

1 **Sharing mating opportunities by coalition males in stump-tailed macaques: elucidation of**
2 **ecological mechanism by diversion of PvS model**

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21 **ABSTRACT**

22 Cooperation, or the act of benefiting others at the cost of the benefactor's fitness, has been a
23 central issue in evolutionary theory. Non-human animals sometimes show coalitions or male-
24 male “cooperation” to confront a male rival and challenge the rank hierarchy. Here we observed
25 novel types of coalitions in wild stump-tailed macaques (*Macaca arctoides*); multiple males
26 actively shared the mating opportunities, i.e., a male copulated with a female, while his ally
27 waited his turn and guarded them. Our mathematical simulations revealed that lack of estrous
28 signs, as well as large numbers of males in a group, possibly enhance facultative sharing of
29 females. This is the first demonstration of the sharing of females in non-human primates. , and
30 shed light on the evolutionary theory of cooperation. Overall, our novel observations have
31 revised the existing socioecological models in primate social systems. The characteristics of
32 stump-tailed macaque societies now range from despotism to egalitarianism, and from
33 monopolization of females by a dominant male to male-male coalition coupled with active
34 sharing of mating opportunities, which increases the chances of reproductive success.

35

36 **KEY WORDS**

37 cooperation, sexual traits, socioecological modeling, stump-tailed macaques

38

39 **INTRODUCTION**

40 Cooperation, or the act of benefiting others at the cost of the benefactor's fitness, has attracted the
41 attention of evolutionary biologists as its origins constitute an evolutionary puzzle. The modern
42 theoretical framework for the evolution of cooperation originated from Hamilton's inclusive
43 fitness theory (Axelrod & Hamilton, 1981; Hamilton, 1964) for kin altruism, along with the idea
44 of reciprocity, as proposed by Trivers, for cooperation among non-kin (Trivers, 1971). Humans
45 are unique in showing "hyper-cooperation" owing to their "spontaneous" tendency to be helpful
46 (Burkart et al., 2014). For example, helping, a direct form of cooperation, is observed in humans
47 even from infancy, whereas this is rare or absent in non-human animals, especially helping of
48 non-relatives (Tomasello & Vaish, 2013).

49 Male reproductive success in a multi-male multi-female group is often skewed in the
50 favor of high-ranking males (Kutsukake & Nunn, 2006). Subordinate males may gain more
51 opportunities of copulation by forming a coalition to jointly confront the top-ranking male than
52 by competing individually against each other. Previous studies have developed a mathematical
53 framework for investigating the underlying mechanisms of coalition formation and mitigating
54 the existing reproductive skew both when the formation of coalition does or does not change
55 male ranks (Pandit & van Schaik, 2003) (Van Schaik, Pandit, & Vogel, 2006). While this
56 framework is comprehensive enough to cover different coalition varieties, such as all-down,
57 bridging, and all-up coalitions (Van Schaik et al., 2006), it is still limited by the fact that it only
58 considers the mitigating or leveling effect of coalition formation on the reproductive skew. There
59 is a yet another possibility; two or more top-ranking males may form a coalition to exclude
60 lower-ranking males from mating opportunities, as a result of which the reproductive skew
61 favoring dominant males is strengthened or steepened. However, this type of coalition is, while

62 intuitively conceivable, not expected to be observed frequently. This is because even if two or
63 more top-ranking males are able to jointly exclude other males, the mating opportunities thus
64 obtained may be monopolized by the single top-ranking male after all, unless he actively shares
65 the spoil with his allies. In other words, the top-ranking male has to pay for others' help.

66 We observed the behavior which theoretically possible but rarely observed described
67 above in the wild population of stump-tailed macaques (*Macaca arctoides*) in Thailand. That is
68 "coalition-like" behavior, which is, certain dominant males guard and actively share mating
69 opportunities (Fig 1).

70



71

72 Figure 1. The male (FTH-M01) and his ally (FTH-M02) simultaneously engaged in the
73 copulation with one female (FHT-F11), not showing any agonistic conflicts between the two
74 “competitive” males; at that time, one male (right male) mounted over the female inserting penis,
75 while the other male (left) “waited for his turn”, touching the female hinds.

76
77 The reason why we denote it as “coalition-like” is because, according to the strict
78 definition of behavioral studies on primates, it cannot be a coalition because this behavior is not
79 occur in the context of aggression. Generally, a “coalition” means the behavior which is formed
80 when one animal intervenes in an ongoing conflict between two parties to support one side
81 (Widdig, Streich, & Tembrock, 2000). In brief, coalition is defined as joint aggression by
82 multiple individuals against common targets (van Schaik, Pandit, & Vogel, 2006). In that
83 respect, the “coalition-like” behavior observed in stump-tailed macaques discussing here is a bit
84 different behavior from that observed in other species. It is not a bond between individuals that is
85 observed in the context of conflict/aggression, but rather as a bond between males in the context
86 of mating to monopolize the opportunity to copulate with females. The coalition forming in
87 stump-tailed macaques is that an alpha male forms a coalition with one or two male(s), and they
88 work together to monopolize one female, eliminate other competitors, and eventually alternate
89 copulating with the monopolized female. This behavior can be interpreted as a “highly
90 cooperative” behavior in which they jointly owing the risk of eliminating other rivals, jointly
91 acquire the female as breeding resource, then share the mating opportunities as acquired benefits
92 together.

93 Cooperative mate guarding by top-ranking males likely affects the distribution of mating
94 opportunities within a group of male stump-tailed macaques. In particular, suppose that the

95 number of sexually receptive females in a group is larger than that would allow the highest-
96 ranking male to monopolize reproduction (i.e., complete contest competition), but smaller than
97 that would lead to complete scramble competition. In such cases, top-ranking males may be able
98 to exclude subordinates more efficiently from mating competition by guarding females
99 collaboratively than by doing so individually. This raises the possibility that dominant males may
100 gain a fitness benefit by having cooperative partners despite the cost of sharing mating
101 opportunities with them.

102 Male collaboration that results in modification of within-group resource allocation has
103 been theoretically investigated in the context of primate coalition formation (Pandit & Van
104 Schaik, 2003; van Schaik, Pandit, & Vogel, 2004; van Schaik et al., 2006). Assuming that payoff
105 distribution within a group follows the priority-of-access model (Altmann, 1962), Pandit and van
106 Schaik (2003) developed a mathematical model of leveling coalition, in which a skew in the
107 access to females in favor of dominant males is mitigated by coalition formation of middle- to
108 low-ranking males. Although our cases of cooperative mate guarding in stump-tailed macaques
109 do not associate with overt expression of coordinated aggression by multiple males on one or
110 more targets, a definitive feature of animal coalition (Pandit & Van Schaik, 2003), they are
111 comparable with male-male coalitions in the way that they modify group-wise allocation of
112 mating opportunities. More specifically, since those who collaboratively mate-guard in stump-
113 tailed macaque groups are top-ranking males, the behavior is similar to all-down or conservative
114 coalition, that is, coalition of higher-rankers against a lower-ranker (Chapais, 1995; van Schaik et
115 al., 2004, 2006).

