Cooperation for copulation: a novel ecological mechanism underlying the evolution of coalition for sharing mating opportunities

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Abstract: Cooperation, or the act of benefiting others at the cost of the benefactor's fitness, has been a central issue in evolutionary theory. Non-human animals sometimes show coalitions or male-male “cooperation” to confront a male rival and challenge the rank hierarchy. Here we observed novel types of coalitions in wild stump-tailed macaques; multiple males actively shared the mating opportunities, i.e., a male copulated with a female, while his ally waited his turn and guarded them. Our mathematical simulations revealed that lack of estrous signs, as well as large numbers of males in a group, possibly enhance facultative sharing of females. This is the first demonstration of the sharing of females in non-human primates, and shed light on the evolutionary theory of cooperation.

Key words: cooperation, sexual traits, socioecological modeling, stump-tailed macaques

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INTRODUCTION

Cooperation, or the act of benefiting others at the cost of the benefactor's fitness, has attracted the attention of evolutionary biologists as its origins constitute an evolutionary puzzle. The modern theoretical framework for the evolution of cooperation originated from Hamilton's inclusive fitness theory [1,2] for kin altruism, along with the idea of reciprocity, as proposed by Trivers, for cooperation among non-kin [3]. Humans are unique in showing "hyper-cooperation" owing to their "spontaneous" tendency to be helpful [4]. For example, helping, a direct form of cooperation, is observed in humans even from infancy, whereas this is rare or absent in non-human animals, especially helping of non-relatives [5].

The formation of coalitions may be considered as a form of cooperative behavior in non-human animals. Coalition is often defined as joint aggression by multiple individuals against common targets [6]. An individual may, for example, intervene in a conflict involving his/her ally to provide agonistic support, where the cost of the intervention may be compensated by reciprocal support by the ally in future. The first observations of coalition formation involving unrelated individuals were reported in pioneer studies on primate societies, such as in baboons [7], as had been predicted by Trivers. For example, unrelated male baboons form coalitions to exclude non-allies from access to females [7–9]. Non-kin coalition has also been documented in male lions, who jointly guard females against the invading coalitions of other males [10,11]. So far, coalition beyond kinship has been reported in several species, including chimpanzees[12]. Coalition formation in male chimpanzees is particularly interesting because of its potential relevance for the origins of human patrilineal societies[13].

Male reproductive success in a multi-male multi-female group is often skewed in the favor of high-ranking males [14]. Subordinate males may gain more opportunities of copulation by forming a coalition to jointly confront the top-ranking male than by competing individually against each other. Previous studies have developed a mathematical framework for investigating the underlying mechanisms of coalition formation and mitigating the existing reproductive skew both when the formation of coalition does or does not change male ranks [15] [6]. While this framework is comprehensive enough to cover different coalition varieties, such as all-down, bridging, and all-up coalitions [6], it is still limited by the fact that it only considers the mitigating or leveling effect of coalition formation on the reproductive skew. There is a yet another possibility; two or more top-ranking males may form a coalition to exclude lower-ranking males from mating opportunities, as a result of which the reproductive skew favoring dominant males is strengthened or steepened. However, this type of coalition is, while intuitively conceivable, not expected to be observed frequently. This is because even if two or more top-ranking males are able to jointly exclude other males, the mating opportunities thus obtained may be monopolized by the single top-ranking male after all, unless he actively shares the spoil with his allies. In other words, the top-ranking male has to pay for others' help.

In this study, we report a novel observation of coalition formation among dominant males to guard and actively share mating opportunities in stump-tailed macaques (*Macaca arctoides*). At a glance, the physical appearances of stump-tailed macaques are typical of *Macaca* species, without anything spectacular such as the long nose in proboscis monkeys [16] or the bright facial coloration on mandrills [17]. Nevertheless, they possess unique morphological and behavioral features, indicating that sperm competition may play a major role in this species [18]. For example, the glans penis of adult males is longer than those in other *Macaca* species [18,19]. They also exhibit unique copulatory behavior, which consists of a brief series of pelvic thrusts, followed by a long period of "post-ejaculatory pair sit," interpreted as male guarding his mate [20]. While stump-tailed macaque is usually a single mount ejaculator [18,21], in which males ejaculate in a single bout of mounting, they sometimes engage in "serial copulations," or a behavioral sequence composed of multiple mounting on a single female with penile insertion within a short time interval, each of which often terminates with ejaculation [22,23]. These various characteristics are predicted to have evolved due to male-male competition triggered by females' strategies for concealing estrus signs, as discussed previously [24,25]. In this study, we have first described our novel findings regarding the fieldwork on groups of stump-tailed macaques and then analyzed the logic underlying these observations using mathematical modeling. Finally, we have attempted to integrate the knowledge available till date to understand the reproductive ecology of the species.

METHODS

Study site and animals

A wild population of stump-tailed macaques inhabiting the Khao Krapuk Khao Taomor non-hunting area in the Phetchaburi Province of central Thailand (99°44' E, 12°48' N, encompassing an area of 3.5–4 km^2) was observed. This site consists primarily of secondary forests, including stands of bamboo and agricultural areas. The macaques also visited areas immediately adjacent to this site (including a nearby temple, cassava and pineapple plantations, and human settlements) on a daily basis. The macaques were occasionally fed by humans, both locals and tourists, on the temple grounds or along the roadside. This population was first reported in June of 1984, at which time there were only 22 individuals. Since then, it has grown to a large population, including at least 391 individuals, who were divided into five groups, namely, Ting, Nadam, Third, Fourth, and Wngklm groups (Table 1) by 2017. The Wngklm group separated from the Third group in November–December 2015. All adults (completely mature monkeys), most subadults (sexually mature but not completely developed), and some juveniles (sexually immature, around 3 years of age) were identified based on facial characteristics. This population is geographically isolated from the other populations, and no new immigrant males from other sites were detected during this study period [24,for related democratic information, see 25].

Daily observations

AT performed the 21-month field observations for the five groups, between September 25, 2015 to June 15, 2017. In total, the animals were observed for 289 days (970.7 hours). The monkeys were followed daily between 09:00 and 17:00 h; the group that was first encountered each day was followed for as long as possible. When the target group could not be followed further (e.g., when the monkeys travelled along cliffs), the observation of the target group was terminated, and another group was seek out and followed.

Copulation definitions and analysis

All copulations during our observation were recorded using video cameras (JVC GZ-RX500 and Sony HDR-PJ675) and their descriptions were noted. Here, a single copulation was defined as a single event consisting of single mount-insertion-separation irrespective of ejaculation, based on the previous report [22]. In total, 433 cases of single copulation events were recorded. Next, the occurrence time of a single copulation event was measured, and the inter-copulation intervals (ICIs) of all recorded single copulation events that occurred multiple times in a day were calculated for defining copulation bout. A "serial copulation bout" was defined as the copulation series including more than four single copulation events, of which every ICI was less than 30 min (for the rationale of the interval criterion see Figure 1). This definition was modified for quantitativeness from the relatively ambiguous definition of the previous studies [22,23]. The other bout was defined as "non-serial copulation bout". For all copulation events and copulation bouts, the IDs of the males and females involved were recorded. The observed counts of the copulation events and bouts of those involved simultaneously in the same serial copulation bout were determined.

Estimation of parameters

Based on the priority-of-access model (PvS model), we estimated the despotic parameter, β, using nonlinear regression analysis for the count data of copulation events. For strict evaluation of the copulation success, only count data of copulation events with ejaculations were used. Then, the males were descending-sorted by copulation event counts for each group, and assigned the "dominance rank"; for example, the male who showed frequent counts of ejaculated copulation event was considered the 1st male in a group. Rank order (i) was fitted to count data (x_i) of copulation events based on the formula (1) or (2) of the PvS model using the nonlinear regression function of Python (curve_fit method in scipy.optimize module). In addition, R^2 values were reported for showing the goodness-of-fitting.

