

1 **Mate sharing in male stump-tailed macaques as a possible case of coalition-**
2 **like behavior to modify the group-wise fitness distribution**

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17 **ABSTRACT**

18 In multi-male multi-female groups of animals, male reproductive success is often skewed toward
19 top-ranking males. Coalition formation by middle- to low-rankers can be seen as a collaborative
20 effort to modify the distribution of reproductive success within the group, so that they gain more
21 than they would do otherwise. It has been pointed out, on the other hand, that a coalition of top-
22 ranking males could hardly be profitable in the sense that they would gain little additional benefit
23 from making collaborative effort. Here we report our novel observation of facultative sharing of
24 mating opportunities among males in a wild population of stump-tailed macaques (*Macaca*
25 *arctoides*) as a possible case of coalition-like behavior in which dominant males jointly guard
26 females from mating with subordinate males and actively share mating opportunities within the
27 allies. First, we report our novel observation of facultative sharing of mating opportunities in
28 male stump-tailed macaques, where two or more males remain in close proximity to and copulate
29 with a female in turn without contesting or sneaking. Second, considering the kind of coalition
30 formation in which dominant males collaboratively exclude subordinates from mating
31 competition and thereby strengthen the reproductive skew that already exists, we specify, by
32 means of mathematical modeling, the condition for this kind of coalition formation to be
33 selectively favored. Finally, we derive predictions about the occurrence of the coalition-like
34 behavior depending on ecological and demographic factors, and test them empirically using data
35 from the five groups of stump-tailed macaques in our study population.

36

37 **KEY WORDS**

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

39

40 Male reproductive success in a multi-male multi-female group is often skewed in favor of high-
41 ranking males (Kutsukake & Nunn, 2006). As a countermeasure, low-ranking males may
42 collaborate to modify the distribution of reproductive success within group so that they gain
43 more than they would do otherwise. Male collaboration that results in modification of within-
44 group resource allocation has been theoretically investigated in the context of coalition or
45 alliance formation (Pandit & van Schaik, 2003; van Schaik et al., 2004, 2006). Assuming that a
46 male's share of mating opportunity decreases monotonically with descending rank position,
47 Pandit & van Schaik (2003) developed a mathematical model of leveling coalition, in which a
48 skew in the access to females in favor of dominant males is mitigated by coalition formation of
49 middle- to low-ranking males. While animal coalition is typically manifested as a coordinated
50 aggression by multiple individuals on one or more targets (Bissonnette et al., 2009; Smith et al.,
51 2010) or an individual's intervention in an ongoing conflict between two parties to support one
52 side (Widdig et al., 2000), the Pandit-van Schaik model is potentially applicable to any case
53 where male-male collaboration serves to flatten the group-wise fitness distribution, even in the
54 absence of overt expression of coordinated aggression.

55 In Pandit & van Schaik's (2003) terminology, a coalition of males ranking below the
56 target (i.e., revolutionary or all-up coalition; (Chapais, 1995; van Schaik et al., 2006) is profitable
57 in the sense that it confers, if successful, a fitness benefit to all coalition members. Hence,
58 whenever the coalition is also feasible, that is, if the subordinates are able to jointly beat the
59 dominant target, this type of coalition is predicted to occur. In contrast, a coalition of top-ranking
60 males against a lower-ranker (i.e., conservative or all-down coalition; (Chapais, 1995; van
61 Schaik et al., 2006) would not be profitable because each of the top-rankers can beat the target
62 even without help. A simplest implication from the Pandit-van Schaik model is, therefore, that

63 male-male collaboration to modify the group-wise distribution of reproductive success is more
64 likely to occur among middle- to low-ranking males than among top-rankers (Pandit & van
65 Schaik, 2003; van Schaik et al., 2004, 2006). The expectation is at least partially supported in
66 some species of primates (Bercovitch, 1988; Noë & Sluifster, 1995), but not in others (Young et
67 al., 2014).

68 In this article, we report a novel observation of facultative sharing of mating
69 opportunities among males in a wild population of stump-tailed macaques (*Macaca arctoides*).
70 We regard the observed mate sharing as facultative because there the males copulate with a
71 female in turn without contesting or sneaking. As an illustration, Fig. 1 shows two male stump-
72 tailed macaques sharing a female without exhibiting any sign of antagonism, where the male on
73 the right is copulating with the female while the male on the left is waiting for his turn. In some,
74 but not all, groups in our study population of stump-tailed macaques, the alpha (i.e., the highest-
75 ranking) male forms a coalition-like unit with one or more other males in the same group. The
76 allied males seem to jointly guard a female from mating with other males, while within the
77 coalition-like unit they share the mating opportunities.

78 Strictly speaking, the observed collaborative unit of males is not to be called a "coalition"
79 as it lacks an overt expression of coordinated aggression; nonetheless, we choose to refer to it as
80 "coalition like" because it is a form of male-male collaboration that can potentially modify the
81 group-wise distribution of male reproductive success, as the genuine coalition does in the Pandit-
82 van Schaik model. In particular, suppose that the number of sexually receptive females in a
83 group is larger than that would allow the alpha male to monopolize reproduction (i.e., complete
84 contest competition), but smaller than that would lead to complete scramble competition. In such
85 cases, top-ranking males may be able to exclude subordinates more efficiently from mating

86 competition by guarding females collaboratively than by doing so individually. This raises the
87 possibility that dominant males may gain a fitness benefit by having collaborative partners
88 despite the cost of sharing mating opportunities with them.

89 Since mate sharing in stump-tailed macaques occurs around the alpha male, it is similar
90 to all-down coalition. Within the framework of Pandit and van Schaik's (2003) leveling coalition,
91 however, all-down coalition is not predicted to occur. Instead, the mate sharing by dominant
92 males may be better represented as a novel kind of coalition formation that deprives subordinate
93 males of mating opportunities, whereby "steepens" the reproductive skew. For the purpose of
94 investigating the coalition-like behavior in stump-tailed macaques, we extend the Pandit-van
95 Schaik model by allowing all-down coalition to enhance the efficiency with which top-ranking
96 males keep subordinates from mating, as a result of which the reproductive skew is strengthened.
97 To keep the model simple and tractable, we do not explicitly specify the underlying mechanism
98 by which subordinates are excluded. A recent study by Pandit, Pradhan, & van Schaik (2020)
99 took a different approach to a similar question. They extended the original Pandit-van Schaik
100 model by incorporating a specific mechanism to realize more skewed resource allocation,
101 namely, higher-rankers' usurping of resources owned by lower-rankers. However, since Pandit et
102 al.'s (2020) model is designed to explore the origins of class formation in human societies, and
103 non-human primates are unlikely to meet the presumption that individuals possess exploitable or
104 tradable resources, it is not applicable to the current context.