116 Within the framework of Pandit and van Schaik (2003), however, all-down coalition is
117 not predicted to occur. This is because higher-rankers have nothing to gain from forming a

118 coalition to "level" the reproductive skew, for they have priority of access to females any way
119 (Pandit, Pradhan, & van Schaik, 2020; van Schaik et al., 2006). Instead, cooperative mate
120 guarding by top-ranking males should be better represented as a novel kind of coalition
121 formation that deprives lower-ranking males of mating opportunities, whereby "steepens" the
122 skew. For the purpose of investigating cooperative mate guarding in stump-tailed macaques, this
123 paper extends the Pandit-van Schaik model by allowing all-down coalition to enhance the
124 efficiency with which top-ranking males keep subordinates from mating, as a result of which the
125 reproductive skew is heightened. To keep the model simple and tractable, we choose not to
126 explicitly specify the underlying mechanism by which subordinates are excluded. Alternatively,
127 a recent study by Pandit et al. (2020) has extended the original Pandit-van Schaik model by
128 incorporating a specific mechanism to realize more skewed resource allocation, namely, higher-
129 rankers' usurping of resources owned by lower-rankers. Pandit et al.'s (2020) model is designed
130 to explore the origins of class formation in human societies, and non-human primates are
131 unlikely to meet the presumption that individuals possess exploitable or tradable resources.

132 In this study, we have first described our findings regarding the fieldwork on groups of
133 stump-tailed macaques and then analyzed the logic underlying these observations using
134 mathematical modeling.

135

136 **METHODS**

137 Study site and animals

138 A wild population of stump-tailed macaques inhabiting the Khao Krapuk Khao Taomor non-
139 hunting area in the Phetchaburi Province of central Thailand (99°44' E, 12°48' N, encompassing
140 an area of 3.5–4 km²) was observed. This site consists primarily of secondary forests, including

141 stands of bamboo and agricultural areas. The macaques also visited areas immediately adjacent
142 to this site (including a nearby temple, cassava and pineapple plantations, and human
143 settlements) on a daily basis. The macaques were occasionally fed by humans, both locals and
144 tourists, on the temple grounds or along the roadside. This population was first reported in June
145 of 1984, at which time there were only 22 individuals. Since then, it has grown to a large
146 population, including at least 391 individuals, who were divided into five groups, namely, Ting,
147 Nadam, Third, Fourth, and Wngklm groups (Table S1 in Supplementary Materials) by 2017. The
148 Wngklm group separated from the Third group in November–December 2015. All adults
149 (completely mature monkeys), most subadults (sexually mature but not completely developed),
150 and some juveniles (sexually immature, around 3 years of age) were identified based on facial
151 characteristics. This population is geographically isolated from the other populations, and no new
152 immigrant males from other sites were detected during this study period (Toyoda &
153 Malaivijitnond, 2018; Toyoda, Maruhashi, Malaivijitnond, & Koda, 2017).

154 Stump-tailed macaques are reported as non-seasonal breeders in general (some local
155 populations/captive groups show seasonality, but Thailand is not in that range). We add this info
156 with references. Whether or not the stump-tailed macaque male can detect the fertile status of
157 female by some questionable are still not clear. One paper suggested that male could detect
158 female ovulation by vagina testing behavior, however, my data comparing the timing of serial
159 copulation occurred and the giving-birth date of the females suggested that more than half of
160 copulations occurred in non-fertileable period (unpublished data). At least, to human observers,
161 female's estrus signals are totally undetectable, however, it's still possible that males are using
162 some cues which human cannot detect.

163

164 Daily observations

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

171

172 Copulation definitions and analysis

173 All copulations during our observation were recorded using video cameras (JVC GZ-RX500 and
174 Sony HDR-PJ675) and their descriptions were noted. Here, a single copulation was defined as a
175 single event consisting of single mount-insertion-separation irrespective of ejaculation, based on
176 the previous report (Estep, Bruce, Johnston, & Gordon, 1984). In total, 433 cases of single
177 copulation events were recorded. Next, the occurrence time of a single copulation event was
178 measured, and the inter-copulation intervals (ICIs) of all recorded single copulation events that
179 occurred multiple times in a day were calculated for defining copulation bout. A “serial
180 copulation bout” was defined as the copulation series including more than four single copulation
181 events, of which every ICI was less than 30 min (for the rationale of the interval criterion see
182 Figure 1). This definition was modified for quantitiveness from the relatively ambiguous
183 definition of the previous studies (Brereton, 1994; Estep et al., 1984). The other bout was defined
184 as “non-serial copulation bout”. For all copulation events and copulation bouts, the IDs of the
185 males and females involved were recorded. The observed counts of the copulation events and
186 bouts of those involved simultaneously in the same serial copulation bout were determined.

187

188 Estimation of parameters

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

198

199 Mathematical model

200 To understand the logic behind the novel male-male coalition identified in stump-tailed
201 macaques, we developed a simple mathematical model based on the framework developed by
202 Pandit and van Schaik (Pandit & van Schaik, 2003). Our motivation for the mathematical
203 modeling was two-fold. First, it is intuitively conceivable that concealed ovulation, as in stump-
204 tailed macaques, hinders the alpha male from guarding all fertilizations, and thus necessitates
205 collaboration of two or more dominant males for reproductive monopoly. However, it is unclear
206 as to whether and under what circumstances the alpha male tolerates one or more allies
207 copulating with females. Second, we have observed within-species variation in the occurrence of
208 male-male coalition in stump-tailed macaques: it occurs in the Ting, Nadam, and Fourth groups,

209 but not in the Third and Wngklm groups (see Figure 2). If our model for the underlying logic of
210 male-male coalition is correct, it should also explain this pattern of within-species variation.

211 We considered a group of N males and a constant number of females. In the case of a
212 linear order of dominance among the males, the relative access of the i th male to females, x_i , in
213 the absence of male-male coalition is described by the priority-of-access model (Altmann, 1962),
214 namely,

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

215 where β represents the degree to which dominant males can monopolize mating opportunities
216 ($0 < \beta < 1$).

