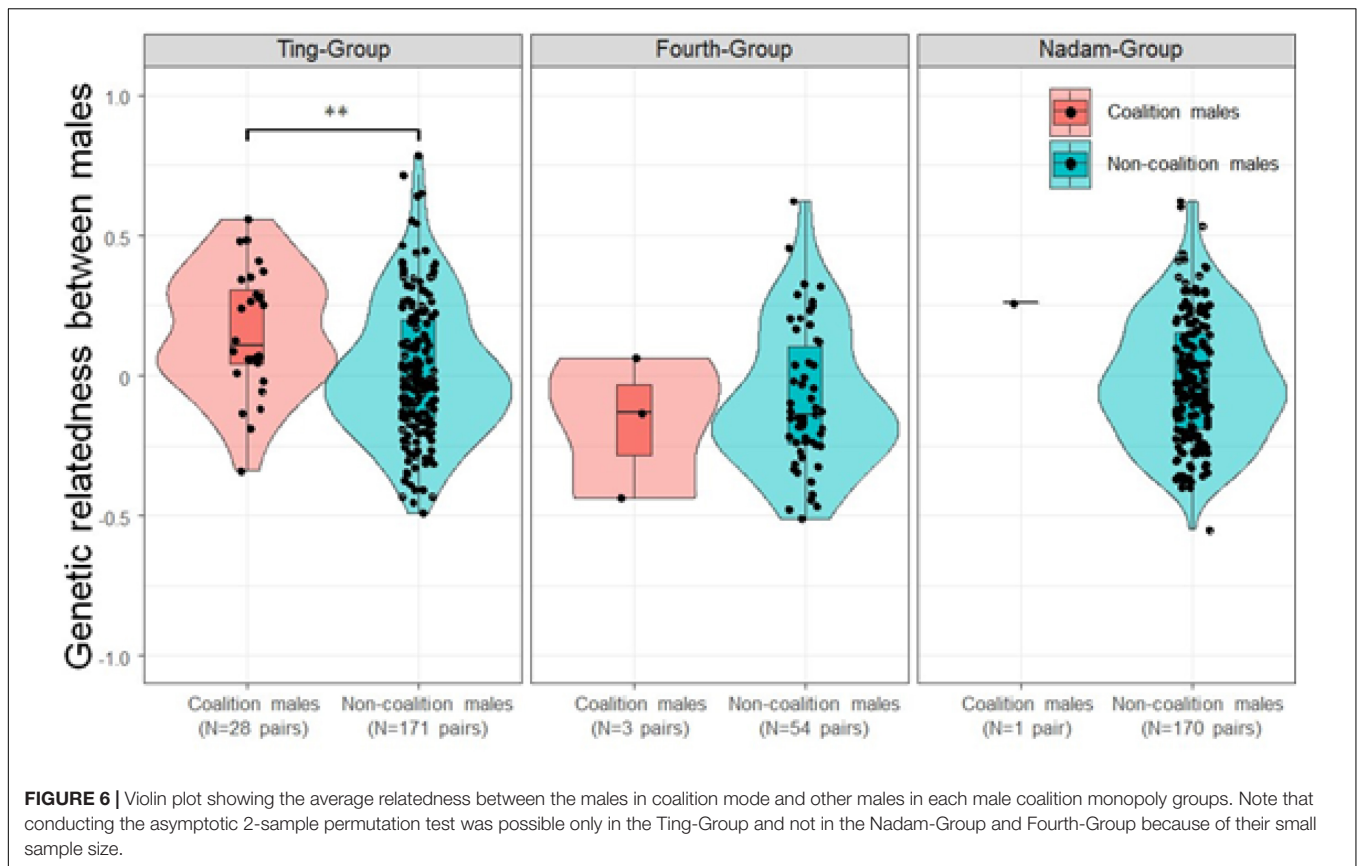
male dyad of the Nadam-Group was assigned as HS, and the three male dyads of the Fourth-Group were assigned as unrelated (but not significant in all cases).

On the other hand, it was not certain that a particular combination of relationships can be affirmed as PO, FS, or HS. Therefore, to verify the accuracy of categorical judgment by ML-RELATE, based on the dataset of mothers and infants with clear consanguinity, we calculated the false negative rate for not judging the mother as PO and the false positive rate for judging extra-group females that should be non-consanguineous to the infant as PO, FS, and HS. The false negative rate was 26.9% and the false positive rate was 31.3%. These results were possibly because too few loci were analyzed for evaluating the pedigree relationship using ML-RELATE. Indeed, the data set used for analysis contained many mother–infant pairs; therefore, the proportions of the samples were biased. In the pedigree relationship estimated using ML-RELATE, combinations of males with the same age were determined to be POs; these were clearly incorrect estimations based on our field observations (**Supplementary Table 3**). Therefore, we could not deny that the males forming the coalition include "fathers and sons (PO)" or "brothers (FS)."