105 In what follows, we describe our observation of facultative mate sharing among male
106 stump-tailed macaques, develop a mathematical model to explore the underlying mechanism of
107 the behavior, and empirically test predictions derived from the model.

108

109 **METHODS**

110 Study site and animals

111 A wild population of stump-tailed macaques inhabiting the Khao Krapuk Khao Taomor non-
112 hunting area in the Phetchaburi Province of central Thailand (99°44' E, 12°48' N, encompassing
113 an area of 3.5–4 km²) was observed. This site consists primarily of secondary forests, including
114 stands of bamboo and agricultural areas. The macaques also visited areas immediately adjacent
115 to this site (including a nearby temple, cassava and pineapple plantations, and human
116 settlements) on a daily basis. The macaques were occasionally fed by humans, both locals and
117 tourists, on the temple grounds or along the roadside. This population was first documented in
118 June of 1984, at which time there were only 22 individuals. Since then, it has grown to a large
119 population, including at least 391 individuals (97 adult males, 124 adult females, 114 infants
120 (≤ 2 years), and 56 subadult unidentified subjects, who were divided into five groups, namely,
121 Ting, Nadam, Third, Fourth, and Wngklm groups (Table S1 in Supplementary Materials) by
122 2017. The Wngklm group separated from the Third group in November–December 2015. All
123 adults (completely mature monkeys), most subadults (sexually mature but not completely
124 developed), and some juveniles (sexually immature, around 3 years of age) were identified based
125 on facial characteristics. This population is geographically isolated from the other populations,
126 and no new immigrant males from other sites were detected during the study period ([Toyoda et](#)
127 [al., 2017](#); [Toyoda & Malaivijitnond, 2018](#)).

128 Stump-tailed macaques are reported in general as non-seasonal breeders (some local
129 populations/captive groups show seasonality, but that is not the case for the populations in
130 Thailand). No clear sign of estrus is observed in females, and thus it is not possible, at least for
131 human observers, to detect ovulation. Concealed ovulation is generally considered to affect the

132 distribution of male reproductive success by hindering the alpha male from monopolizing fertile
133 females. It should be noted, however, that there is an ongoing debate about whether or not males
134 can infer reproductive status of females. One paper has suggested that males can detect female
135 ovulation by vagina testing behavior (Cerdeña-Molina et al., 2006) although this is not congruent
136 with our data suggesting that more than half of copulations occurred in non-fertile period
137 (Toyoda, unpublished data).

138

139 Daily observations

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

146 All copulations during our observation were recorded using video cameras (JVC GZ-
147 RX500 and Sony HDR-PJ675) and their descriptions were noted.

148

149 Data on copulation

150 Following a previous report (Estep et al., 1984), *single copulation* was defined as a sequence of
151 copulating behavior consisting of mount, insertion, and separation, irrespective of the presence
152 or absence of ejaculation. The starting and ending times of each single copulation were recorded,
153 and the inter-copulation intervals (ICIs) of all adjacent events of single copulations recorded
154 within a day were calculated. A series of single copulations by a female at an interval of less than

155 30 min was considered collectively as a *serial copulation bout* if it included four or more single
156 copulations. We adopted this definition for its improved objectivity as compared with the
157 relatively ambiguous definition in previous studies (Brereton, 1994; Estep et al., 1984). Each of
158 all single copulations not included in any serial copulation bouts was considered a *non-serial*
159 *copulation bout*.

160

161 Mathematical model

162 To understand the logic behind the coalition-like behavior in male stump-tailed macaques, we
163 designed a simple mathematical model based on the framework developed by Pandit & van
164 Schaik (2003). Our motivation for the mathematical modeling was two-fold. First, it is intuitively
165 conceivable that concealed ovulation, as in stump-tailed macaques, hinders the alpha male from
166 guarding all fertilizations, and thus necessitates collaboration of two or more dominant males for
167 reproductive monopoly. However, it is unclear as to whether and under what circumstances the
168 alpha male tolerates one or more allies copulating with females. Second, we observed within-
169 species variation in the occurrence of the coalition-like behavior: it occurs in the Ting, Nadam,
170 and Fourth groups, but not in the Third and Wngklm groups (see Results section). If our logic is
171 sound, the model should also explain this pattern of within-species variation.

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

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

176 where β represents the degree to which dominant males can monopolize mating opportunities,
177 called the despotic parameter ($0 < \beta < 1$).

178 Ecological and demographic factors have been suggested to affect β (van Schaik et al.,
179 2006). Of these, cryptic ovulation in females probably reduces β as it prevents dominant males
180 from guarding each female intensively only during her fertile period. Thus, compared to species
181 in which ovulation is advertised, species with cryptic ovulation are expected to have smaller β .
182 Other factors, such as the number of females in the group, the relative strengths of dominant
183 males, and the female preference for or against dominant males, are also likely to affect β . As
184 the latter factors may vary within a species, we expect that different groups of stump-tailed
185 macaques are characterized by different β values.

186 There may exist circumstances such that it is beneficial for top-ranking males to form a
187 coalition to guard potentially fertile females in a collaborative manner and share copulation
188 opportunities among the allies. The effect of this behavior on the distribution of male
189 reproductive success can be represented by the following equation:

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

190 where we assume $1 < s < 1/\beta$. Parameter s reflects the effect of male-male coalition to
191 "steepen," instead of "flatten," the male reproductive skew, where larger s indicates higher
192 reproductive monopolization by dominant males. It should be emphasized that our parameter s
193 differs from α , the similar parameter in the Pandit- van Schaik model, the latter of which
194 captures the effect of coalition among subordinate males to level the reproductive skew (i.e.,
195 $0 \leq \alpha \leq 1$).