217 Ecological and demographic factors have been suggested to affect β (Van Schaik et al.,
218 2006). Of these, cryptic ovulation in females probably reduces β as it prevents dominant males
219 from guarding each female intensively only during her fertile periods. Thus, compared to species
220 in which ovulation is advertised, species with cryptic ovulation are expected to have small β . In
221 contrast, other factors, such as the number of females in the group, the relative strengths of
222 dominant males, and the female preference for or against dominant males, are also likely to
223 affect β . As the latter factors may vary within a species, we expect that different groups of
224 stump-tailed macaques are characterized by different β values.

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

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

230 where we assume $1 < s < 1/\beta$. Parameter s reflects the effect of male-male coalition to
231 "steepen" the male reproductive skew, where larger s indicates higher reproductive
232 monopolization by dominant males. It should be emphasized that our parameter s differs from α ,
233 the similar parameter in Pandit and van Schaik's (2003) model, which considered the effect of
234 coalition among subordinate males to "level" the reproductive skew (i.e., $0 \leq \alpha \leq 1$). As this
235 type of male-male coalition is by definition conservative (Chapais, 1995) or all-down (van
236 Schaik et al., 2004), it is always feasible as no single male outside the coalition can prevent it
237 from occurring (Pandit & van Schaik, 2003).

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

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

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

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

245 while in the presence of coalition,

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

246 Regarding the second component, we assume that the first components of males forming a
247 coalition are multiplied by $1 - c$, where c represents the cost of coalition ($0 < c < 1$), while

248 those of non-coalition males are multiplied by 1. Therefore, for the i th male, joining a coalition
 249 is profitable if and only if

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

250 or equivalently,

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

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

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

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

255 Equation (8) immediately shows that $s(1-c) > 1$ is necessary for any coalition to be viable;
 256 otherwise, $m^* < 1$ always holds. It also shows that the right-hand side of (8) increases with N
 257 (Figure 2a, 2b). For large N , the upper boundary of the coalition size is obtained approximately
 258 using

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

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

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

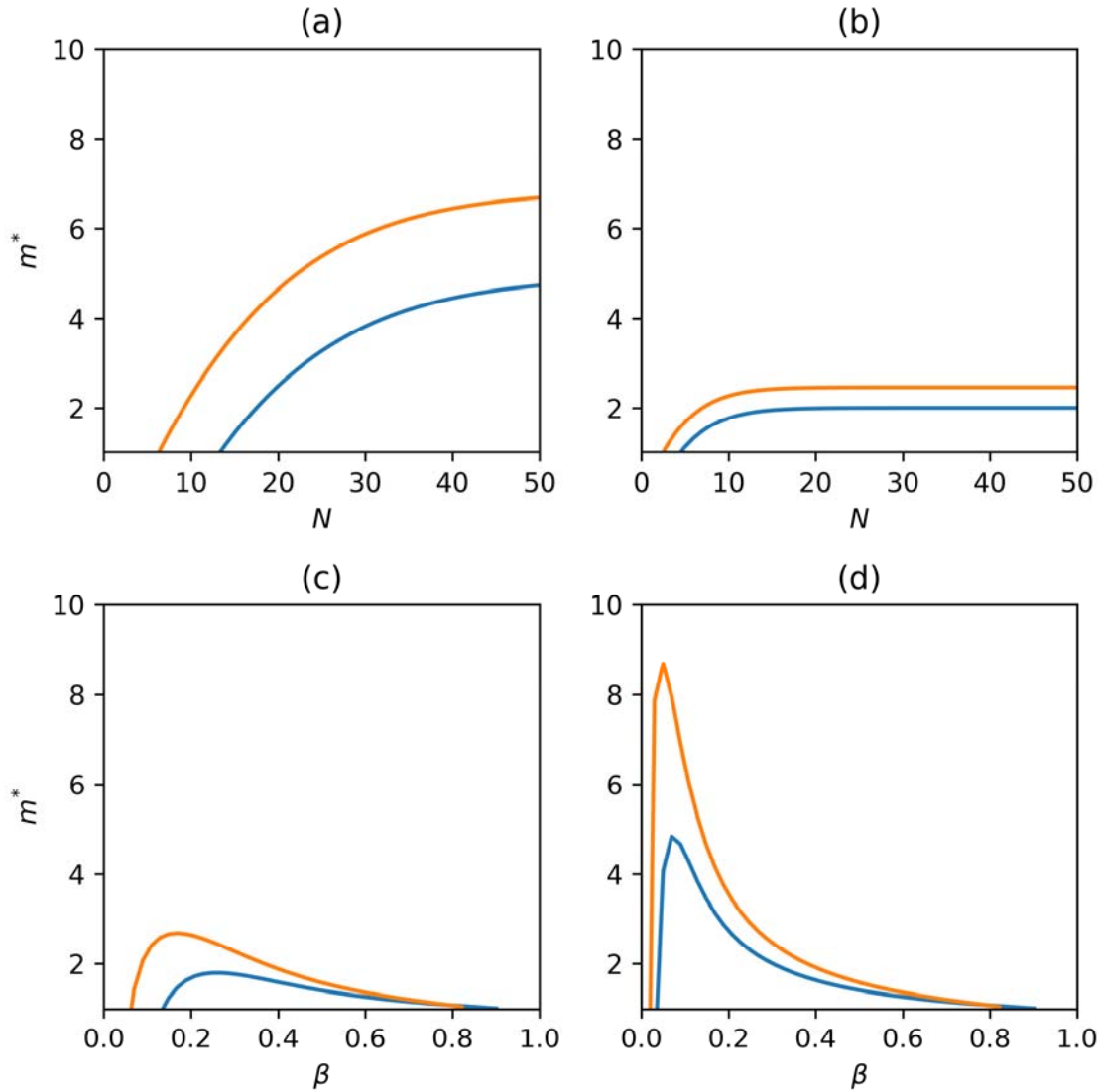
261 indicating that as β approaches zero, m^* diverges to minus infinity. In general, however, the
262 dependence of m^* on β is not monotonic (Figure 2c, 2d).

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

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

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

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Figure 2. 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) $N=40$.

276 Ethics approval

277 All data acquisitions and procedures during the fieldwork were approved by the National
278 Research Council of Thailand (NRCT, Permission No. 0002/6910) and the Department of
279 National Parks, Wildlife and Plant Conservation of Thailand (DNPT). We also complied with the
280 guidelines for field studies of the Primate Research Institute, Kyoto University.