A common conclusion of the relatedness analysis of pairs formed by male coalitions using GenAlEx and ML-RELATE was that the coalition males of the Ting-Group contained potentially highly related male pairs, but that there was no

evidence of relatedness between coalition males in Nadam-Group and Fourth-Group.

DISCUSSION

Copulatory Behavior in Relation to Male–Male Coalition and Paternity

This study is the first to describe the detailed copulatory behaviors of *M. arctoides* in the wild. It, therefore, provides a complete depiction of their unique mating strategies, especially the coalition mode of forming male–male alliances with shared mating opportunities, which has never been reported in other female-philopatric primates. Echoing the observation of copulatory behavior in this study, Fooden (1990) noted the unique copulation, especially the so-called serial copulation, in *M. arctoides* to be strikingly different from other phylogenetically close macaque species, such as *M. sylvanus* and *M. radiata*. Additionally, as reported in captive *M. arctoides* (Estep et al., 1984; Brereton, 1994), in this study, we also found that only a few males monopolized the mating opportunities even in the free-ranging groups. Although the dominance rank was not systematically tested in this study, males who monopolized mating opportunities in our study were seemingly higher-ranking males in the groups as shown by previous studies on *M. arctoides* in captivity (Gouzoules, 1974; Niemeyer and Chamove, 1983; Estep et al., 1988). Furthermore, in this study, the distribution

of copulations among females was not prominently skewed as observed in case of males; however, it was not evenly distributed, which is similar to previous findings of studies on *M. arctoides* in captivity (Estep et al., 1984; Brereton, 1994).

Although basic copulatory behaviors in free-ranging populations are comparable to those in captivity, our notable findings were the copulatory behaviors in relation to two different mating strategies by males, which has not been reported even in free-ranging populations (Richter et al., 2009). In this study, coalition mode was observed in three out of five study groups while engaging in serial copulations, as reported by Toyoda et al. (2020b). Based on the analysis, focusing on the number of males monopolizing the copulations within groups, we elucidated about two different group types with different mating strategies, i.e., single-male monopoly and male coalition monopoly. Nearly 80% of copulations were monopolized by a single male or several males (coalition mode). Because monopolizing access to fertile females is one of the universal strategies in non-human primates to maximize the reproductive success for males, e.g., chimpanzees (Nishida, 1990), mandrills (Setchell et al., 2005) and long-tailed macaques (Engelhardt et al., 2006), both mating strategies would be successful.

Nonetheless, based on the genetic data assessing the paternity of infants in the study groups, benefits and drawbacks in two different mating strategies were revealed. If only one male can monopolize the females within the groups, such as the Third-Group and Wngklm-Group, it would be the best reproductive strategy. In reality, however, such a strategy allowed for opportunistic/sneaky copulations by other males with a relatively high probability. Thus, the degree of mating success did not reflect the reproductive success in the single-male monopoly group. Indeed, in the single-male monopolized groups, the peripheral males in whom copulations were never observed sired the same number of infants as the males that monopolized the observed copulations in the Third- and Wngklm-Groups (**Table 1**). Thus, opportunistic/sneaky copulations may serve as an effective strategy for those peripheral or non-group males who cannot constantly access females. Contrary to a study in captivity that showed that alpha males effectively achieved a virtual monopoly in siring an offspring (Hearn and Bauers, 1994), monitoring all group females by only one or a few males may be difficult in free-ranging populations. In fact, in an experimental study of captive *M. arctoides*, when higher-ranking males were removed from their view in captivity, lower-ranking males started copulating more frequently (Estep et al., 1988), supporting the fact that opportunistic/sneaky copulations commonly occur in natural habitats where subordinates have more opportunity to escape the view of dominant males for copulations.

Contrastingly, the males in coalition mode could successfully share their mating and reproductive success in the male coalition monopoly group, especially in the Ting-Group. Paternity determination by microsatellite analysis showed that reproductive success among the male coalition was almost equally distributed. In addition, compared with the single-male monopolized groups, males of the male coalition monopoly groups could successfully copulate with a larger number females in the group, suggesting that male copulation would effectively

guard females against opportunistic/sneaky copulations by other rival males. Coalition formation is not only beneficial to cover a larger number of females as mating partners but also allows males to be more vigilant and capable of detecting other rival males approaching the females. Thus, advantageous factors, such as an effective mating guard, triggered male–male coalitions in *M. arctoides*, particularly in a larger group, as observed in the Ting-Group. Although it has been suggested that *M. arctoides* relies on non-visual cues to assess female reproductive status (Murray et al., 1985; Cerda-Molina et al., 2006), it has been noted to be a non-seasonal breeder, and the lack of visual signals, such as the swelling of the female's perineum (Napier and Napier, 1967; Bertrand, 1969; Heldstab et al., 2021), supports the idea that keeping a constant watch on both females and rival males would be profitable by multiple males in a coalition compared with a single male in larger groups.