Mathematical model

To understand the logic behind the novel male-male coalition identified in stump-tailed macaques, we developed a simple mathematical model based on the framework developed by Pandit and van Schaik [15]. Our motivation for the mathematical modeling was two-fold. First, it is intuitively conceivable that concealed ovulation, as in stump-tailed macaques, hinders the alpha male from guarding all fertilizations, and thus necessitates collaboration of two or more dominant males for reproductive monopoly. However, it is unclear as to whether and under what circumstances the alpha male tolerates one or more allies copulating with females. Second, we have observed within-species variation in the occurrence of male-male coalition in stump-tailed macaques: it occurs in the Ting, Nadam, and Fourth groups, but not in the Third and Wngklm groups (see Figure 2). If our model for the underlying logic of male-male coalition is correct, it should also explain this pattern of within-species variation.

We considered a group of N males and a constant number of females. In the case of a linear order of dominance among the males, the relative access of the ith male to females, x_i, in the absence of male-male coalition is described by the priority-of-access model [26], namely,

$$x_i = (1-\beta)^{i-1}x_1, \quad (1)$$

where β represents the degree to which dominant males can monopolize mating opportunities ($0 < \beta < 1$).

Ecological and demographic factors have been suggested to affect β [6]. Of these, cryptic ovulation in females probably reduces β as it prevents dominant males from guarding each female intensively only during her fertile periods. Thus, compared to species in which ovulation is advertised, species with cryptic ovulation are expected to have small β. In contrast, other factors, such as the number of females in the group, the relative strengths of dominant males, and the female preference for or against dominant males, are also likely to affect β. As the latter factors may vary within a species, we expect that different groups of stump-tailed macaques are characterized by different β values.

In groups with relatively small β, it may be beneficial for top-ranking males to form a novel type of coalition in which allied males guard potentially fertile females in a collaborative manner to exclude subordinate males from copulation opportunities, which are then simultaneously shared among the allies. This type of coalition may be represented by the following equation:

$$x_i = (1 - s\beta)^{i-1} x_1, \quad (2)$$

where we assume $1 < s < 1/\beta$. Parameter s reflects the effect of male-male coalition to "steepen" the male reproductive skew, where larger s indicates higher reproductive monopolization by dominant males. It should be emphasized that our parameter s differs from α, the similar parameter in Pandit and van Schaik's (2003) model, which considered the effect of coalition among subordinate males to "level" the reproductive skew (i.e., $0 \leq \alpha \leq 1$). As this type of male-male coalition is by definition conservative [27] or all-down [28], it is always feasible as no single male outside the coalition can prevent it from occurring [15].

To evaluate the profitability of a male-male coalition, the cost and benefit of coalition formation has to be defined. We considered two components of a particular male's fitness: the ratio of the mating opportunities gained by that male to all the mating opportunities, and the cost of coalition associated with the additional effort of collaborating with others. As for the first component, y_i denotes the proportion of mating opportunities obtained by the ith male among all matings; in other words,

$$y_i = \frac{x_i}{\sum_{j=1}^{N} x_j}. \quad (3)$$

From (1) and (2), in the absence of male-male coalition, we obtain

$$y_i = \frac{\beta(1-\beta)^{i-1}}{1-(1-\beta)^N}, \quad (4)$$

while in the presence of coalition,

$$y_i = \frac{s\beta(1-s\beta)^{i-1}}{1-(1-s\beta)^N}. \quad (5)$$

Regarding the second component, we assume that the first components of males forming a coalition are multiplied by $1 - c$, where c represents the cost of coalition ($0 < c < 1$), while those of non-coalition males are multiplied by 1. Therefore, for the ith male, joining a coalition is profitable if and only if

$$\frac{s\beta(1-s\beta)^{i-1}}{1-(1-s\beta)^N}(1-c) > \frac{\beta(1-\beta)^{i-1}}{1-(1-\beta)^N}, \quad (6)$$

or equivalently,

$$\left(\frac{1-s\beta}{1-\beta}\right)^{i-1} > \frac{1}{s(1-c)} \frac{1-(1-s\beta)^N}{1-(1-\beta)^N}. \quad (7)$$

As $1 - s\beta < 1 - \beta$, the left-hand side of (7) decreases with increasing i; thus, whenever (7) holds for the mth male ($m \geq 2$), it also holds for the first to $m - 1$th males.

Therefore, from (7), we derive the upper boundary of coalition size, m^*, for specific β, N, s, and c as

$$m^* = 1 + \frac{\log[s(1-c)] - \log\dfrac{1-(1-s\beta)^N}{1-(1-\beta)^N}}{\log\dfrac{1-\beta}{1-s\beta}}. \quad (8)$$

Equation (8) immediately shows that $s(1-c) > 1$ is necessary for any coalition to be viable; otherwise, $m^* < 1$ always holds. It also shows that the right-hand side of (8) increases with N (Figure 3a, 3b). For large N, the upper boundary of the coalition size is obtained approximately using

$$m^* \approx 1 + \frac{\log[s(1-c)]}{\log\dfrac{1-\beta}{1-s\beta}}, \quad (9)$$

which decreases with increasing β whenever $s(1-c) > 1$. On the other hand, when β is small, (8) is approximated by

$$m^* \approx 1 + \frac{\log(1-c)}{\log[1+(s-1)\beta]}, \quad (10)$$

indicating that as β approaches zero, m^* diverges to minus infinity. In general, however, the dependence of m^* on β is not monotonic (Figure 3c, 3d).

For coalition of at least two males (i.e., $m^* > 2$), (9) shows that β should be smaller than a threshold, specified by

$$\beta < \frac{s(1-c)-1}{s^2(1-c)-1}. \quad (11)$$

Hence, for any coalition to occur, β has to be relatively small, but not extremely small. Figure 5 illustrates the combinations of N and β values, for which $m^* > 2$ (based on (8)).

RESULTS

Behavioral analysis

During our 21 months of field observations, we counted 433 cases of copulations (defined as a single event consisting of single mount-insertion-separation, see Materials and method section) from five subject groups (391 individuals consisting of 97 adult males, 124 adult females, 114 infants ($\leq$ 2 years), and 56 subadult unidentified subjects (see Toyoda et al 2018). The inter-copulation intervals (ICI) of all recorded single copulation events that occurred multiple times between the female and male(s) in a day ($N_{ICI} = 206$) were measured; the median with ranges of ICI were 7 (0–359) min (Figure 1), and 95% events occurred within 30 min ICI. We defined the serial copulation bout as the copulation series including more than four single copulation events, of which every ICI was less than 30 min, which partially followed the definitions of the previous study [22,23] (for details, see Materials and method section). Out of the 433 copulation events, 213 (49.2 %) cases occurred in serial copulation bouts, i.e., repeated single mount-insertion-separation copulation event with one female recipient partner. In contrast, 220 (50.8%) cases occurred as non-serial copulations. In total, 26 serial copulation bouts (number of single copulation events with ejaculation per bout, median: 6.0 times; range: 1–31 times) were recorded in the five-subject groups (Ting group: 9 times; Nadam: 4; Third: 5; Fourth: 6; Wngklm: 2, for details see Table 2 and Figure 4). Thus, almost 50% of single copulation events occurred as a part of the serial copulation bout. The seven cases of serial copulations in the Third and Wngklm groups were of alpha males (named TRD-M01 and WKM-M01 for Third and Wngklm groups, respectively), i.e., one male maintained the proximity to females and was involved in most of the copulations. In total, we recorded 80 copulations include 68 ejaculatory copulations (81.8% of all copulation occurrences, 86.1% of all ejaculated copulation) of TRD-M01, and 26 copulations 22 ejaculatory copulations (59.1%, 78.6%) of WKM-M01 as well, indicating their monopoly over copulations (Figure 2, see "alpha-male-monopoly type).