281 Conflicts of interest/Competing interests

282 Authors declare no competing interests.

283

284

285 **RESULTS**

286 Behavioral analysis

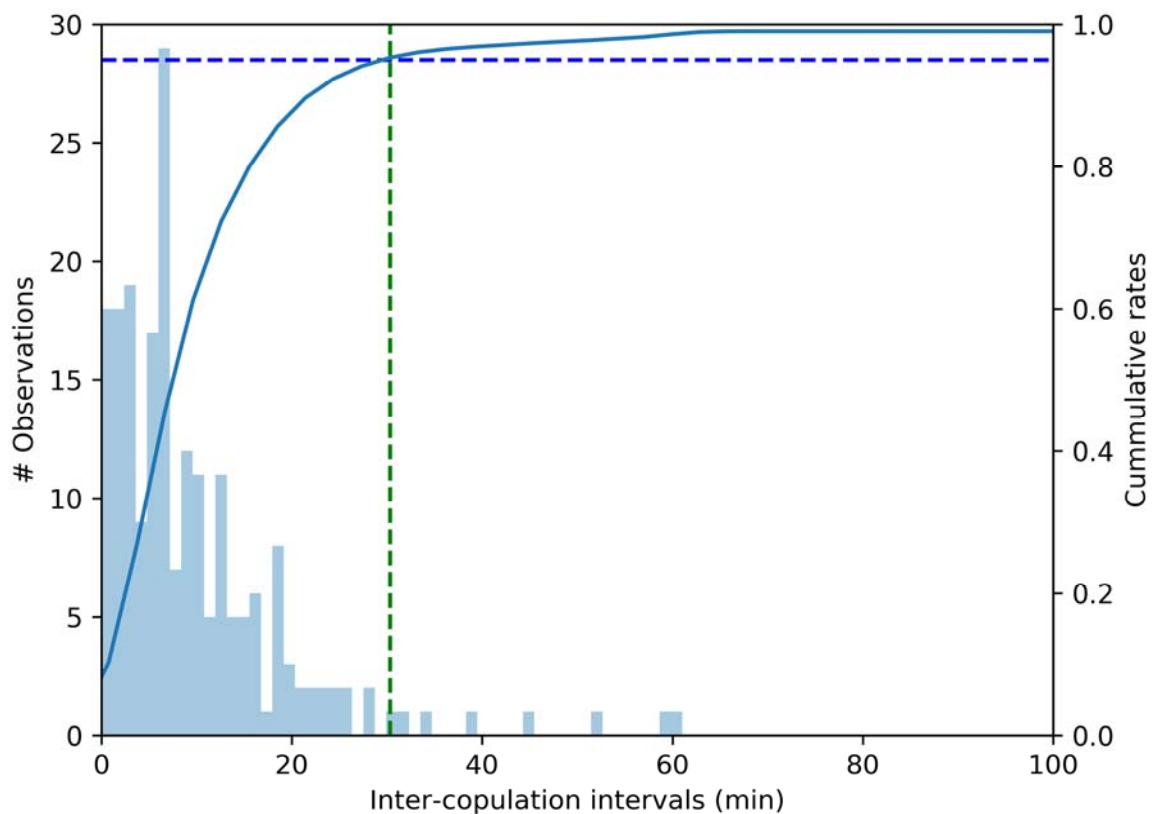
287 During our 21 months of field observations, we counted 433 cases of copulations (defined as a
288 single event consisting of single mount-insertion-separation, see Materials and method section)
289 from five subject groups (391 individuals consisting of 97 adult males, 124 adult females, 114
290 infants (≤ 2 years), and 56 subadult unidentified subjects (see Toyoda et al 2018). The inter-
291 copulation intervals (ICI) of all recorded single copulation events that occurred multiple times
292 between the female and male(s) in a day ($N_{ICI} = 206$) were measured; the median with ranges of
293 ICI were 7 (0–359) min (Figure 3), and 95% events occurred within 30 min ICI. We defined the
294 serial copulation bout as the copulation series including more than four single copulation events,
295 of which every ICI was less than 30 min, which partially followed the definitions of the previous
296 study (Brereton, 1994; Estep et al., 1984) (for details, see Materials and method section). Out of
297 the 433 copulation events, 213 (49.2 %) cases occurred in serial copulation bouts, i.e., repeated
298 single mount-insertion-separation copulation event with one female recipient partner. In contrast,

299 220 (50.8%) cases occurred as non-serial copulations. In total, 26 serial copulation bouts
300 (number of single copulation events with ejaculation per bout, median: 6.0 times; range: 1–31
301 times) were recorded in the five-subject groups (Ting group: 9 times; Nadam: 4; Third: 5;
302 Fourth: 6; Wngklm: 2, for details see Table S2 and Figure S1 in Supplementary Materials). Thus,
303 almost 50% of single copulation events occurred as a part of the serial copulation bout. The
304 seven cases of serial copulations in the Third and Wngklm groups were of alpha males (named
305 TRD-M01 and WKM-M01 for Third and Wngklm groups, respectively), i.e., one male
306 maintained the proximity to females and was involved in most of the copulations. In total, we
307 recorded 80 copulations include 68 ejaculatory copulations (81.8% of all copulation occurrences,
308 86.1% of all ejaculated copulation) of TRD-M01, and 26 copulations 22 ejaculatory copulations
309 (59.1%, 78.6%) of WKM-M01 as well, indicating their monopoly over copulations (Figure 2, see
310 “alpha-male-monopoly type).

311 In contrast, the serial copulation patterns of the Ting, Nadam, and Fourth groups
312 differed from those of the Third and Wngklm groups (Figure 4, see “coalition” type).
313 Interestingly, we observed that multiple males were involved in a single serial copulation bout;
314 each of the males first performed the single mount-insertion-separation copulation event several
315 times and the other male(s) maintained close proximity to the copulating male-female pair
316 without any agonistic interaction, after which the males serially changed positions as copulators
317 (Figure 4). These multi-male serial copulation bouts were observed 26 times in total (Table S2).
318 Six, two, and three males were involved in the multi-male serial copulations for the Ting, Nadam
319 and Fourth groups, respectively. The number of bouts where two males were involved
320 simultaneously was 10, while the number for those involving three males was 16 (Table S2).
321 Serial copulation bouts involving four or more males were never observed. The membership of