Nonetheless, this result should be interpreted with caution because the results of paternity determination showed that reproductive success did not reflect mating success even in the male coalition monopoly group, i.e., the Fourth-Group. In other words, despite the fact that the male coalition conducted most of the ejaculatory copulations, their reproductive success was lower than expected from the number of observed copulations, indicating that peripheral or non-group males have higher reproductive success than expected. Differing group size, particularly the number of males in groups, might have led to this inconsistency between the Ting- (30 adult males in total) and Fourth-Groups (16 males). A higher number of males in a group would allow males to organize multiple combinations of coalition formation, enabling more males to have copulation opportunities with females, as observed in the Ting-Group. Therefore, the gap between mating and reproductive success may be less prominent. In the case of the Fourth-Group, despite the observed male–male coalition, a single combination of coalition formation involving only three males was detected, which possibly induced the prominent skew of mating success in group males owing to the number of group males being lower than in the Ting-Group. Thus, in male coalition monopoly groups, the number of group males in relation to the number of males involved in the coalition formation and monopolizing copulation opportunities is key in explaining whether the group males can fairly share their mating and reproductive success.

Sneaky/Opportunistic Copulation in Relation to Partner Preference by Females

The gap between mating and reproductive success has been reported in other primates. A study on chimpanzees showed that while only alpha males monopolized females to achieve paternity, other high- and middle-ranking males achieved paternity through opportunistic mating (Constable et al., 2001), concluding that such mating may be an effective strategy for non-alpha males because they cannot monopolize females. In addition, several studies evaluating paternity in free-ranging *M. fuscata* showed a similar tendency that mating success does

not necessarily result in high reproductive success, with this inconsistency being explained by female mate choice (Inoue et al., 1990; Soltis et al., 2001; Hayakawa, 2008). Indeed, mating success was positively correlated with male dominance in *M. fuscata*; however, paternity tests showed that higher-ranking males did not sire the infants within groups (Inoue et al., 1993). These results are consistent with the fact that *M. fuscata* females copulated with higher-ranking males with long tenures during the non-ovulation period. However, lower-ranking males with shorter tenures are selected as mating partners during the ovulation period (Inoue and Takenaka, 2008). Furthermore, a study on *M. mulatta* showed that dominance was not associated with reproductive success, with 4 of the 11 infants being sired by males from other social groups, and the four infants of unknown paternity were sired either by males who were not observed mating with the females or the lower-ranking males who were not fingerprinted (Berard et al., 1993). This result supports the fact that females prefer low-ranking or non-group males as "less familiar" or "novel" partners as suggested in *M. fuscata* (Takahata et al., 1999). Although female preference in *M. arctoides* has not been studied well, an experimental study revealed that female proceptive behavior increases in the absence of high-ranking males (Estep et al., 1988), indicating that similar to that in other *Macaca* spp., effects of female preference is an important factor in understanding the gap between mating and reproductive success in *M. arctoides*.

Sneaky/opportunistic copulations in relation to female preference may be explained well by the number of group males in *M. arctoides*; although, female preferences are commonly difficult to assess (Clutton-Brock and McAuliffe, 2009). In the two study groups with a small number of males (Fourth- and Wngklm-Group), infants were mostly not sired by the male(s) monopolizing the mating opportunity in the groups but were sired by other rival males within groups or other groups. In theory, it should be easier to monitor all group members and detect sneaking copulations if females do not actively move away from the center of the group to follow less familiar or novel male partners within groups or in other groups. Therefore, given the observed low mating success by sneaking males but with relatively high reproductive success, it would be assumed that reproductive partner choice (not mating partner choice) is strongly affected by female preferences in those two study groups with a small number of males. Thus, because there were not many options for reproductive partner choice within Fourth- and Wngklm-Groups, females might have actively sought less familiar or novel partners as reported in other macaque species (Takahata et al., 1999). Furthermore, the two study groups with a larger number of males, especially in the Ting-Group, showed a less prominent gap between mating and reproductive success with less sneaky/opportunistic reproductive success, supporting our opinion that the number of males influence the level of female preference in *M. arctoides*.