In contrast, the serial copulation patterns of the Ting, Nadam, and Fourth groups differed from those of the Third and Wngklm groups (Figure 2, see "coalition type). Interestingly, we observed that multiple males were involved in a single serial copulation bout; each of the males first performed the single mount-insertion-separation copulation event several times and the other male(s) maintained close proximity to the copulating male-female pair without any agonistic interaction, after which the males serially changed positions as copulators (Figure 5). These multi-male serial copulation bouts were observed 26 times in total (Table 2). Six, two, and three males were involved in the multi-male serial copulations for the Ting, Nadam and Fourth groups, respectively. The number of bouts where two males were involved simultaneously was 10, while the number for those involving three males was 16 (Table 2). Serial copulation bouts involving four or more males were never observed. The membership of the males involved in the multiple serial copulations was stable; the same male members were always involved in maintaining close proximities and participating in the copulations (Table 2). Consequently, male members, who were tolerant of each other's approaching a female, dominantly occupied the copulatory opportunities; 108 (93.1%), 30 (96.8%), and 68 (95.8%) copulations were recorded for the Ting, Nadam, and Fourth groups, respectively (Table 2, Figure 2). The occupancy rates of copulations for the coalition were apparently higher than those of non-coalition males. Thus, we concluded that the males formed a stable coalition for sharing copulation opportunities.

Mathematical modeling analysis

Our mathematical modeling analysis indicates the presence of conditions under which formation of a coalition by the top-ranking males with other males to guard and share mating opportunities might be beneficial. Hence, we have established a theoretical basis for the occurrence of the novel male-male competition observed in stump-tailed macaques. Regarding the within-species variation in the occurrence of male-male coalition, two qualitative predictions were derived: first, a large coalition is more likely to be observed in larger male groups (Figure 6); second, among sufficiently large male groups, a coalition is more likely to occur in a group where the extent of reproductive monopolization by dominant males is relatively small, unless it is extremely small (Figure 6).

We evaluated the above predictions for within-species variation on the basis of our observational data from the five groups of stump-tailed macaques. For each group, we estimated β', which denotes either β in (1) or $s\beta$ in (2) based on whether male-male coalition is absent (Third, Wngklm) or present (Ting, Nadam, Fourth), respectively. For this purpose, the observed number of copulations in which ejaculation is confirmed for the ith male is used as the observed value of x_i. β' is estimated using the means of non-linear fitting of (1) or (2) to the observations

(Figure 7). Figure 8 shows the estimates of β' and the numbers of males, N, in the five groups. It is to be noted that the vertical axis represents $s\beta$ for Ting, Nadam, and Fourth, such that β in these groups without male-male coalition will be lower than these values. Consistent with the model predictions, the Ting group, in which the largest coalition ($m = 6$) was observed, had the combination of the largest N and the smallest β' (and thus β) among the five groups. In addition, as predicted, Fourth ($m = 3$) and Nadam ($m = 2$), the two other groups in which coalitions were observed, have the second and third lowest values of β' (and thus β), respectively. On the other hand, male-male coalition is absent in the Third group with the second largest N, which might appear to contradict our predictions. We tentatively interpret this as a result of large β' in this group; in other words, β may be too large to satisfy (11), although a quantitative evaluation of this claim has been challenging so far. In sum, we concluded that our model accounts well for the patterns of within-species variation in the male-male coalition observed in stump-tailed macaques.

DISCUSSION

To the best of our knowledge, this is the first mammalian observation of collaborative mate guarding by males, followed by facultative sharing of mating opportunities. Males in other species, such as chimpanzees, olive baboons, and lions, also collaborate to guard females against other males. The "cooperative mate guarding by coalition males" in these species appear to be similar to those in the stump-tailed macaque; however, they fundamentally differ in social relationships between/among coalition allies or non-allies. The stump-tailed macaque forms multi-male multi-female societies, which includes a large number of males in the group, among which only certain individuals tolerate sexual competition and show exclusive attitude toward others. Male allies in a coalition exclude rivals and then share the mating opportunities with each other. Thus, coalitions of stump-tailed macaques act as dominant males' strategy for overcoming reproductive competition within a group, by sharing the mating opportunities, as well as by excluding other rivals. In the case of lions, a pride is the unit of a group, which mainly consists of females and only few males, who collectively defend the females from other invasive males. This is similar to coalitions of stump-tailed macaques, although alpha (the highest ranking) males mostly monopolize the mating opportunities, whereas subordinate allies may either have no access to the females or are allowed limited number of copulations, albeit not through active sharing. Similarly, olive baboons are a well-known species forming male-male "coalition for reproduction", but differ from the stump-tailed macaques regarding the formation of coalitions. The subordinate baboons form a coalition to jointly attack the dominant male, thereby increasing their future access to females, while not showing any active sharing of copulations. The observations made with one chimpanzee group might be comparable to our observations regarding the stump-tailed macaque, where active sharing copulation (a female copulated with 8 males within a short period) was observed [29]. However, these were considered exceptions only in the Ngogo population, which are considerably larger than the other populations [see section of 'Contrasts with other chimpanzee communities' in 29].

In stark contrast, stump-tailed macaques showed active sharing of mating opportunities that they jointly obtain among the male allies. In this novel type of coalition, the alpha male appeared to pay a reproductive cost by giving mating opportunities away to benefit his allies, and the subordinate males in return repay in terms collaborative work efforts, as a result of which they gain reproductive advantage as a team. Furthermore, the cooperation among three males is another novel feature. Generally, coalition formation has been observed in the context of aggression, characterized by triadic relations, such as the attacker, attack recipient, and supporter. In the cognitive aspect, coalition formation may require higher abilities of social cognition, termed "triadic awareness" [30–33], where the individual must recognize not only the dyadic relationship between two individuals, but also the relationships with other individuals [34]. The collaboration among three individuals, which is rarely observed in non-human animals, may require the more expanded capacity of social cognition in this species. Hence, we consider coalition formation in stump-tailed macaques as a unique instance of male-male cooperation to achieve reproductive gain, which we believe is rare in non-human animals.

Why do male stump-tailed macaques, unlike males of closely related species, exhibit this peculiar behavior? To put it in another way, what are the socio-ecological factors in stump-tailed macaques that may have favored the evolution of this behavior? Here, we tentatively hypothesize that the absence of signs of ovulation in female stump-tailed macaques is key to understanding the evolution of male-male coalition, followed by facultative sharing. In many primate species, the females exhibit visual or olfactory signs of ovulation during the fertile period of the reproductive cycle. Conspicuous estrous signals such as sexual swellings enhance male-male competition, providing females more opportunities for mate choice [35–37]. Advertisement of female reproductive status is often seen in Old World monkeys living in multi-male multi-female societies, such as most macaques, baboons, and chimpanzees [35–37]. When female reproductive status is advertised, it is relatively easy for the alpha male to monopolize fertilizations, as in that case he can concentrate all his guarding efforts on the females fertile at that moment. On the other hand, when female ovulation is cryptic, the alpha male is no longer able to adopt the selective guarding strategy, and reproductive monopoly is only possible if all cycling females are guarded all the time. Our hypothesis is that the difficulty in establishing reproductive monopoly by the alpha male due to concealed ovulation may have promoted coalition formation of top-ranking males. Despite the low copulating frequency, it is surprising that the males adopt a strategy to efficiently monopolize and share the copulating opportunities—a critical reproductive resource—among multiple coalition males.

Our discovery of male-male coalition, followed by active sharing of mating opportunities in stump-tailed macaques, demands a revision of the existing socioecological models in primate social systems. To the best of our knowledge, this is the first documented case in non-human primates of non-kin collaborative effort for acquiring resources based on active sharing among allies. We have hypothesized that the lack of estrous signs in female stump-tailed macaques, unlike many Old World monkeys, is a key factor enhancing male-male coalition coupled with active sharing. Concealed ovulation is likely to reduce the extent to which fertilizations are monopolized by dominant males. In our mathematical model, this effect is represented by the reduction in parameter β. The model predicts that male-male coalition is more likely to occur when β is small, confirming the logical consistency of our hypothesis. From the female's perspective, monopolization by dominant males is indicative of limited opportunities for females to select mates, particularly when they prefer copulations with subordinate or out-group males. Thus, concealed ovulation may be considered as a female strategy to facilitate mate choice. Further extending the argument, the formation of coalition followed by active sharing of mating opportunities may be a counter strategy of dominant males. In other words, being unable to control female reproduction on his own, the alpha male may be better suited surrendering some fertilization opportunities to elicit cooperation by subordinates. Hence, the intensified sperm competition in stump-tailed macaques may be a joint consequence of female concealment of fertility states and male sharing of mating opportunities. In addition, a potentially relevant observation is that female stump-tailed macaques do not produce copulation calls [38]. Although the function of female copulation calls is still a matter of contention [39,40], a possible interpretation is that female stump-tailed macaques do not make any effort to induce male mate guarding.