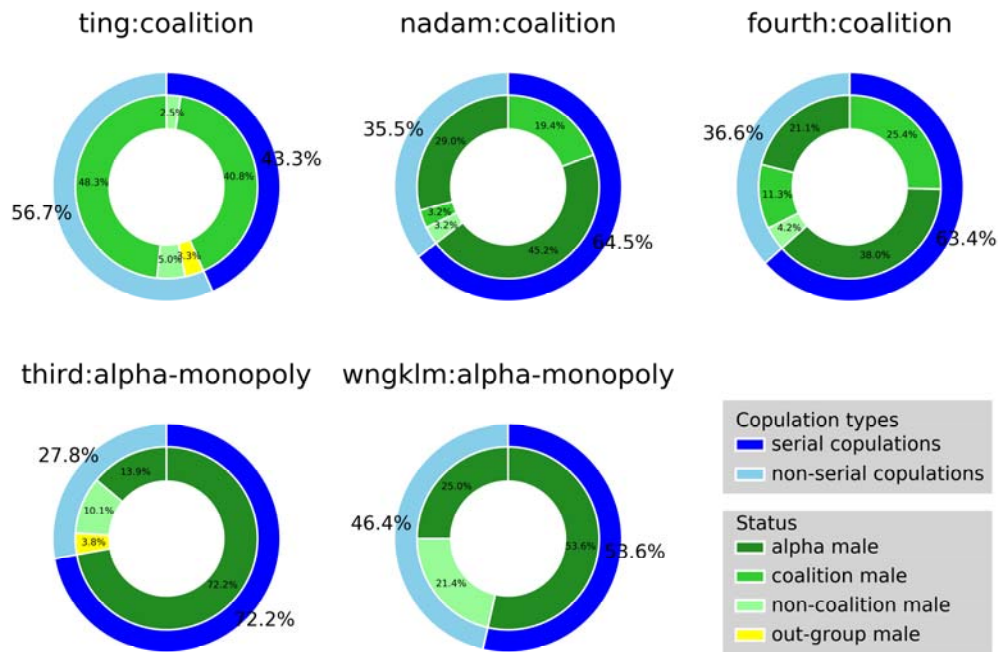
322 the males involved in the multiple serial copulations was stable; the same male members were
323 always involved in maintaining close proximities and participating in the copulations (Table S2).
324 Consequently, male members, who were tolerant of each other's approaching a female,
325 dominantly occupied the copulatory opportunities; 108 (93.1%), 30 (96.8%), and 68 (95.8%)
326 copulations were recorded for the Ting, Nadam, and Fourth groups, respectively (Table S2,
327 Figure 4). The occupancy rates of copulations for the coalition were apparently higher than those
328 of non-coalition males. Thus, we concluded that the males formed a stable coalition for sharing
329 copulation opportunities.

330



331

332 Figure 3. Occurrences of the inter-copulatory event intervals (ICIs) of all recorded single
 333 copulation events occurred multiple times in a day (N_ICI=206). Note that the cases of only one
 334 copulation within a day were excluded for the calculations of ICIs because the intervals should
 335 be defined by the two consecutive events.
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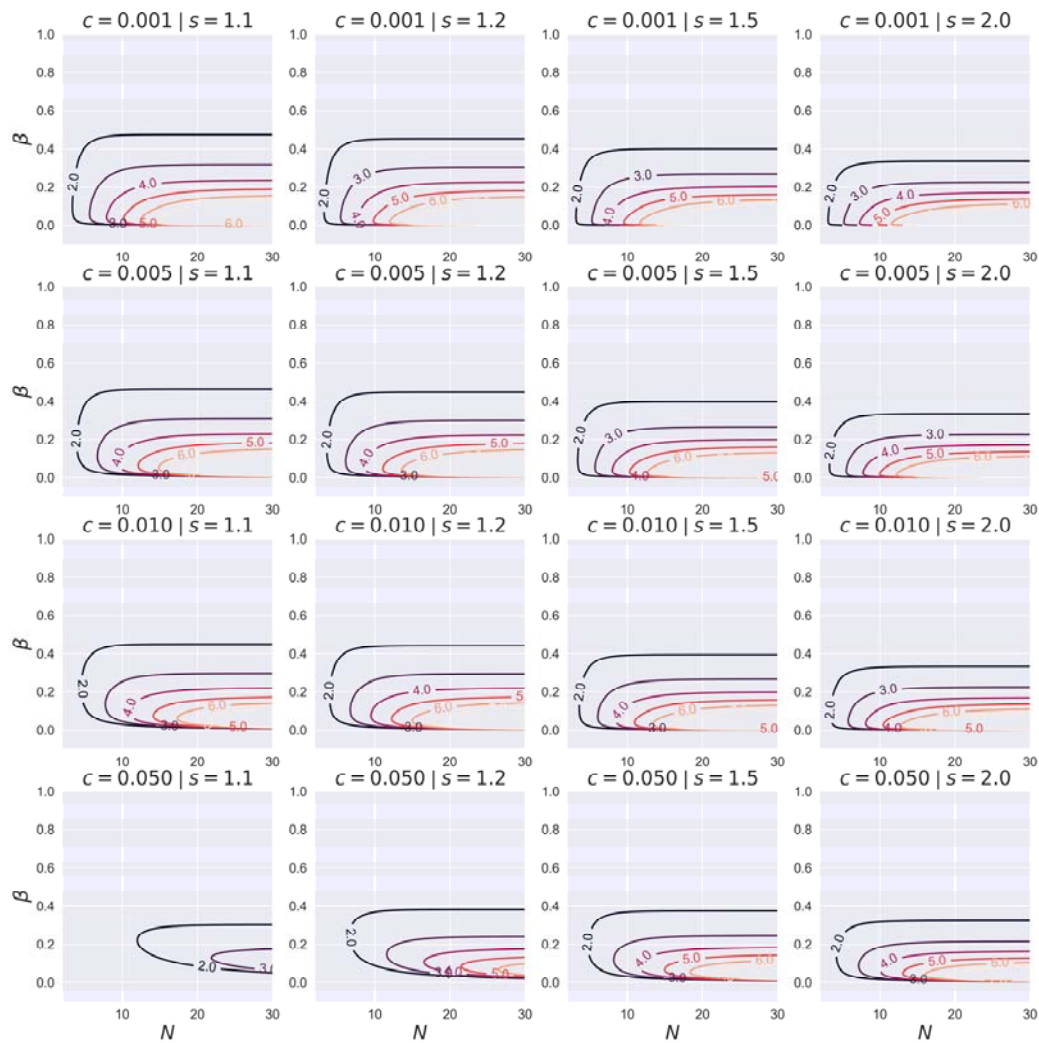
337
 338 Figure 4. Ratios of copulation events (with an ejaculation) for social status, i.e., coalition males
 339 (coalitions), males outside of coalitions in a group (non-coalitions), a male solely dominating
 340 copulations (alpha), and non-group member males (out-group), for each group.

