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1 Original Article

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3 Reproductive success of two male morphs in a free-ranging population of Bornean
4 orangutans

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47 **Abstract**

48 The reproductive success of male primates is not always associated with dominance status.

49 For example, even though male orangutans exhibit intra-sexual dimorphism and clear

50 dominance relationships exist among males, previous studies have reported that both

51 morphs are able to sire offspring. The present study aimed to compare the reproductive

52 success of two male morphs, and to determine whether unflanged males sired offspring

53 in a free-ranging population of Bornean orangutans, using 12 microsatellite loci to

54 determine the paternity of eight infants. A single flanged male sired most of the offspring

55 from parous females, and an unflanged male sired a firstborn. This is consistent with our
56 observation that the dominant flanged male showed little interest in nulliparous females,
57 whereas the unflanged males frequently mated with them. This suggests that the dominant
58 flanged male monopolizes the fertilization of parous females and that unflanged males
59 take advantage of any mating opportunities that arise in the absence of the flanged male,
60 even though the conception probability of nulliparous females is relatively low.

61

62 **Keywords:** paternity analysis; male dominance; bimaturism; Bornean orangutan; *Pongo*
63 *pygmaeus*; free-ranging population

64 Introduction

65 In most mammals, males compete to fertilize reproductive females (Trivers
66 1972), and previous studies of social primates suggest that dominant males usually have
67 more access to fertile females and sire more offspring than subordinate males (Altmann
68 1962; Cowlshaw and Dunbar 1991; Kutsukake and Nunn 2006). However, genetic
69 analyses have revealed that the most dominant male is not always the most successful sire
70 (Ellis 1995; Majolo et al. 2012) and dominant males' monopolization of fertilization can
71 be reduced by female estrus synchrony, the number of rival males (Kutsukake and Nunn
72 2006; Ostner et al. 2008), and the alternative reproductive tactics of subordinate males
73 (Setchell 2008).

74 Unlike other great apes, wild orangutans lead a semi-solitary lifestyle (Delgado
75 and van Schaik 2000). Orangutans are characterized by male bimaturation, a phenomenon
76 in which sexually mature males exhibit intra-sexual dimorphism and that might have
77 evolved as a result of intense male-male competition (Utami Atmoko et al. 2009a). In this
78 system, the dominant morphs, which are called "flanged males" (FLMs), have large
79 bodies and fully developed secondary sexual characteristics, including prominent cheek
80 pads, long fur, and a throat sack, whereas the subordinate morphs, which are called
81 "unflanged males" (UFMs), have skeletally mature female-sized bodies and lack

82 secondary sexual characteristics (Delgado and van Schaik 2000). In addition to their
83 contrasting morphology, the two male morphs also exhibit different social behavior
84 (Utami Atmoko et al. 2009a). For example, FLMs are highly competitive, as evidenced
85 by wounds on their faces and bodies (Utami Atmoko et al. 2009a), whereas UFMs are
86 usually more tolerant, thereby obscuring the dominance relationships among UFMs
87 (Utami Atmoko et al. 2009a).

88 Previous studies have also reported that the dominant and subordinate orangutan
89 morphs also differ in their mating behavior. For example, FLMs primarily copulate during
90 their consortship with females (Galdikas 1985a; Mitani 1985), whereas UFMs often
91 perform forced copulations (Galdikas 1985b; Mitani 1985) and often do so in the absence
92 of FLMs (Utami Atmoko et al. 2009b). These observations suggest that FLMs sire more
93 offspring than UFMs. However, it has been reported that both male morphs can sire
94 offspring (Utami et al. 2002; Goossens et al. 2006), and paternity studies have reported
95 that almost half of Sumatran orangutan offspring are sired by UFMs, whereas most
96 Bornean orangutan offspring are sired by FLMs (Utami Atmoko et al. 2009b). Banes et
97 al. (2015), who sampled a mixed population of wild-born and ex-captive Bornean
98 orangutans, also reported that a dominant FLM sired most of the population's offspring.

99 However, orangutan paternity studies have been based on molecular genetic

100 analyses and have generally lacked behavioral observation. In addition, Utami Atmoko et
101 al. (2009b) pointed out that UFM's sire most firstborn offspring in Sumatra. Yet, this has
102 never been investigated in Bornean orangutans, and the paternity studies that have been
103 conducted in Borneo (e.g., Goossens et al. 2006; Banes et al. 2015) provide no
104 information regarding female parity or offspring birth order.

105 Accordingly, the present study aimed to compare the reproductive success of the
106 dominant and subordinate male morphs in Borneo, and to determine whether the firstborn
107 offspring of female Bornean orangutans are sired by UFM's. The present study focused
108 on a free-ranging population that was primarily composed of rehabilitated orangutans in
109 Kabili Sepilok Forest Reserve, because the females of the population have been regularly
110 monitored and their parity has been documented. To complement the paternity analyses,
111 the behavior of the males was also observed.

112

113 **Methods**

114 *Study Site*

115 Sample collection and behavioral observation were conducted by the author TT
116 with the help of local assistants in the Kabili Sepilok Forest Reserve (KSFR), which
117 comprises ~4200 ha of lowland dipterocarp forest and harbors ~200 orangutans

118 (Ancrenaz et al. 2005). The Sepilok Orangutan Rehabilitation Centre (SORC; 05°51.841'
119 N, 117°57.003' E), which was established in 1964, is located adjacent to KSFR and has
120 managed a rehabilitation project in which orphaned Bornean orangutans (*P. pygmaeus*
121 *morio*) are rescued from the state of Sabah, Malaysia and then released into the reserve
122 (Kuze et al. 2008). The SORC has established feeding platforms (Fig. 1), which the
123 rehabilitated orangutans visit voluntarily, and supplies the orangutans with supplemental
124 food (mainly bananas and sugarcane) twice a day (10:00 and 15:00 h).