The present study has also revealed the importance of the number of males in a group as a predictor for the formation of copulation coalitions among dominant males. In other words, male-male coalition is more likely to be formed when there are more males in a group. In our field site, we observed five groups of stump-tailed macaques consisting of 391 individuals, or on an average 78.2 individuals per group. The relatively large group size is primarily due to the semi-provisioning conditions in our study site, and this factor also appears to affect the socioeconomic sex ratio, i.e., the ratio of the number of adult females to the number of adult males. The average socioeconomic sex ratio in our sample is 1.33, while those that have been previously reported for other populations of stump-tailed macaques are approximately 5.7 [18]. The smaller socioeconomic sex ratio indicates more intense male-male contest. Hence, both large number of males per group and small socioeconomic ratio may have facilitated the occurrence of coalition formation by dominant males in our study population.

Per our observational data, the coalition sizes were two or three, but did not exceed four; however, our current model predicts the monotonic increase of the coalition size over four, depending on the number of males in a group. This “discrepancy” might indicate three as the limit of the coalition size in non-human animals. Actually, psychological experiments on cooperative tasks revealed possibilities of collaboration by two or three subjects, but difficulties were encountered with four or more subjects even in chimpanzees, probably due to the limitations of social cognition. For the recognition of quadradic relations, an individual has to recognize the possible combinations of dyadic and triadic relations, exponentially increasing the socio-cognitive loading in the brain. Thus, such a socio-cognitive background might limit the coalition size in stump-tailed macaques. In contrast, humans have evolved a hyper-cooperative manner beyond the triadic allies, as suggested by the Machiavellian intelligence hypothesis.

We have also observed within-species variation to the extent to which copulations are monopolized by dominant males, which is represented by β in our model. Despite the marked ecological similarities between groups, the estimated β' ranged from 0.30 to 0.97. In the Third ($\beta' = 0.97$) and Wngklm ($\beta' = 0.78$) groups, copulations were almost completely monopolized by the alpha males, a situation that is called "despotic." This contrasts with the conventional classification of primate societies, in which stump-tailed macaques are characterized as having "egalitarian" societies [41], or class 3 social systems [42]. The traditional classification intends to place each species on a single position on the despotic-egalitarian spectrum, based largely on the species-level characterizations of ecological factors, such as whether or not a given species is seasonal breeder, or the abundance and spatial distribution of food resources [43]. However, our observations clearly suggest that the level of despotism as indicated by β is determined not necessarily in such a top-down manner, but in a more bottom-up way, such that it may vary within species according to the idiosyncrasies of each group. For example, our field observation indicates that the despotic nature of the Third group may have been caused not only by the physical strength of the alpha male, THR-M01, but by the absence of competent rivals; in fact, other males seem either too old or immature to challenge him. Therefore, it appears that bottom-up mechanisms determine β in each group, which then determines whether the alpha male will adopt the solo monopolization strategy or the coalition strategy.

Finally, our model predicts the future dynamics in the stump-tailed macaque groups. For example, when youngsters in the Third group become sufficiently mature to challenge the alpha male, and as a consequence β is reduced, our model predicts that the alpha male will form coalition with other males. We expect that a longitudinal observation of wild stump-tailed macaques will confirm these model predictions. In conclusion, stump-tailed macaques are characterized by societies ranging from despotism to egalitarianism, and from monopolization of females by a dominant male to male-male coalition coupled with active sharing of mating opportunities. Future studies on wild stump-tailed macaques may shed new light on the origins and evolution of altruism and cooperation in mammalian societies, including the hyper-cooperation in human societies.

References and Notes:

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Table 1.

Group	Adult males	Adult females	Infant[1]	Unidentified[2]	Total
Ting	30	33	39	18	120
Nadam	20	30	21	4	75
Third	23	23	20	13	79
Fourth	16	27	22	9	74
Wngklm	8	11	12	12	43
Total	97	124	114	56	391

Age-sex composition of each group in Khao Krapuk Khao Taomor non-hunting area. [1]Infants were 0–2 year-old monkeys. [2]Unidentified monkeys were all subadult monkeys who were not stably observed in the group, the numbers of which have been reported above.

Table 2.

Table 2-1. All serial copulation bouts of Ting group

Bout-id	Group	Observed date	Female	Male: TNG-M02	Male: TNG-M07	Male: TNG-M04	Male: TNG-M08	Male: TNG-M09	Male: TNG-M30	Male: TNG-M18	Male: TNG-M03	Male: TNG-M17	Total (N)
ting-1	Ting	2015/10/23	TNG-F11	7(4)	4(4)	-	-	-	-	-	1(0)	-	12(8)
ting-2	Ting	2015/11/8	TNG-F23	8(8)	6(6)	-	-	-	-	-	-	-	14(14)
ting-3	Ting	2015/12/30	TNG-F05	1(1)	3(3)	-	-	2(2)	-	-	-	-	6(6)
ting-4	Ting	2016/1/28	TNG-F10	-	-	-	-	1(0)	-	2(2)	-	1(0)	4(2)
ting-5	Ting	2016/10/13	TNG-F18	6(6)	1(1)	-	-	-	-	-	-	-	7(7)
ting-6	Ting	2016/10/13	TNG-F18	4(4)	-	-	-	-	-	-	-	-	4(4)
ting-7	Ting	2016/11/3	TNG-F32	-	-	4(3)	2(0)	-	2(1)	-	-	-	8(4)
ting-8	Ting	2017/2/1	TNG-F09	3(3)	1(0)	-	-	-	-	-	-	-	4(3)
ting-9	Ting	2017/2/8	TNG-F11	0	4(3)	-	1(1)	-	-	-	-	-	5(4)

Table 2-2. All serial copulation bouts of Nadam group

Bout-id	Group	Observed date	Female	Male: NDM-M01	Male: NDM-M03	Total
nadam-1	Nadam	2015/12/19	NDM-F07	4(4)	-	4(4)
nadam-2	Nadam	2016/2/9	NDM-F12	3(3)	3(3)	6(6)
nadam-3	Nadam	2016/6/14	NDM-F01	3(3)	2(2)	5(5)
nadam-4	Nadam	2016/6/23	NDM-F25	4(4)	2(1)	6(5)

Table 2-3. All serial copulation bouts of Third group

Bout-id	Group	Observed date	Female	Male: TRD-M01	Total
third-1	Third	2015/12/24	TRD-F25	16(16)	16(16)
third-2	Third	2016/10/3	TRD-F24	31(31)	31(31)
third-3	Third	2016/10/12	TRD-F16	4(1)	4(1)
third-4	Third	2016/11/14	TRD-F16	6(1)	6(1)
third-5	Third	2017/1/18	TRD-F29	8(8)	8(8)

Table 2-4. All serial copulation bouts of Fourth group

Bout-id	Group	Observed date	Female	Male: FTH-M01	Male: FTH-M02	Male: FTH-M15	Total
fourth-1	Fourth	2015/10/10	FTH-F13	8(8)	1(1)	-	9(9)
fourth-2	Fourth	2015/10/24	FTH-F13	11(11)	3(3)	-	14(14)
fourth-3	Fourth	2016/6/16	FTH-F08	-	7(6)	-	7(6)
fourth-4	Fourth	2016/7/21	FTH-F02	4(4)	-	-	4(4)
fourth-5	Fourth	2016/7/23	FTH-F11	4(4)	-	-	4(4)
fourth-6	Fourth	2016/10/25	FTH-F11	2(2)	1(1)	7(7)	10(10)

Table 2-5. All serial copulation bouts of Wngklm group

Bout-id	Group	Observed date	Female	Male: WKM-M01	Total
wngklm-1	Wngklm	2016/2/2	WKM-F04	6(6)	6(6)
wngklm-2	Wngklm	2016/8/23	WKM-F11	9(9)	9(9)

All rows in the tables represent a single copulation bout and indicate the “Group”, “Observed Dates”, “Female ID”, and “Male ID” involved in the bout. The numbers represent the count numbers of copulation event (in parentheses are the number of copulations with ejaculation).