341
 342 Mathematical modeling analysis

343 Our mathematical modeling analysis indicates the presence of conditions under which formation
 344 of a coalition by the top-ranking males with other males to guard and share mating opportunities

345 might be beneficial. Hence, we have established a theoretical basis for the occurrence of the
346 novel male-male competition observed in stump-tailed macaques. Regarding the within-species
347 variation in the occurrence of male-male coalition, two qualitative predictions were derived: first,
348 a large coalition is more likely to be observed in larger male groups (Figure 5); second, among
349 sufficiently large male groups, a coalition is more likely to occur in a group where the extent of
350 reproductive monopolization by dominant males is relatively small, unless it is extremely small
351 (Figure 5).

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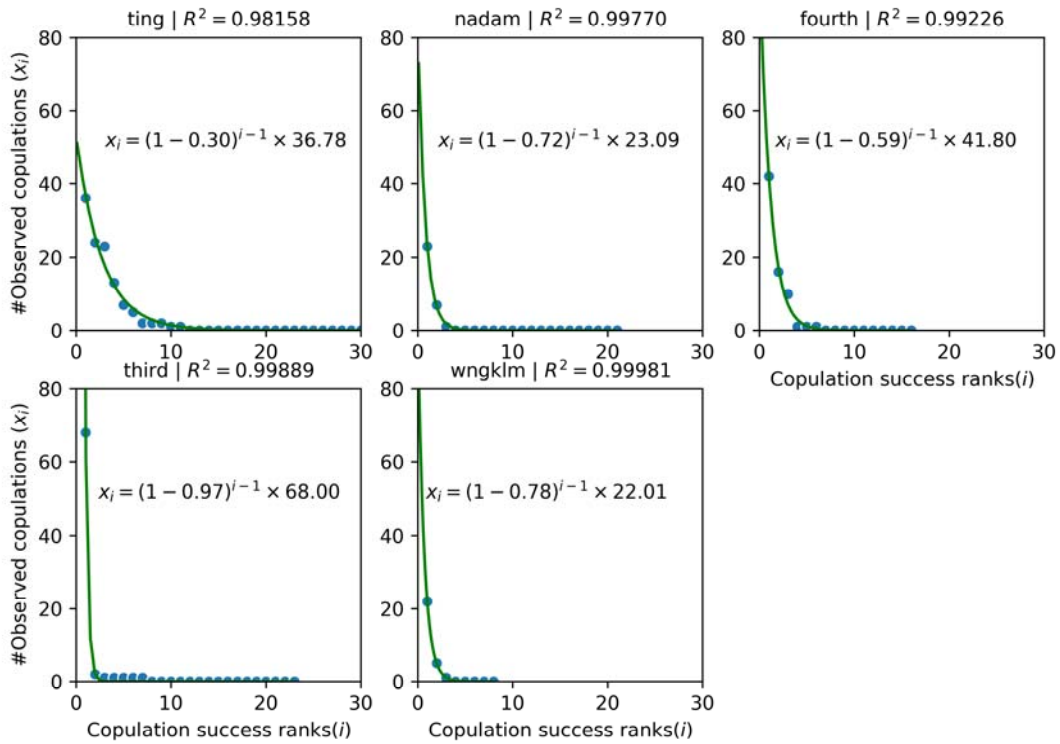
354 Figure 5. Combinations of $N \in [1, 30]$ and $\beta \in (0, 1)$ values for which coalition of more than two
355 males is possible (i.e., $m^* > 2$) for several parameter s and c (see plot titles). Each contour
356 represents the coalition size ($m^* > 2$).

357

358 We evaluated the above predictions for within-species variation on the basis of our
359 observational data from the five groups of stump-tailed macaques. For each group, we estimated

360 β' , which denotes either β in (1) or $s\beta$ in (2) based on whether male-male coalition is absent
361 (Third, Wngklm) or present (Ting, Nadam, Fourth), respectively. For this purpose, the observed
362 number of copulations in which ejaculation is confirmed for the i th male is used as the observed
363 value of x_i . β' is estimated using the means of non-linear fitting of (1) or (2) to the observations
364 (Figure 6). Figure 7 shows the estimates of β' and the numbers of males, N , in the five groups. It
365 is to be noted that the vertical axis represents $s\beta$ for Ting, Nadam, and Fourth, such that β in
366 these groups without male-male coalition will be lower than these values. Consistent with the
367 model predictions, the Ting group, in which the largest coalition ($m = 6$) was observed, had the
368 combination of the largest N and the smallest β' (and thus β) among the five groups. In addition,
369 as predicted, Fourth ($m = 3$) and Nadam ($m = 2$), the two other groups in which coalitions were
370 observed, have the second and third lowest values of β' (and thus β), respectively. On the other
371 hand, male-male coalition is absent in the Third group with the second largest N , which might
372 appear to contradict our predictions. We tentatively interpret this as a result of large β' in this
373 group; in other words, β may be too large to satisfy (11), although a quantitative evaluation of
374 this claim has been challenging so far. In sum, we concluded that our model accounts well for
375 the patterns of within-species variation in the male-male coalition observed in stump-tailed
376 macaques.