196 To evaluate the profitability of a male-male coalition, the cost and benefit of
197 collaboration has to be defined. We considered two components of a particular male's fitness: the

198 ratio of the mating opportunities gained by that male to all the existing mating opportunities,
199 which approximates the male's share of paternity, and the cost associated with the additional
200 effort of collaborating with others. As for the first component, y_i denotes the proportion of
201 mating opportunities obtained by the i th male among all matings; that is,

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

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

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

203 while in the presence of a coalition,

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

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

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

208 or equivalently,

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

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

211

212 Estimation of parameters

213 We estimated the despotic parameter, β in (1) or $s\beta$ in (2), using nonlinear regression analysis on
214 the observed distribution of the number of copulations, as a proxy to the reproductive success,
215 among males in each of the five groups. For the purpose of better approximating male
216 reproductive success, we considered only those single copulations for which ejaculation was
217 confirmed. Males were sorted according to the number of copulations by the descending order,
218 and a rank order, i , was assigned to each of them. We used the rank among males in the number
219 of copulations as a substitute for the dominance rank in the Pandit-van Schaik model, assuming
220 that coalition formation does not change the dominance ranks of the coalition members of the
221 target. The i th male's number of copulations, x_i , was regressed on the rank order, i , to estimate β
222 in (1) or $s\beta$ in (2) using the nonlinear regression function of Python (curve_fit method in SciPy
223 optimize module). In addition, R^2 values were reported for showing the goodness-of-fitting.

224

225 Ethics approval

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

230

231 **RESULTS**

232 Description of the observed behavior

233 We counted 433 cases of single copulations (defined as a single mount-insertion-separation
234 sequence, see Methods section) from the five subject groups. The median and range of the inter-
235 copulation intervals (ICIs; $N_{ICI} = 206$) were 7 and 0-359 min, respectively, and 95% of the ICIs

236 were 30 min or shorter (Fig. 2). Out of the 433 copulations, 213 (49.2 %) cases occurred in serial
237 copulation bouts, while 220 (50.8%) occurred as non-serial copulation bouts. In total, 26 serial
238 copulation bouts were recorded in the five groups (nine cases in the Ting group, four in Nadam,
239 five in Third, six in Fourth, and two in Wngklm; for details see Table S2 and Fig. S1 in
240 Supplementary Materials), among which the median and range of the per-bout number of single
241 copulations resulting in ejaculation were 6 and 1-31 times, respectively.

242 In the Third and Wngklm groups, a single male was responsible for all of the five and
243 two serial copulation bouts, respectively. These were the same males as those considered as the
244 alpha males throughout the study period on the basis of behavioral observation (named TRD-
245 M01 and WKM-M01 for the Third and Wngklm groups, respectively), i.e., in these groups the
246 alpha males remained in the proximity of a female and copulated repeatedly. Pooling serial and
247 non-serial copulation bouts, we recorded 80 single copulations by TRD-M01, of which 68 were
248 associated with ejaculation, amounting to 81.8% of all copulations and 86.1% of all ejaculated
249 copulations in the Third group. Similarly, we observed 26 single copulations including 22
250 ejaculatory copulations by WKM-M01, which were 59.1% of all copulations and 78.6% of all
251 ejaculatory copulations in the Wngklm group. These indicate that the alpha males were able to
252 obtain considerable portion of copulation opportunities on their own in the Third and Wngklm
253 groups (Fig. 3, see "alpha-monopoly" type).

254 In contrast, we observed serial copulation bouts involving multiple males in the Ting,
255 Nadam, and Fourth groups (Fig. 3, see "coalition" type). Interestingly, in each such multi-male
256 serial copulation bout, males copulated with a female in turn without overt conflict; that is, while
257 one male copulated with a female, the other male(s) maintained close proximity to the copulating
258 pair, and only after one male performed several sequences of copulatory behaviors (i.e., mount,

259 insertion, and separation), did another male take over the role as the copulator (see Fig. 1). In
260 total, 14 cases of multi-male serial copulation bouts were observed, of which nine cases involved
261 two males and five involved three males, and in no cases four or more males were involved
262 (Table S2). The identities of the males sharing females were highly stable, particularly in the
263 Nadam and Fourth groups, in which the numbers of males participated in at least one case of
264 multi-male serial copulation bout were two and three, respectively, including NDM-M01 in
265 Nadam and FTH-M01 in Fourth, who were considered as the alpha males throughout the study
266 period. In the Ting group, where a clear dominance order was not established during the study
267 period among several dominant males, there were nine males that participated in at least one case
268 of multi-male serial copulation bout (Table S2). In addition, there were 108, 30, and 68
269 ejaculated copulations by those males that participated in at least one case of multi-male serial
270 copulation bout in the Ting, Nadam, and Fourth groups, respectively, which amounted to 93.1%,
271 96.8%, and 95.8% of all ejaculated copulations excluding those done by outgroup males (Table
272 S2, Fig. 3). This suggests that the copulation opportunities in the Ting, Nadam, and Fourth
273 groups were obtained almost exclusively by those males who were members of the facultative
274 mate sharing. From these findings, we hypothesize that those males sharing a female function as
275 a coalition-like unit to jointly guard females from mating with other males and actively share the
276 secured mating opportunities within the unit.

277

278 Mathematical analysis

279 Our mathematical analysis specifies the condition for a coalition by the i highest-ranking males
280 to be profitable (i.e., (7)). Since a coalition of top-rankers is always feasible, such a coalition is
281 predicted to occur whenever (7) holds.

282 Regarding within-species variation in the occurrence of coalition formation, we
283 investigate how ecological and demographic factors, which may vary among groups of stump-
284 tailed macaques, affect the profitability condition (7). We derive from (7) the upper bound of
285 coalition size, m^* , for given β , N , s , and c as

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

286 Equation (8) immediately shows that $s(1-c) > 1$ is necessary for any coalition to be profitable;
287 otherwise, $m^* < 1$ always holds. It also shows that the right-hand side of (8) increases with N
288 (Fig. 4a, 4b).

289 For large N , the upper bound of the coalition size is obtained approximately as

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

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

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

292 indicating that as β approaches zero, m^* diverges to minus infinity. In general, the dependence
293 of m^* on β is not monotonic (Fig. 4c, 4d). For coalition of at least two males (i.e., $m^* > 2$), (9)
294 shows that β should be smaller than a threshold, specified by

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

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

297 In summary, we have established the theoretical possibility of coalition formation by
298 dominant males to steepen the reproductive skew that already exists, providing a formal
299 foundation for our hypothesis of coalition-like behavior in male stump-tailed macaques. We have
300 also specified the condition for this kind of coalition to occur, from which the following two
301 predictions are derived: first, a large coalition is more likely to be observed in larger male groups
302 (Fig. 5); and second, among sufficiently large male groups, a coalition is more likely to occur in
303 a group where the extent of reproductive monopolization by dominant males is relatively small,
304 unless it is extremely small (Fig. 5). If, as we have hypothesized, coalition-like behavior
305 underlies the observed facultative mate sharing in stump-tailed macaques, patterns of within-
306 species variation in the occurrence of the facultative mate sharing are expected to follow these
307 predictions.