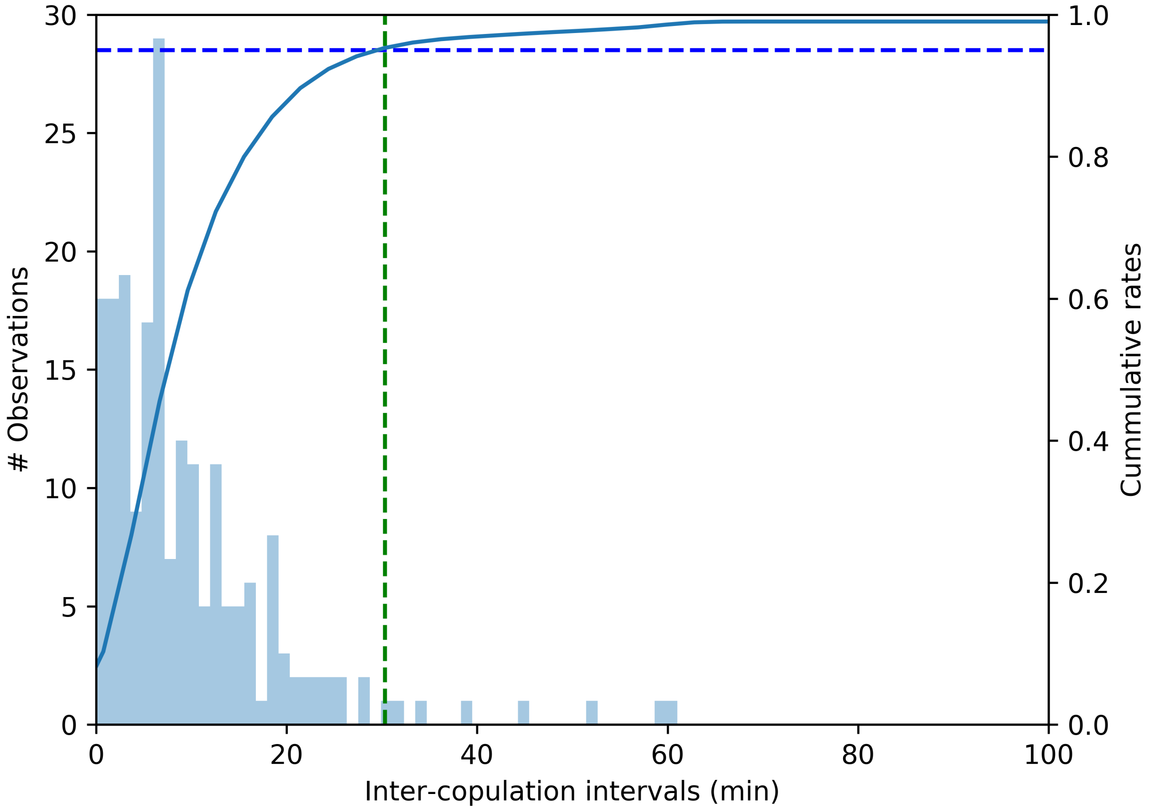


Figure 1. Occurrences of the inter-copulatory event intervals (ICIs) of all recorded single copulation events occurred multiple times in a day (N_ICI=206). Note that the cases of only one copulation within a day were excluded for the calculations of ICIs because the intervals should be defined by the two consecutive events. 5

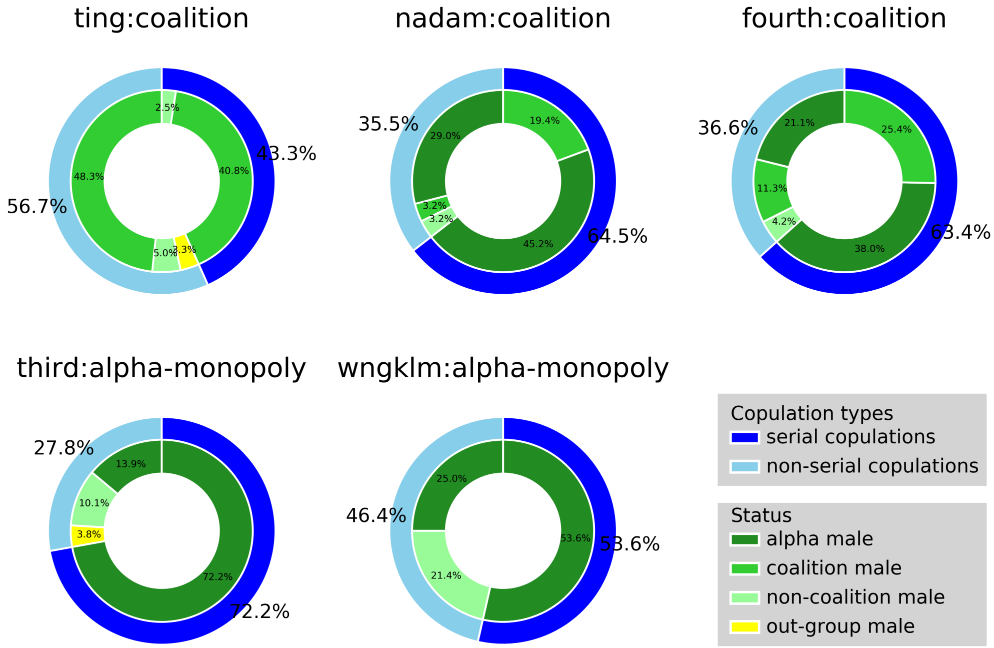


Figure 2. Ratios of copulation events (with an ejaculation) for social status, i.e., coalition males (coalitions), males outside of coalitions in a group (non-coalitions), a male solely dominating copulations (alpha), and non-group member males (out-group), for each group.