377

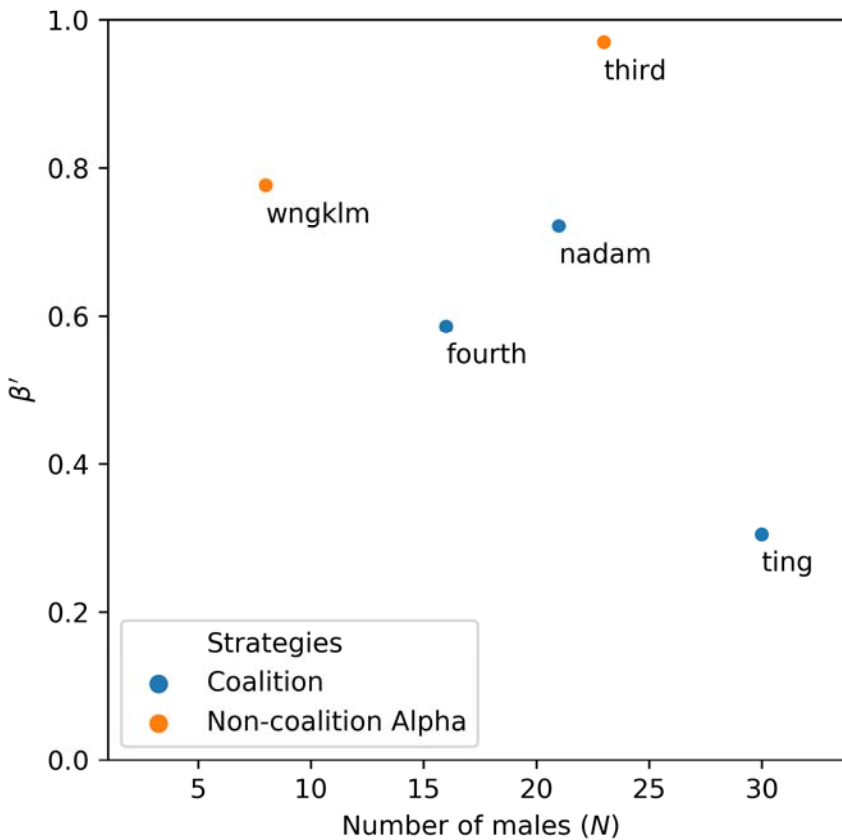


378

379 Figure 6. Nonlinear fitting of copulation occurrences with copulation success ranks. The formula

380 in the plot area shows the estimated parameters, and plot title showed the R^2 .

381



382

383 Figure 7. The estimates of β' and the numbers of males, N , in the five groups.

384

385 DISCUSSION

386 To the best of our knowledge, this is the first mammalian observation of collaborative
387 mate guarding by males, followed by facultative sharing of mating opportunities. Males in other
388 species, such as chimpanzees, olive baboons, and lions, also collaborate to guard females against
389 other males. The "cooperative mate guarding by coalition males" in these species appear to be
390 similar to those in the stump-tailed macaque; however, they fundamentally differ in social
391 relationships between/among coalition allies or non-allies. The stump-tailed macaque forms
392 multi-male multi-female societies, which includes a large number of males in the group, among

393 which only certain individuals tolerate sexual competition and show exclusive attitude toward
394 others. Male allies in a coalition exclude rivals and then share the mating opportunities with each
395 other. Thus, coalitions of stump-tailed macaques act as dominant males' strategy for overcoming
396 reproductive competition within a group, by sharing the mating opportunities, as well as by
397 excluding other rivals. In the case of lions, a pride is the unit of a group, which mainly consists
398 of females and only few males, who collectively defend the females from other invasive males.
399 This is similar to coalitions of stump-tailed macaques, although alpha (the highest ranking) males
400 mostly monopolize the mating opportunities, whereas subordinate allies may either have no
401 access to the females or are allowed limited number of copulations, albeit not through active
402 sharing. Similarly, olive baboons are a well-known species forming male-male "coalition for
403 reproduction" but differ from the stump-tailed macaques regarding the formation of coalitions.
404 The subordinate baboons form a coalition to jointly attack the dominant male, thereby increasing
405 their future access to females, while not showing any active sharing of copulations. The
406 observations made with one chimpanzee group might be comparable to our observations
407 regarding the stump-tailed macaque, where active sharing copulation (a female copulated with 8
408 males within a short period) was observed (Watts, 1998). However, these were considered
409 exceptions only in the Ngogo population, which are considerably larger than the other
410 populations (Watts, 1998).

411 In stark contrast, stump-tailed macaques showed active sharing of mating opportunities
412 that they jointly obtain among the male allies. In this novel type of coalition, the alpha male
413 appeared to pay a reproductive cost by giving mating opportunities away to benefit his allies, and
414 the subordinate males in return repay in terms collaborative work efforts, as a result of which
415 they gain reproductive advantage as a team. Furthermore, the cooperation among three males is

416 another novel feature. Generally, coalition formation has been observed in the context of
417 aggression, characterized by triadic relations, such as the attacker, attack recipient, and
418 supporter. In the cognitive aspect, coalition formation may require higher abilities of social
419 cognition, termed "triadic awareness" (Harcourt, de Waal, & others, 1992; Paxton et al., 2010;
420 Schino, Tiddi, & Di Sorrentino, 2006; Silk, 1999), where the individual must recognize not only
421 the dyadic relationship between two individuals, but also the relationships with other individuals
422 (Hemelrijk, Puga-Gonzalez, & Steinhauser, 2013). The collaboration among three individuals,
423 which is rarely observed in non-human animals, may require the more expanded capacity of
424 social cognition in this species. Hence, we consider coalition formation in stump-tailed macaques
425 as a unique instance of male-male cooperation to achieve reproductive gain, which we believe is
426 rare in non-human animals.

427 Why do male stump-tailed macaques, unlike males of closely related species, exhibit this
428 peculiar behavior? To put it in another way, what are the socio-ecological factors in stump-tailed
429 macaques that may have favored the evolution of this behavior? Here, we tentatively hypothesize
430 that the absence of signs of ovulation in female stump-tailed macaques is key to understanding
431 the evolution of male-male coalition, followed by facultative sharing. In many primate species,
432 the females exhibit visual or olfactory signs of ovulation during the fertile period of the
433 reproductive cycle. Conspicuous estrous signals such as sexual swellings enhance male-male
434 competition, providing females more opportunities for mate choice (C. L Nunn, van Schaik, &
435 Zinner, 2001; Charles L. Nunn, 1999; Zinner, van Schaik, Nunn, & Kappeler, 2004).
436 Advertisement of female reproductive status is often seen in Old World monkeys living in multi-
437 male multi-female societies, such as most macaques, baboons, and chimpanzees (C. L Nunn et
438 al., 2001; Charles L. Nunn, 1999; Zinner et al., 2004). When female reproductive status is

439 advertised, it is relatively easy for the alpha male to monopolize fertilizations, as in that case he
440 can concentrate all his guarding efforts on the females fertile at that moment. On the other hand,
441 when female ovulation is cryptic, the alpha male is no longer able to adopt the selective guarding
442 strategy, and reproductive monopoly is only possible if all cycling females are guarded all the
443 time. Our hypothesis is that the difficulty in establishing reproductive monopoly by the alpha
444 male due to concealed ovulation may have promoted coalition formation of top-ranking males.
445 Despite the low copulating frequency, it is surprising that the males adopt a strategy to efficiently
446 monopolize and share the copulating opportunities—a critical reproductive resource—among
447 multiple coalition males.