308

309 Test of model predictions

310 We evaluated the above predictions for within-species variation on the basis of our observational
311 data from the five groups of stump-tailed macaques. For each group, we estimated the despotic
312 parameter, β' , that was supposed to be either unmodified (i.e., $\beta' = \beta$ for Third and Wngklm) or
313 modified (i.e., $\beta' = s\beta$ for Ting, Nadam, and Fourth) by male coalition-like behavior. Non-linear
314 regression analysis returned the following estimates of β' : 0.30, 0.72, 0.97, 0.59, and 0.78 for
315 Ting, Nadam, Third, Fourth, and Wngklm, respectively (Fig. 6).

316 Figure 7 shows the estimates of β' and the numbers of males, N , in the five groups. It is
317 to be noted that the vertical axis represents β for Third and Wngklm and $s\beta$ for Ting, Nadam,
318 and Fourth, so that the unmodified despotic parameter β in the latter three groups would be
319 lower than these values. Consistent with the model predictions, the Ting group, in which there

320 were nine males who participated at least one multi-male serial copulation bout ($m = 9$), had the
321 combination of the largest N and the smallest β' (and thus β) among the five groups. In addition,
322 as predicted, Fourth ($m = 3$) and Nadam ($m = 2$), the two other groups in which multi-male
323 serial copulation bouts were observed, had the second and third lowest values of β' (and thus β),
324 respectively. On the other hand, multi-male serial copulation bout is absent in the Third group
325 with the second largest N , which might appear to contradict our predictions. We tentatively
326 interpret this as a result of large β' in this group; in other words, β may be too large to satisfy
327 (11), although a quantitative evaluation of this claim has been challenging so far. In sum, we
328 conclude that our model accounts well for the patterns of within-species variation in the
329 coalition-like behavior in stump-tailed macaques.

330

331 **DISCUSSION**

332 Our observations, together with mathematical analysis and empirical test of model predictions,
333 suggest that the alpha male of stump-tailed macaques form a coalition-like unit with one or more
334 males in the group to jointly secure mating opportunities and actively share them within the unit.
335 To the best of our knowledge, this is the first mammalian observation of collaborative mate
336 guarding by males, followed by facultative sharing of mating opportunities. While males in other
337 species, such as chimpanzees, olive baboons, and lions, also collaborate to guard females against
338 other males, the coalition-like behavior in stump-tailed macaques differs from them in the
339 following aspects. In the case of lions, a group of females with a few males, called a pride, is
340 formed and the males collectively defend the females from other invasive males. The alpha male
341 mostly monopolizes the mating opportunities, and the subordinate allies have either no access to
342 the females or only limited access not through active sharing (Bygott et al., 1979; Packer &

343 [Pusey, 1982](#)). This is in contrast to the case of stump-tailed macaques, where a coalition-like unit
344 is formed by a few males in a large multi-male multi-female group to exclude other males in the
345 same group from mating competition, and the mating opportunities thus secured are actively
346 shared within the unit. Similarly, in olive baboons, subordinate males form a coalition to jointly
347 attack a dominant male, thereby increasing their future access to females. However, unlike
348 stump-tailed macaques, olive baboons do not actively share copulations ([Bercovitch, 1988](#)). On
349 the other hand, the observed case of a chimpanzee female copulating with eight males within a
350 short time period ([Watts, 1998](#)) might be comparable to the facultative mate sharing in the
351 stump-tailed macaque, although this was considered exceptional, observed only in the Ngogo
352 population, which is considerably larger than the other populations ([Watts, 1998](#)).

353 A remarkable feature of the coalition-like behavior in stump-tailed macaques is that the
354 alpha male appears to pay a reproductive cost by giving mating opportunities away to his allies,
355 who in return offer collaborative work efforts, and as a result they gain reproductive advantage
356 as a team. Another point deserving attention is that coalition formation manifested as joint
357 aggression on a target may involve triadic awareness among the attacker, helper, and target
358 ([Harcourt & de Waal, 1992](#); [Paxton et al., 2010](#); [Schino, Tiddi, & Di Sorrentino, 2006](#); [Silk,](#)
359 [1999](#)), which is deemed to be cognitively more demanding than understanding the dyadic
360 relationship between the self and another individual ([Hemelrijk et al., 2013](#)). For that matter, the
361 coalition-like behavior in stump-tailed macaques, which sometimes involves collaboration
362 among more than two individuals, may also require extra capacity of social cognition and that
363 may be why similar behavior is rare in non-human animals.

364 Why do male stump-tailed macaques, unlike males of closely related species, exhibit this
365 peculiar behavior? To put it in another way, what are the socio-ecological factors in stump-tailed

366 macaques that may have favored the evolution of this behavior? Here, we propose that the
367 absence of signs of ovulation in female stump-tailed macaques may be a key. In many primate
368 species, females exhibit visual or olfactory signs of ovulation during the fertile period of the
369 reproductive cycle. Conspicuous estrous signals such as sexual swellings enhance male-male
370 competition, providing females more opportunities for mate choice (Nunn, 1999; Nunn, van
371 Schaik, & Zinner, 2001; Zinner et al., 2004). Advertisement of female reproductive status is
372 often seen in Old World monkeys living in multi-male multi-female societies, such as most
373 macaques, baboons, and chimpanzees (Nunn, 1999; Nunn et al., 2001; Zinner et al., 2004). When
374 female reproductive status is advertised, it is relatively easy for the alpha male to monopolize
375 fertilizations, as in that case he can concentrate all his guarding efforts on the females fertile at
376 that moment. On the other hand, when female ovulation is cryptic, the alpha male is no longer
377 able to adopt the selective guarding strategy, and reproductive monopoly is only possible if all
378 cycling females are guarded all the time. Our hypothesis is that the difficulty in establishing
379 reproductive monopoly by the alpha male due to concealed ovulation may have promoted the
380 formation of a coalition-like unit among dominant males.