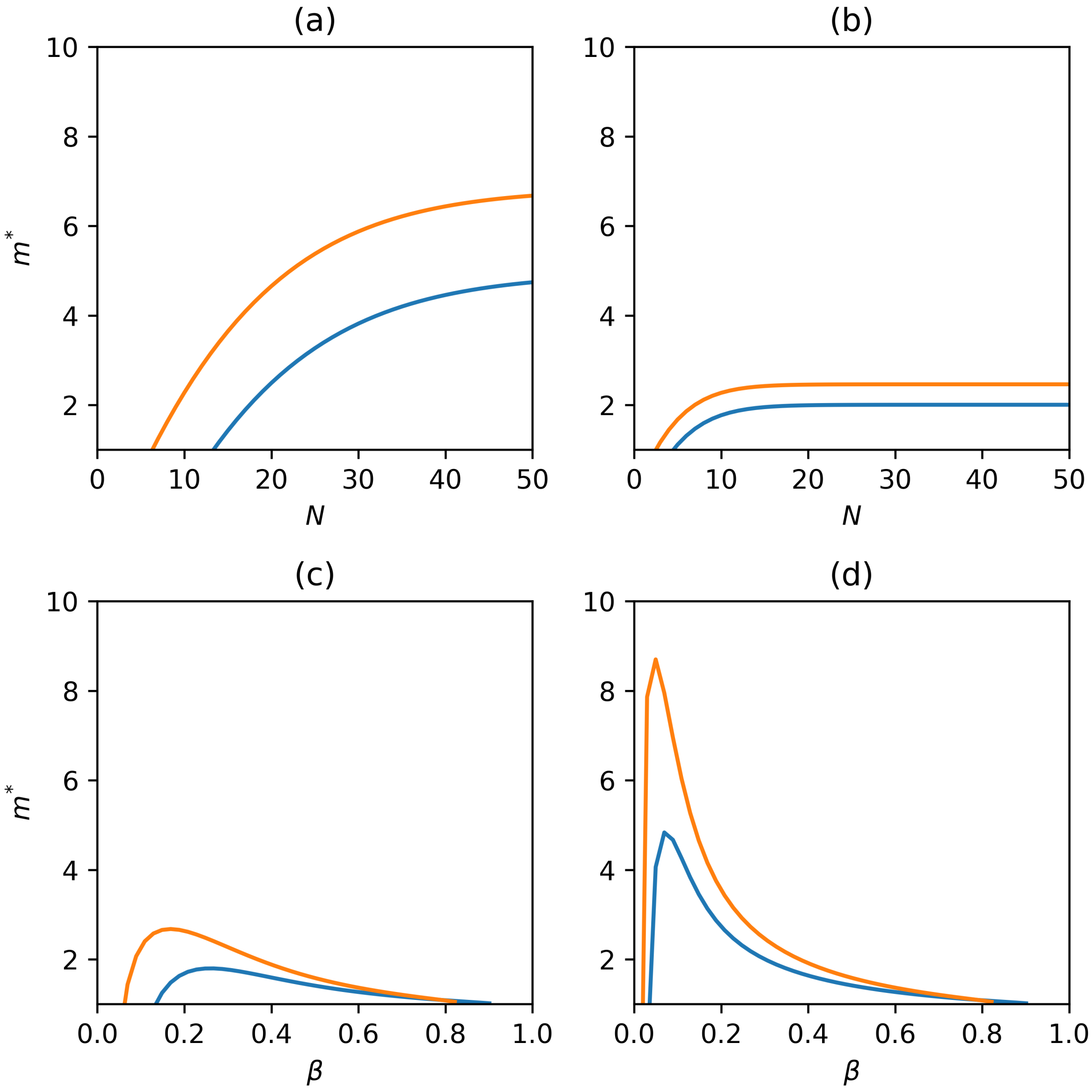
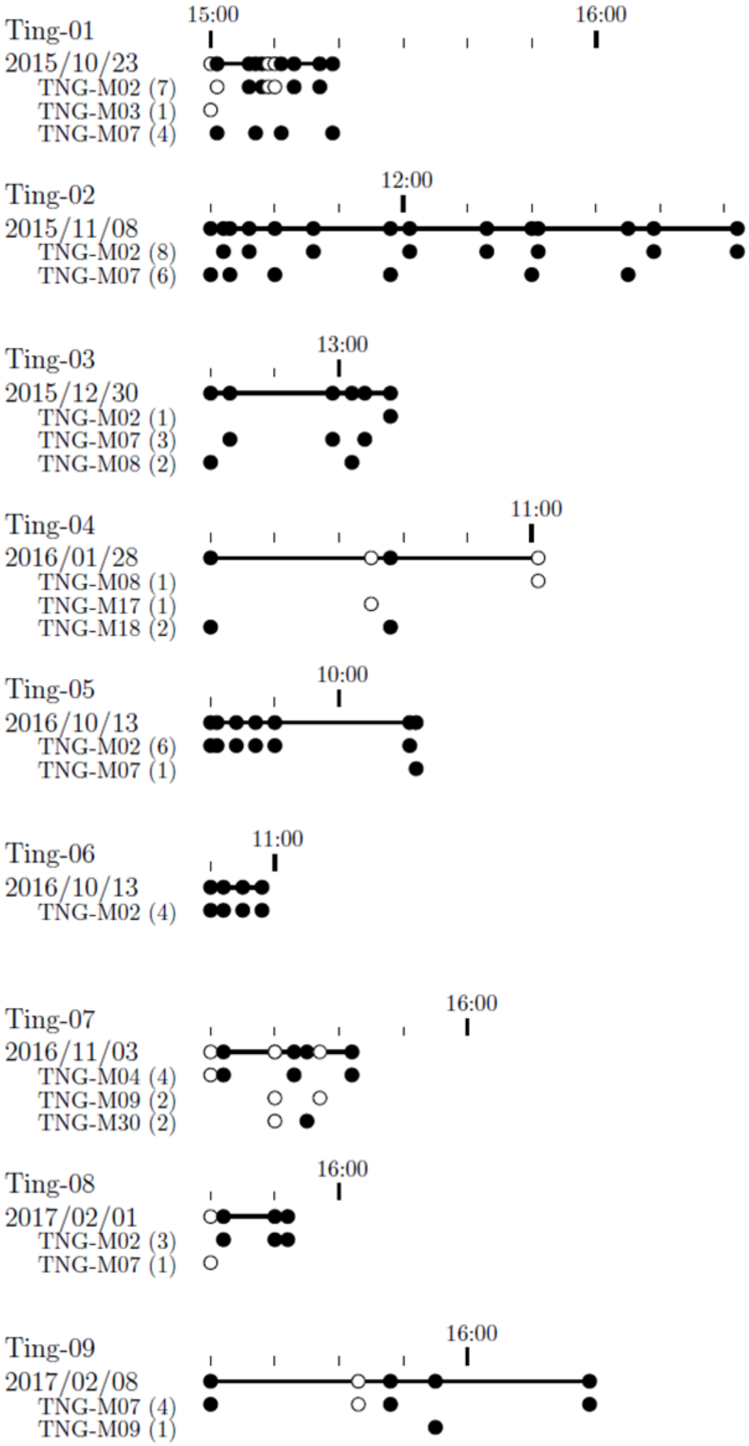
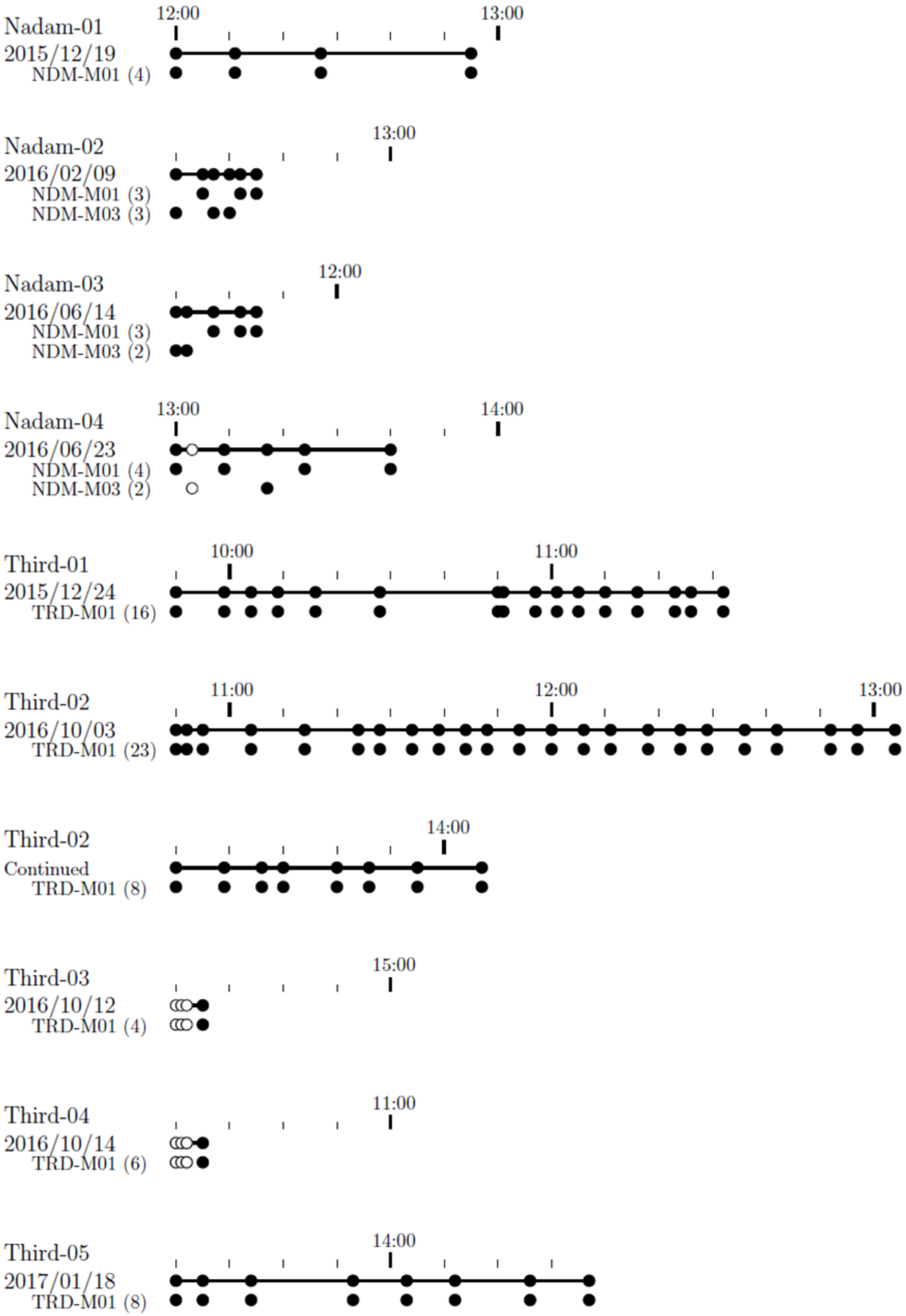