448 Our discovery of male-male coalition, followed by active sharing of mating opportunities
449 in stump-tailed macaques, demands a revision of the existing socioecological models in primate
450 social systems. To the best of our knowledge, this is the first documented case in non-human
451 primates of non-kin collaborative effort for acquiring resources based on active sharing among
452 allies. We have hypothesized that the lack of estrous signs in female stump-tailed macaques,
453 unlike many Old-World monkeys, is a key factor enhancing male-male coalition coupled with
454 active sharing. Concealed ovulation is likely to reduce the extent to which fertilizations are
455 monopolized by dominant males. In our mathematical model, this effect is represented by the
456 reduction in parameter β . The model predicts that male-male coalition is more likely to occur
457 when β is small, confirming the logical consistency of our hypothesis. From the female's
458 perspective, monopolization by dominant males is indicative of limited opportunities for females
459 to select mates, particularly when they prefer copulations with subordinate or out-group males.
460 Thus, concealed ovulation may be considered as a female strategy to facilitate mate choice.
461 Further extending the argument, the formation of coalition followed by active sharing of mating

462 opportunities may be a counter strategy of dominant males. In other words, being unable to
463 control female reproduction on his own, the alpha male may be better suited surrendering some
464 fertilization opportunities to elicit cooperation by subordinates. Hence, the intensified sperm
465 competition in stump-tailed macaques may be a joint consequence of female concealment of
466 fertility states and male sharing of mating opportunities. In addition, a potentially relevant
467 observation is that female stump-tailed macaques do not produce copulation calls (Blurton Jones
468 & Trollope, 1968). Although the function of female copulation calls is still a matter of contention
469 (Bernstein, Sheeran, Wagner, Li, & Koda, 2016; Maestriperi & Roney, 2005), a possible
470 interpretation is that female stump-tailed macaques do not make any effort to induce male mate
471 guarding.

472 The present study has also revealed the importance of the number of males in a group as
473 a predictor for the formation of copulation coalitions among dominant males. In other words,
474 male-male coalition is more likely to be formed when there are more males in a group. In our
475 field site, we observed five groups of stump-tailed macaques consisting of 391 individuals, or on
476 an average 78.2 individuals per group. The relatively large group size is primarily due to the
477 semi-provisioning conditions in our study site, and this factor also appears to affect the
478 socioeconomic sex ratio, i.e., the ratio of the number of adult females to the number of adult
479 males. The average socioeconomic sex ratio in our sample is 1.33, while those that have been
480 previously reported for other populations of stump-tailed macaques are approximately 5.7
481 (Fooden, 1990). The smaller socioeconomic sex ratio indicates more intense male-male contest.
482 Hence, both large number of males per group and small socioeconomic ratio may have facilitated
483 the occurrence of coalition formation by dominant males in our study population.

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

495 We have also observed within-species variation to the extent to which copulations are
496 monopolized by dominant males, which is represented by β in our model. Despite the marked
497 ecological similarities between groups, the estimated β' ranged from 0.30 to 0.97. In the Third
498 ($\beta' = 0.97$) and Wngklm ($\beta' = 0.78$) groups, copulations were almost completely monopolized
499 by the alpha males, a situation that is called "despotic." This contrasts with the conventional
500 classification of primate societies, in which stump-tailed macaques are characterized as having
501 "egalitarian" societies (Matsumura, 1999), or class 3 social systems (Thierry, Singh, &
502 Kaumanns, 2004). The traditional classification intends to place each species on a single position
503 on the despotic-egalitarian spectrum, based largely on the species-level characterizations of
504 ecological factors, such as whether or not a given species is seasonal breeder, or the abundance
505 and spatial distribution of food resources (Sterck, Watts, & van Schaik, 1997). However, our
506 observations clearly suggest that the level of despotism as indicated by β is determined not

507 necessarily in such a top-down manner, but in a more bottom-up way, such that it may vary
508 within species according to the idiosyncrasies of each group. For example, our field observation
509 indicates that the despotic nature of the Third group may have been caused not only by the
510 physical strength of the alpha male, THR-M01, but by the absence of competent rivals; in fact,
511 other males seem either too old or immature to challenge him. Therefore, it appears that bottom-
512 up mechanisms determine β in each group, which then determines whether the alpha male will
513 adopt the solo monopolization strategy or the coalition strategy.

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

524

525 **CONCLUSION**

526 We reported a novel type of animal coalition as a part of male copulatory strategy, and simulated
527 the phenomenon using a mathematical model. We observed novel types of coalitions in wild
528 stump-tailed macaques; multiple males actively shared the mating opportunities. Our

529 mathematical simulations revealed that lack of estrous signs, as well as large numbers of males
530 in a group, possibly enhanced facultative sharing of females.

531

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542

543 **APPENDICES**

544 We have Tables S1, S2, and Figure S1 in Supplementary Materials as separately attached.

545

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644

645 **FIGURE LEGENDS**

646 Figure 1. The male (FTH-M01) and his ally (FTH-M02) simultaneously engaged in the
647 copulation with one female (FHT-F11), not showing any agonistic conflicts between the
648 two “competitive” males; at that time, one male (right male) mounted over the female
649 inserting penis, while the other male (left) “waited for his turn”, touching the female hinds.

650 Figure 2. The dependence of the upper bound of coalition size, m^* , on the number of males, N ,
651 and the extent to which dominant males monopolize matings and/or fertilizations, β , in the
652 absence of coalition formation. The solid and broken curves represent m^* for $s=1.1$ and
653 $s=1.2$, respectively. The upper bound increases and approaches the right-hand side of (9) as

654 N increases (a, b), while the dependence of m^* on β is non-monotonic (c, d). For all
655 panels, $c=0.05$. (a) $\beta=0.1$, (b) $\beta=0.3$, (c) $N=10$, (d) $N=40$.

656 Figure 3. Occurrences of the inter-copulatory event intervals (ICIs) of all recorded single
657 copulation events occurred multiple times in a day ($N_{ICI}=206$). Note that the cases of only
658 one copulation within a day were excluded for the calculations of ICIs because the intervals
659 should be defined by the two consecutive events.

660 Figure 4. Ratios of copulation events (with an ejaculation) for social status, i.e., coalition males
661 (coalitions), males outside of coalitions in a group (non-coalitions), a male solely
662 dominating copulations (alpha), and non-group member males (out-group), for each group.

663 Figure 5. Combinations of $N \in [1,30]$ and $\beta \in (0,1)$ values for which coalition of more than two
664 males is possible (i.e., $m^* > 2$) for several parameter s and c (see plot titles). Each contour
665 represents the coalition size ($m^* > 2$).

666 Figure 6. Nonlinear fitting of copulation occurrences with copulation success ranks. The formula
667 in the plot area shows the estimated parameters, and plot title showed the R^2 .

668 Figure 7. The estimates of β' and the numbers of males, N , in the five groups.