381 Our discovery of the formation of a coalition-like unit, followed by active sharing of
382 mating opportunities, in male stump-tailed macaques demands a revision of the existing
383 socioecological models in primate social systems. As far as we are aware, this is the first
384 documented case in non-human primates of collaborative effort for acquiring resources based on
385 active sharing among the collaborators. We have hypothesized that the lack of estrous signs in
386 female stump-tailed macaques, unlike many Old-World monkeys, is a key factor enhancing the
387 coalition-like behavior. Concealed ovulation is likely to reduce the extent to which fertilizations
388 are monopolized by dominant males. In our mathematical model, this effect is represented by the

389 reduction in parameter β . The model predicts that male-male coalition is more likely to occur
390 when β is small, confirming the logical consistency of our hypothesis. From the female's
391 perspective, monopolization by dominant males means limited opportunities for female mate
392 choice, particularly when they prefer copulations with subordinate or out-group males. Thus,
393 concealed ovulation may be considered as a female strategy to facilitate mate choice. Further
394 extending the argument, the formation of coalition followed by active sharing of mating
395 opportunities may be a counter strategy of dominant males. In other words, being unable to
396 control female reproduction on his own, the alpha male may gain more by surrendering some
397 fertilization opportunities to elicit cooperation by subordinates. Hence, the intensified sperm
398 competition in stump-tailed macaques ([García Granados et al., 2014](#)) may be a joint consequence
399 of female concealment of fertility states and male sharing of mating opportunities. In addition, a
400 potentially relevant observation is that female stump-tailed macaques do not produce copulation
401 calls ([Blurton Jones & Trollope, 1968](#)). Although the function of female copulation calls is still a
402 matter of contention ([Bernstein et al., 2016](#); [Maestripieri & Roney, 2005](#)), a possible
403 interpretation is that female stump-tailed macaques do not make any effort to induce male mate
404 guarding.

405 The present study has also revealed the importance of the number of males in a group as
406 a predictor for the formation of coalitions among dominant males. In other words, male-male
407 coalition is more likely to be formed when there are more males in a group. In our field site, we
408 observed five groups of stump-tailed macaques consisting of 391 individuals, or on average 78.2
409 individuals per group. The relatively large group size is primarily due to the semi-provisioning
410 conditions in our study site, and this factor also appears to affect the socioeconomic sex ratio,
411 i.e., the ratio of the number of adult females to the number of adult males. The average

412 socioeconomic sex ratio in our sample is 1.33, while those that have been previously reported for
413 other populations of stump-tailed macaques are approximately 5.7 (Fooden, 1990). The smaller
414 socioeconomic sex ratio indicates more intense male-male competition. Hence, both large
415 number of males per group and small socioeconomic ratio may have facilitated the occurrence of
416 coalition formation by dominant males in our study population.

417 While our model predicts monotonic increase of the coalition size with the increasing
418 number of males in the group, we observed coalitions of two or three males, but never four or
419 more. This discrepancy might indicate that there exist additional factors restricting the coalition
420 size that are not considered in the model. A possible factor is, as mentioned earlier, the limited
421 social cognition in non-human animals. Actually, psychological experiments on cooperative
422 tasks have revealed that collaboration is possible among two or three chimpanzee subjects, but is
423 much more difficult when four or more subjects are involved ((Hirata & Fuwa, 2007; Kaigaishi
424 et al., 2019; Tomonaga et al., 2004)). For the recognition of quadratic relations, an individual
425 has to recognize the possible combinations of dyadic and triadic relations, exponentially
426 increasing the socio-cognitive loading in the brain.

427 We have also observed within-species variation in the extent to which copulations are
428 monopolized by dominant males, which is represented by β in our model. Despite the marked
429 ecological similarities between groups, the estimated β' ranged from 0.30 to 0.97. In the Third
430 ($\beta' = 0.97$) and Wngklm ($\beta' = 0.78$) groups, copulations were almost completely monopolized
431 by the alpha males, a situation that is called "despotic." This contrasts with the conventional
432 classification of primate societies, in which stump-tailed macaques are characterized as having
433 "egalitarian" societies (Matsumura, 1999), or class 3 social systems (Thierry et al., 2004). The
434 traditional classification intends to place each species on a single position on the despotic-

435 egalitarian spectrum, based largely on the species-level characterizations of ecological factors,
436 such as whether or not a given species is seasonal breeder, or the abundance and spatial
437 distribution of food resources (Sterck et al., 1997). However, our observations clearly suggest
438 that the level of despotism as indicated by β is determined not necessarily in such a top-down
439 manner, but in a more bottom-up way, such that it may vary within species according to the
440 idiosyncrasies of each group. For example, our field observation indicates that the despotic
441 nature of the Third group may have been caused not only by the physical strength of the alpha
442 male, THR-M01, but by the absence of competent rivals; in fact, other males seem either too old
443 or immature to challenge him. Therefore, it appears that bottom-up mechanisms determine β in
444 each group, which then determines whether the alpha male will adopt the solo monopolization
445 strategy or the coalition strategy.

446 Finally, our model predicts the future dynamics in the stump-tailed macaque groups. For
447 example, when youngsters in the Third group become sufficiently mature to challenge the alpha
448 male, and as a consequence β is reduced, our model predicts that the alpha male will form a
449 coalition-like unit with other males. We expect that a longitudinal observation of wild stump-
450 tailed macaques will confirm these model predictions. In conclusion, stump-tailed macaques are
451 characterized by societies ranging from despotism to egalitarianism, and from monopolization of
452 females by a dominant male to male-male coalition coupled with active sharing of mating
453 opportunities. Future studies on wild stump-tailed macaques may shed new light on the origins
454 and evolution of altruism and cooperation in mammalian societies, including the hyper-
455 cooperation in human societies (Burkart et al., 2014).

456

457 **CONCLUSION**

458 We have reported a novel observation of facultative sharing of mating opportunities among
459 males in a wild population of stump-tailed macaques. Our observational data, mathematical
460 analysis, and empirical test of model predictions altogether indicate that the observed behavior
461 can be interpreted as a coalition-like behavior, in which dominant males collaboratively guard
462 females from mating with subordinate males, and actively share the secured mating opportunities
463 within the allies. The mathematical analysis predicts that less intense despotism and greater
464 number of males in a group are to be associated with the coalition-like behavior. We have further
465 argued that the lack of estrus signs in stump-tailed macaque females may be a key factor that
466 accounts for the occurrence of the coalition-like behavior in this species.

467

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479

480 **APPENDICES**

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

482

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610 **FIGURE LEGENDS**

611 Figure 1. Stamp-tailed macaque males (FTH-M01 and FTH-M02) sharing mating opportunities
612 with a female (FHT-F11) without showing any sign of antagonism.

613
614 Figure 2. The distribution of the inter-copulation intervals (ICIs) between two consecutive single
615 copulations that involved the same pair of male and female ($N_{ICI} = 206$). The green broken line
616 represents the critical ICI value below which 95% of the observed ICIs were included. Note that
617 only the cases where the same pair of male and female copulated more than once within a day
618 are included.