Figure 3. The dependence of the upper bound of coalition size, m^*, on the number of males, N, and the extent to which dominant males monopolize matings and/or fertilizations, β, in the absence of coalition formation. The solid and broken curves represent m^* for $s = 1.1$ and $s = 1.2$, respectively. The upper bound increases and approaches the right-hand side of (9) as N increases (a, b), while the dependence of m^* on β is non-monotonic (c, d). For all panels, $c = 0.05$. (a) $\beta = 0.1$, (b) $\beta = 0.3$, (c) $N = 10$, (d) $N = 40$.


Ting-01
2015/10/23
15:00
16:00
TNG-M02 (7)
TNG-M03 (1)
TNG-M07 (4)
Ting-02
2015/11/08
12:00
TNG-M02 (8)
TNG-M07 (6)
Ting-03
2015/12/30
13:00
TNG-M02 (1)
TNG-M07 (3)
TNG-M08 (2)
Ting-04
2016/01/28
11:00
TNG-M08 (1)
TNG-M17 (1)
TNG-M18 (2)
Ting-05
2016/10/13
10:00
TNG-M02 (6)
TNG-M07 (1)
Ting-06
2016/10/13
11:00
TNG-M02 (4)
Ting-07
2016/11/03
16:00
TNG-M04 (4)
TNG-M09 (2)
TNG-M30 (2)
Ting-08
2017/02/01
16:00
TNG-M02 (3)
TNG-M07 (1)
Ting-09
2017/02/08
16:00
TNG-M07 (4)
TNG-M09 (1)


Nadam-01
2015/12/19
NDM-M01 (4)
12:00
13:00
Nadam-02
2016/02/09
NDM-M01 (3)
NDM-M03 (3)
13:00
Nadam-03
2016/06/14
NDM-M01 (3)
NDM-M03 (2)
12:00
Nadam-04
2016/06/23
NDM-M01 (4)
NDM-M03 (2)
13:00
14:00
Third-01
2015/12/24
TRD-M01 (16)
10:00
11:00
Third-02
2016/10/03
TRD-M01 (23)
11:00
12:00
13:00
Third-02
Continued
TRD-M01 (8)
14:00
Third-03
2016/10/12
TRD-M01 (4)
15:00
Third-04
2016/10/14
TRD-M01 (6)
11:00
Third-05
2017/01/18
TRD-M01 (8)
14:00

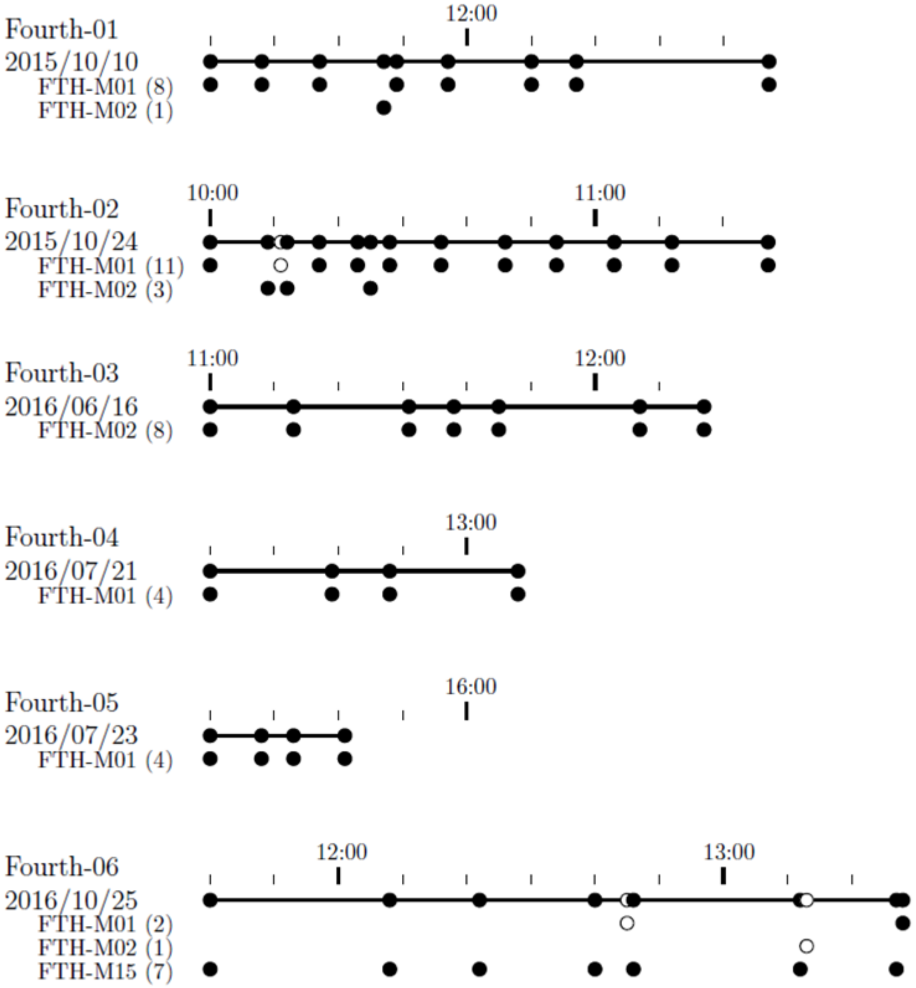


Figure 4. Sequential figure for each event of Serial copulations. Black circles indicate copulations end with ejaculation, and white circles indicate copulations end without ejaculation.

Figure 5. The male (FTH-M01) and his ally (FTH-M02) simultaneously engaged in the copulation with one female (FHT-F11), not showing any agonistic conflicts between the two "competitive" males; at that time, one male (right male) mounted over the female inserting penis, while the other male (left) "waited for his turn", touching the female hinds.