Male Relatedness and Coalition

Genetic analysis focusing on the relatedness among males within groups partly revealed the factor determining the formation of male coalitions. In the Ting-Group, the largest male coalition monopoly group, including several combinations of male–male coalitions, relatedness among the male coalition was significantly higher than that in non-coalition males. Although this result can not immediately imply a "brotherly" coalition among males due to the trade-off issues of coalition formation, it is a reasonable outcome, wherein even if those males are competitors for paternity, the degree of inclusive fitness increases to form a coalition with males who are highly related. This explanation would also be supported by the fact that there was no extreme reproductive skew among the male coalitions in the Ting-Group.

Male–male coalitions or cooperative alliances, often involving close kin, e.g., maternal brothers, have been reported in primates with male philopatry, e.g., chimpanzees, bonobos and spider monkeys (Nishida and Hiraiwa-Hasegawa, 1987; Valero et al., 2006), and males are often tolerant to group males and share copulations with receptive females (Nishida, 1983; Watts, 1998; Strier et al., 2002). Thus, the question to be resolved is under what conditions can the degree of relatedness increase among certain males in a matrilineal social system, such as that of *M. arctoides*, and how the male coalition perceives such higher relatedness. One possibility is the male "parallel dispersal," in which several males migrate from the same group to another group together, as observed in the study groups. During the study period, 36 cases of migration were observed, and 15 cases occurred from the same original group to the same group within 2 weeks after the predecessors moved on (unpublished observation by Toyoda). It is entirely possible that the "familiar" males, born and grown in the same group (possibly with high relatedness), chose them as coalition partners after their transfer to new groups. Male–male coalitions observed in non-human primates, e.g., *Alouatta seniculus* (Pope, 1990) and *Cebus capucinus* (Wikberg et al., 2014), have been suggested to be the results of such parallel dispersal (Jack et al., 2009). Further evaluation of such effects of parallel dispersal on increased relatedness and preference to form male coalitions in the matrilineal social system of *M. arctoides* is necessary in a future study.

However, the combination of low relatedness male–male coalitions in the Ting-Group and similar coalitions between low relatedness males were also prominent in other male coalition monopoly groups. Among primate species with male dispersal, observation of coalitions with non-kin alliances is less frequent in general. Under certain conditions of competition for access to sexually receptive females, such male–male coalitions with non-kin alliances have been observed mostly in the context of aggressive interactions. For instance, males may develop stable alliances with each other to overpower younger higher-ranking rivals in *Papio cynocephalus* (Cheney et al., 1986), to takeover groups of females in *Alouatta seniculus* (Crockett and Sekulic, 1984) and to support other males in agonistic coalitions in *M. radiata* (Silk, 1992) and *Saimiri sciureus* (Mitchell, 1994). Schulke et al. (2010) also demonstrated a causal link between differentiated social bonds and fitness in *M. assamensis* males, especially in the absence of strong kin bias. In both kin and non-kin male–male coalitions, increasing male mating opportunities leading to reproductive success may explain the formation of male–male alliances with either lower or higher relatedness

among members in *M. arctoides,* which is consistent with the findings of previous studies.

Outlook

We followed up with multiple groups of *M. arctoides* over a period of 21 months. We successfully collected genetic samples from nearly all potential sires and approximately half of the mother–child pairs despite studying the population under natural conditions. Consequently, we were able to outline their reproductive success in relation to the mating strategies of males. We also revealed a rare phenomenon by which different social conditions and kinship structures within groups promoted a male–male coalition. In a future study, determining the full set of infant paternity with a longer observation period would provide further understanding of reproductive success spanning the entire lifetime through factors such as the history of males, female mate choice and genetic kinship.

Lastly, non-human primates often are representative reference models for understanding evolutionary trajectories of human cooperative behaviors, including the male–male coalition, which is common in human society (Silk, 2003). Similar to human society, coalition mode forming male–male alliances often occurs among relatives and non-relatives, indicating the complexity and flexibility inherent in the male social bond of *M. arctoides*. *M. arctoides*, thus, may be a useful species to understand the evolutionary functions of friendship, which is a fundamental element of our social life.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by the Department of National Parks, Wildlife and Plant Conservation of Thailand.

AUTHOR CONTRIBUTIONS

AT, TM, and IM conceptualized the initial idea. AT performed the field observation. AT, YK, and KM conducted genetic analysis at the laboratory. SM arranged the sampling and laboratory analyses in Thailand. AT and IM performed and interpreted the statistical analyses and drafted the manuscript. All authors contributed to the final version of the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.802012/full#supplementary-material

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