619
620 Figure 3. Proportions of single copulations with different characteristics to all single copulations
621 in each of the five groups. Only are the single copulations associated with ejaculation included.
622 The outer circle compares the proportions of single copulations that are part of serial copulation
623 bouts and those that are non-serial copulation bouts. The inner circle shows the proportions of
624 single copulations by the alpha males, non-alpha males forming a coalition unit, non-alpha males
625 not forming a coalition unit, and males from outside of the group.

626
627 Figure 4. The dependence of the upper bound of coalition size, m^* , on the number of males, N ,
628 and the despotic parameter, β , in the absence of coalition formation. The blue and orange curves
629 represent m^* for $s = 1.1$ and $s = 1.2$, respectively. For all panels, $c = 0.05$. (a) $\beta = 0.1$, (b)
630 $\beta = 0.3$, (c) $N = 10$, (d) $N = 40$.

631

632 Figure 5. Contour plots of the upper bound of coalition size, m^* , on the $N\beta$ -plane for given
633 values of c and s . Each contour represents (8) for the designated value of m^* .

634

635 Figure 6. The observed distribution of the number of single copulations with ejaculation among
636 males in each of the five groups. The curves represent the results of nonlinear regression
637 analysis. R^2 gives the coefficient of determination.

638

639 Figure 7. The estimates of β^i and the numbers of males, N , in the five groups.

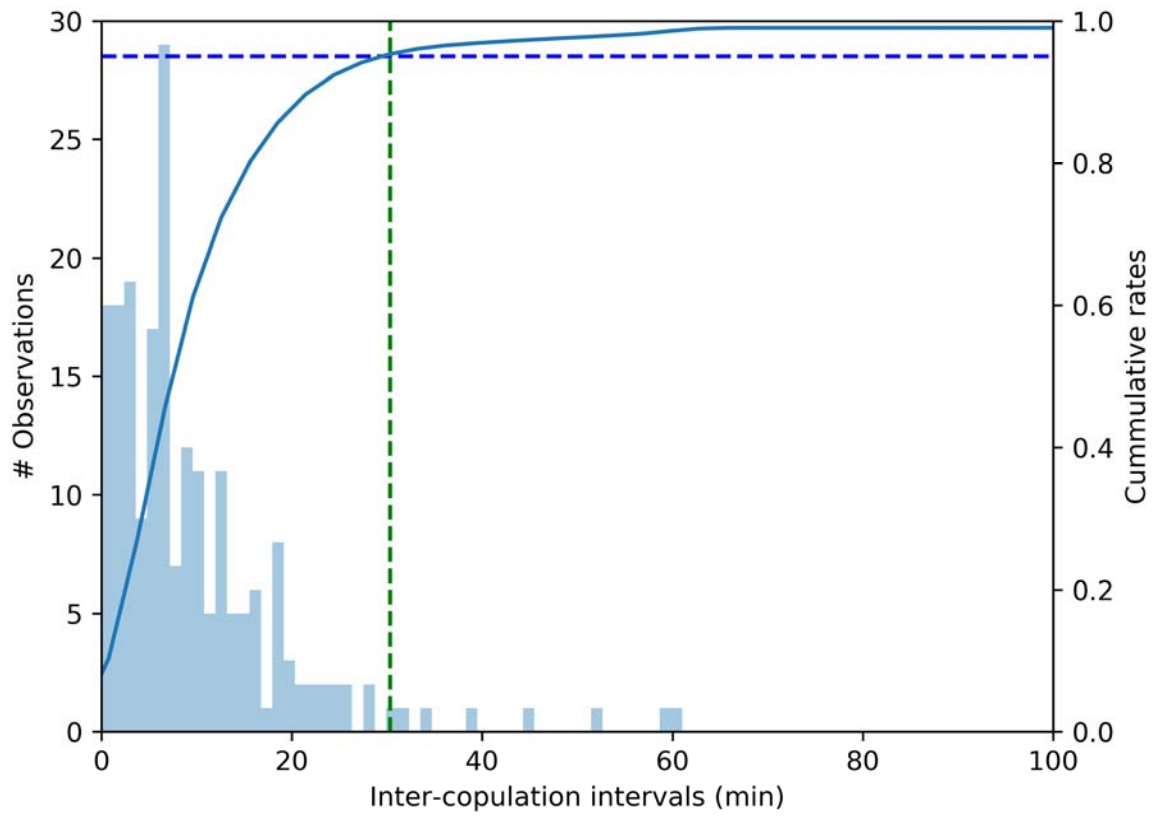
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642 Figure 1

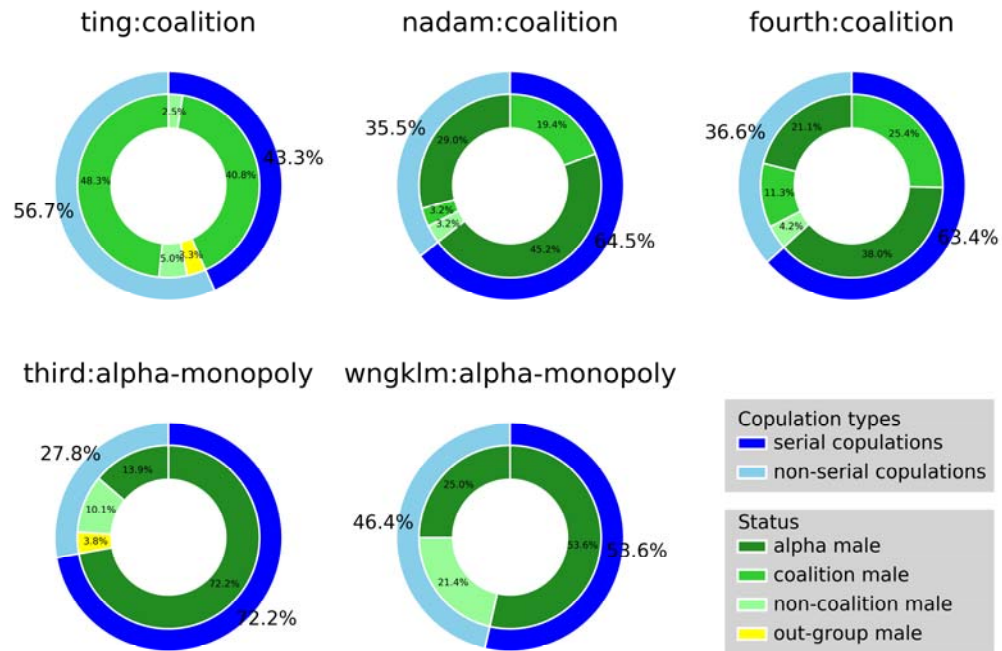
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645 Figure 2