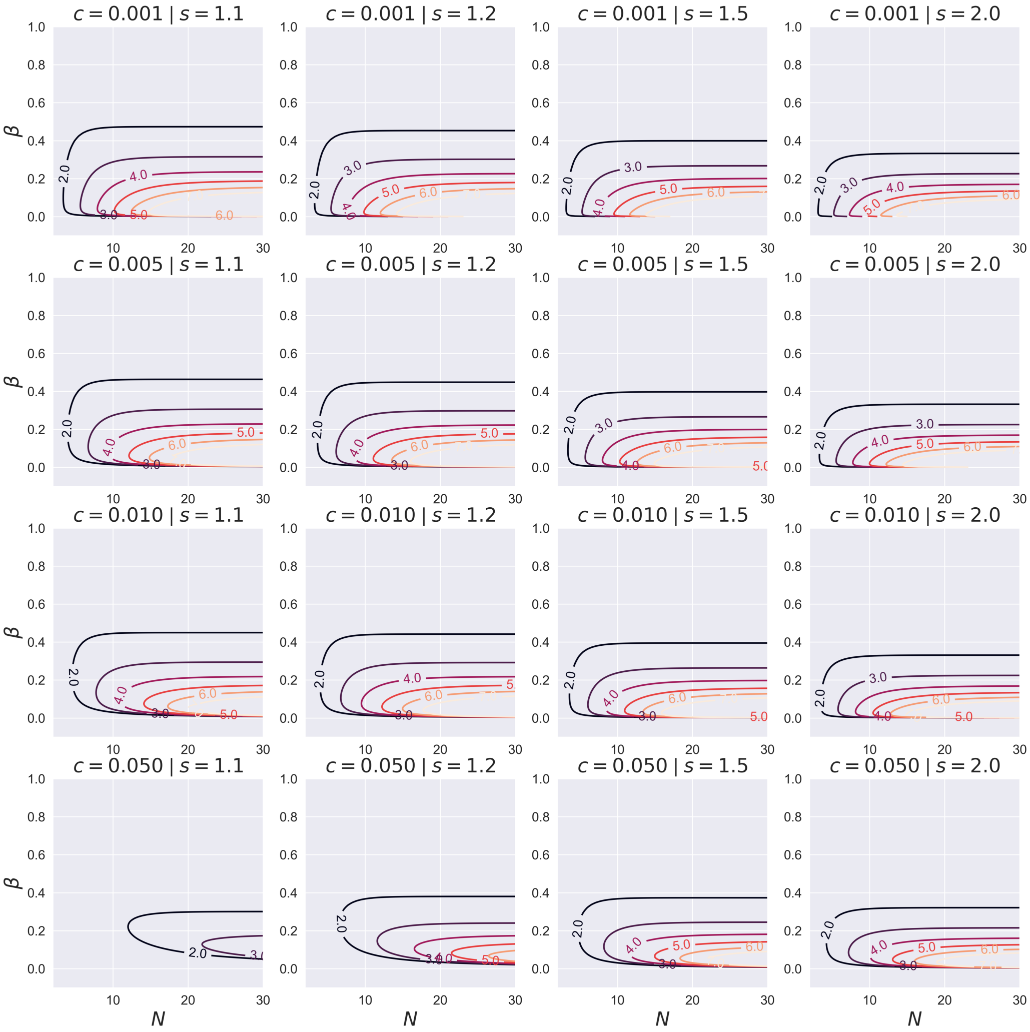


Figure 6. Combinations of $N \in [1{,}30]$ and $\beta \in (0{,}1)$ values for which coalition of more than two males is possible (i.e., $m^* > 2$) for several parameter s and c (see plot titles). Each contour represents the coalition size ($m^* > 2$).

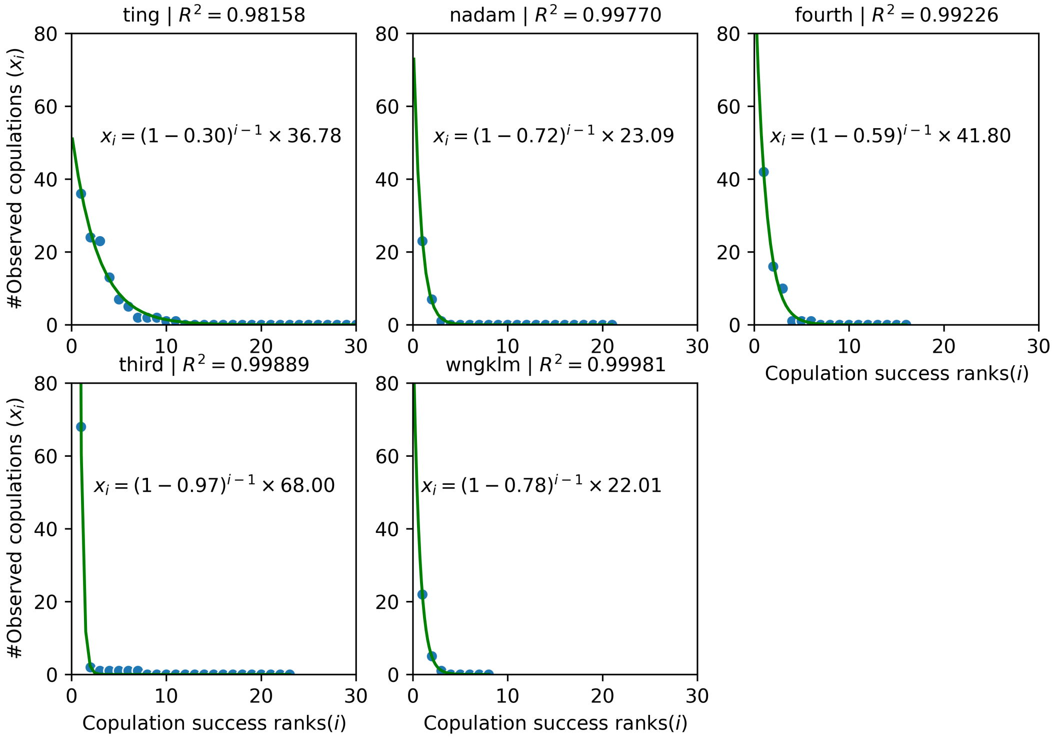


Figure 7. Nonlinear fitting of copulation occurrences with copulation success ranks. The formula in the plot area shows the estimated parameters, and plot title showed the R^2.

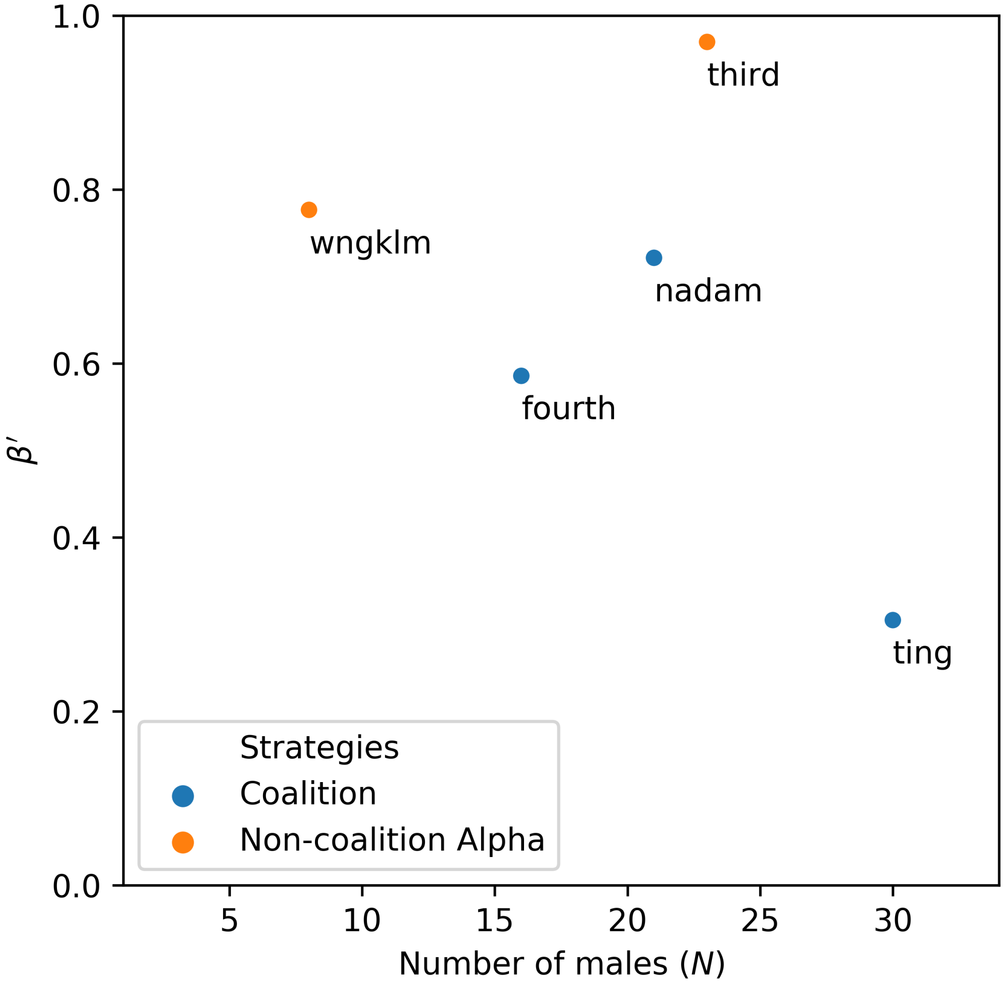


Figure 8. The estimates of β' and the numbers of males, N, in the five groups.