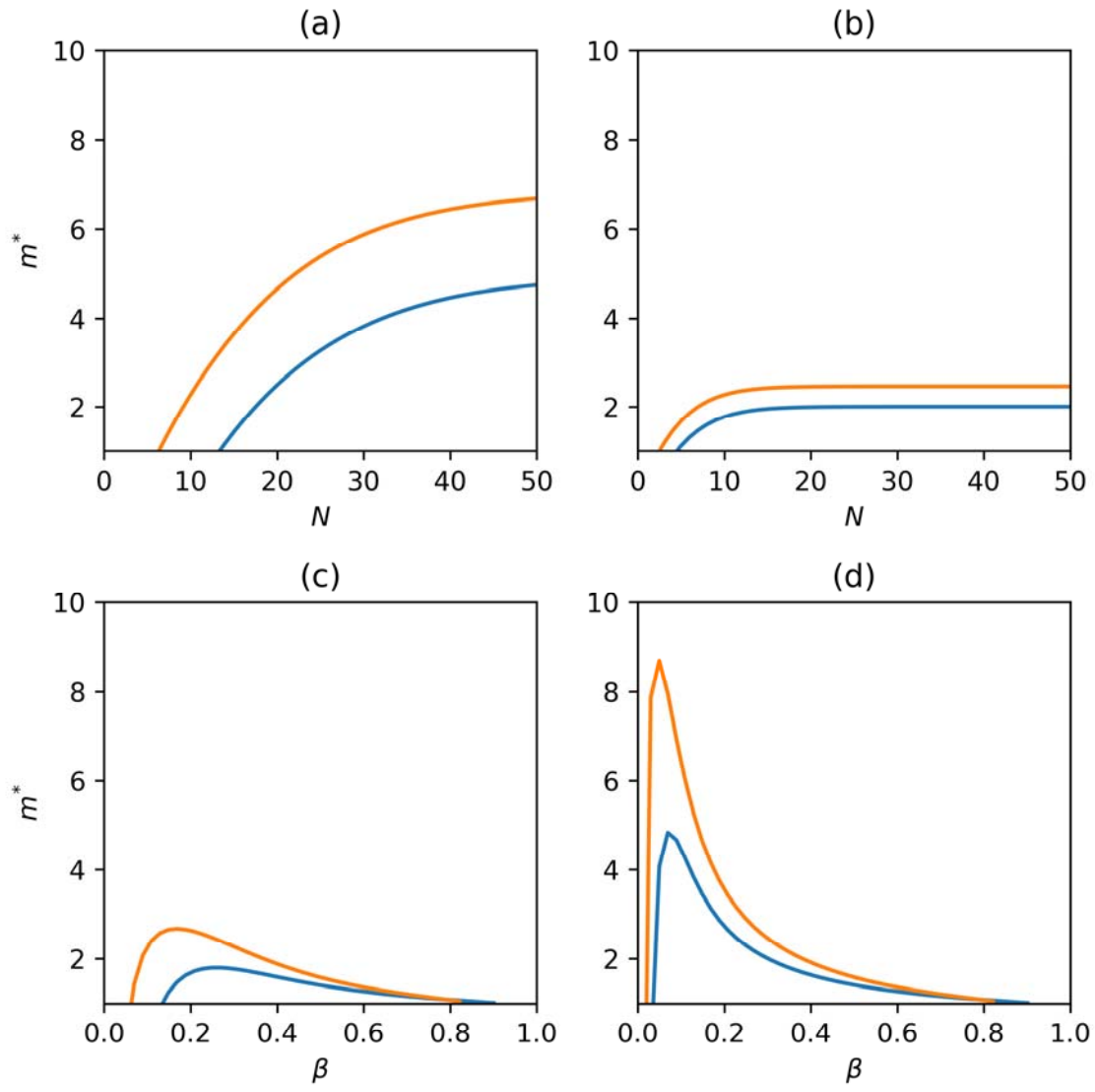
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648 Figure 3

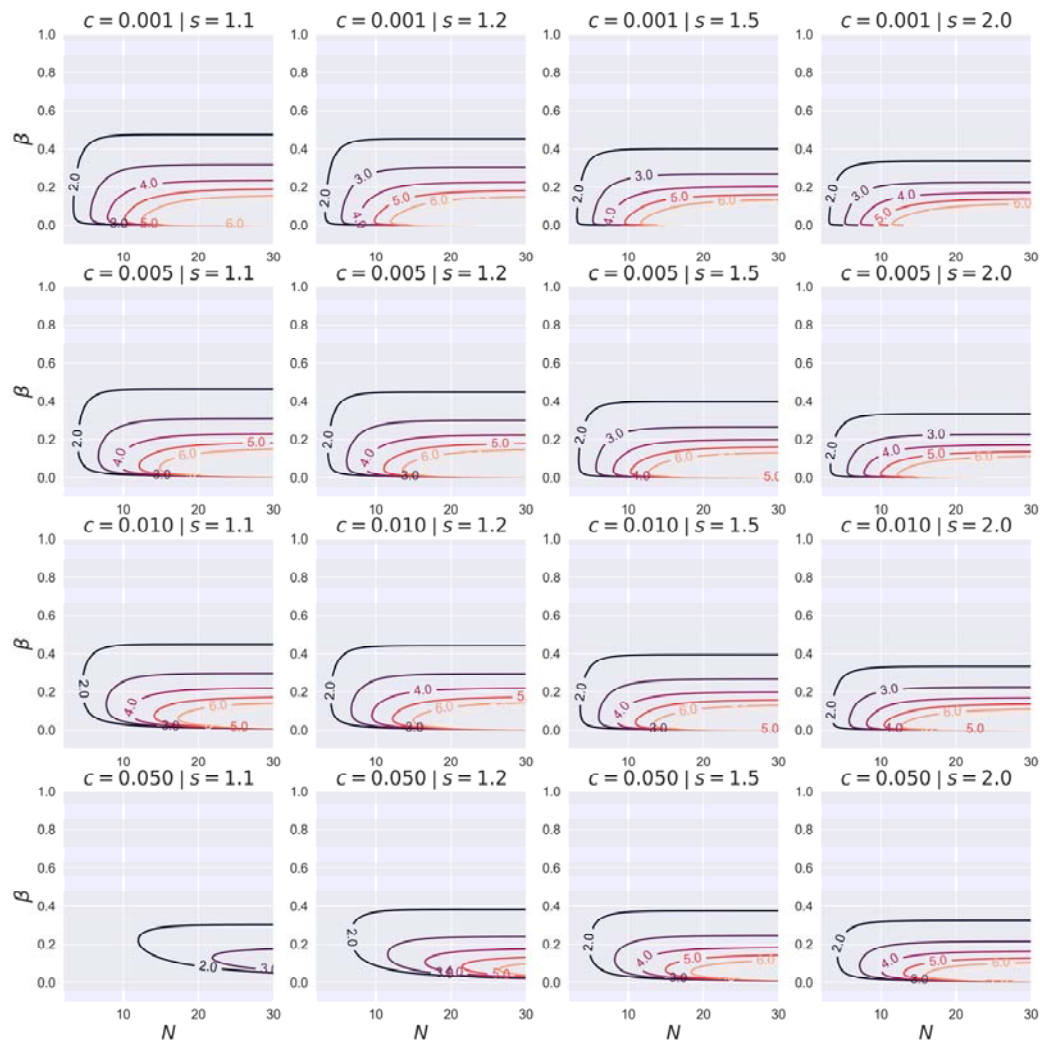
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651 Figure 4

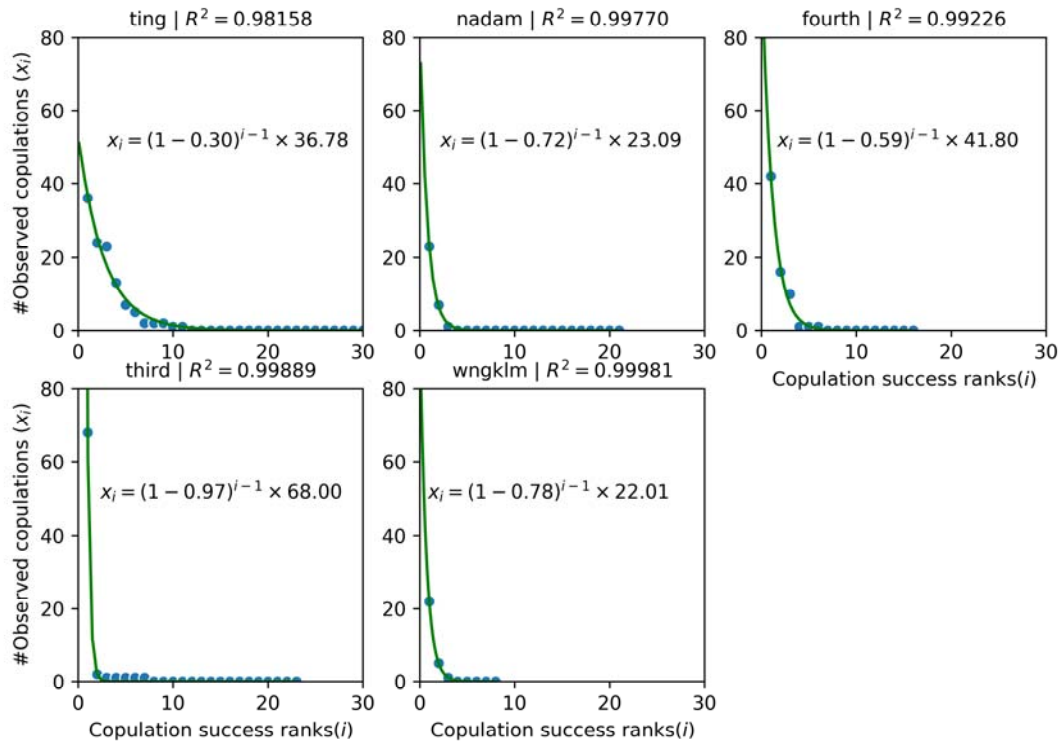
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654 Figure 5

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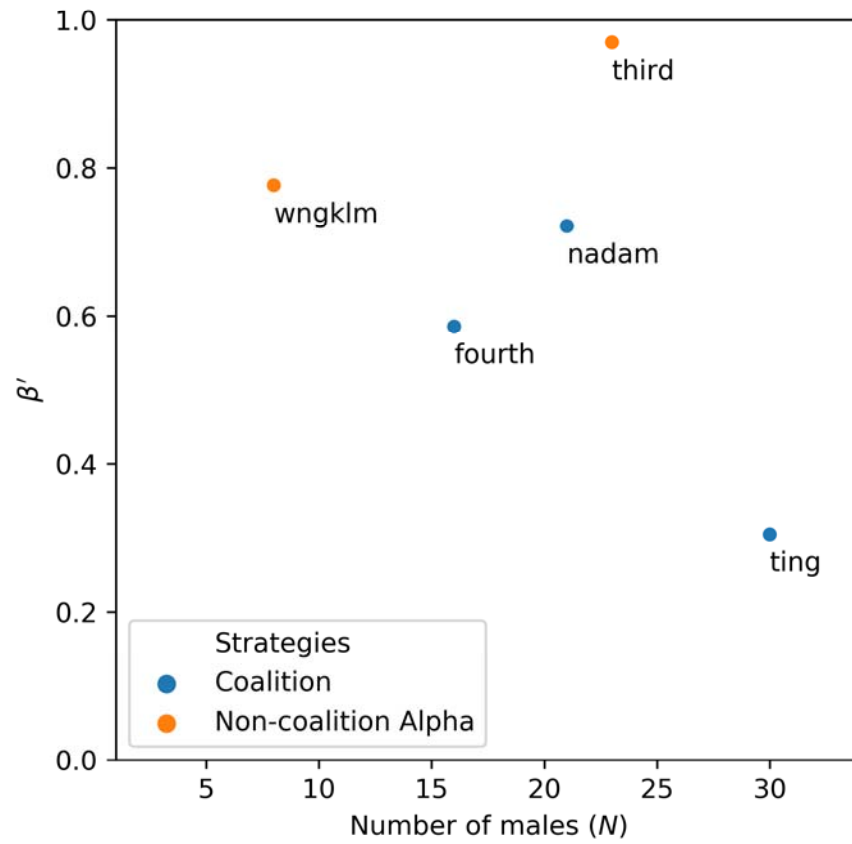


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657

Figure 6

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659

660 Figure 7

661