125

126 *Animals*

127 The present study monitored eight adult orangutans (one FLM, three UFM, and
128 four parous females) between December 2010 and August 2012. The age-sex class of the
129 individuals was determined based on morphology (Wich et al. 2004; Kuze et al. 2005).
130 Reliable information about the rehabilitated orangutans was obtained from the SORC
131 studbook (Table 1). One of the UFM (MK) and two of the parous females (MM and BR)
132 were rehabilitated, and the other two parous females (MR and CL) were descendants of
133 MM and BR. The origin of the other three adult males (CD, RG, and TK) is unknown.
134 One of the population's UFM (MK) and one adult female (BR), along with her offspring,
135 were translocated to another reserve in 2012.

136 The timing of each conception was estimated from the average gestation length
137 (245 d; Graham 1988) and each offspring's birth date, following Knott et al. (2010).
138 Reproductive females were defined as those that lacked dependent infants and that failed
139 to exhibit labial swelling, which only occurs during pregnancy (Delgado and van Schaik,
140 2000). During our study, the adult males were also observed to mate with nulliparous
141 females (6–10 years old), some of which were potentially fertile, since the age at first
142 parturition in the SORC is 8–15 years (Kuze et al. 2008).

143

144 [insert Fig. 1 around here]

145 [insert Table 1 around here]

146

147 *Sample and Data Collection*

148 The behavior of the four adult males and four parous females was monitored
149 during July–August 2010, December 2010–April 2011, and July 2011–August 2012.
150 These periods encompassed three conceptions (MM3, CL3, and MO). Whenever possible,
151 we followed the same animal from the morning to the night nest for a maximum of three
152 consecutive days, in order to record sexual and agonistic interactions with other
153 individuals. The behavior of the individuals was observed for a total of 1557 h (males:

154 438 h; females: 1045 h). During these observations, copulation was recorded when penile
155 intromission was observed.

156

157 *Genotyping and Paternity Analyses*

158 We analyzed the paternity of 22 individuals, but we failed to collect DNA
159 samples from four nulliparous females (TP, RSL, SG, and OT). From 2010 to 2014,
160 seventy-three fresh fecal samples were collected from 19 individuals, which included
161 eight mother-infant units (Table S1). However, three infants (CL3, MM3, and MO) had
162 died before the non-invasive samples were taken. Therefore, we collected muscle and
163 liver tissues from the postmortem specimens, with appropriate permissions from the
164 SORC and Sabah Wildlife Department. Four adult males were genotyped as paternal
165 candidates, although we were unable to collect samples from an FLM that had been
166 occasionally observed in 2009. Following Wich et al. (2004), we estimated that the five
167 young males were less than 14 years old at the time of each conception and, thereby,
168 regarded them as adolescent and excluded them from the paternal analysis. To obtain
169 DNA through non-invasive means, we swabbed the surface of feces from the individuals
170 and then soaked the swabs in tubes that contained lysis buffer (Longmire et al. 1997). The
171 DNA of fecal and post-mortem tissue samples was then extracted using the QIAamp DNA

172 Stool Mini Kit (Qiagen, Valencia, California, USA) and DNeasy Blood & Tissue Kit
173 (Qiagen), respectively. Multiplex polymerase chain reaction (PCR) was performed as
174 described in Inoue et al. (2007), using the QIAGEN multiplex PCR Kit (Qiagen). We then
175 amplified 12 microsatellite loci (Goossens et al. 2006) from each of the DNA samples
176 using two multiplex primer sets: multi1 (*D2s1326*, *D3s2459*, *D5s1457*, *D12s375*,
177 *D16s420*, and *D1s2130*) and multi2 (*D1s550*, *D4s1627*, *D5s1505*, *D6s501*, *D2s141*, and
178 *D13s765*). Because the non-invasive samples had low DNA contents, we needing to
179 account for the low rate of DNA amplification and the resulting genotyping errors (Lampa
180 et al. 2013). For accurate genotyping, homozygous and heterozygous alleles were scored
181 after amplification in three and two independent PCRs, respectively (Lampa et al. 2013).
182 Genotypes for all 12 microsatellite loci were obtained for 22 individuals (Table S1). We
183 estimated the paternity of the offspring using CERVUS 3.0 (Kalinowski et al. 2007), with
184 10,000 simulations and confidence levels of 95% (relaxed) and 99% (strict).

185

186 **Results**

187 *Paternity*

188 Genotypes for all 12 microsatellite loci were generated for 22 individuals (Table
189 S1), and paternity was determined for six of the eight offspring born during the study

190 period (Table 2). No mismatches were observed between the offspring and expected sires
191 at any locus. One FLM (CD) sired five non-firstborn offspring, whereas a UFM (RG)
192 sired a firstborn offspring (SP). Another firstborn (RN) was sired by CD, who has been
193 an FLM since 2010; no information regarding its morph and status in 2004 is available.
194 We could not determine the paternity of two offspring (SL and CH) that were born in June
195 2010, and we failed to collect DNA samples from an FLM that was occasionally observed
196 at the feeding platforms around the estimated timing of these two conceptions (i.e.,
197 October 2009).

198

199 [insert Table 2 around here]

200

201 *Male agonistic interaction*

202 We observed 22 cases of agonistic interactions among the four adult males. All
203 of these interactions occurred in the presence of females, and male dominance relations
204 were established on the basis of these dyadic interactions (Table 3). The FLM (CD) was
205 always dominant over the UFM, and linear dominance was observed among the UFM.
206 The FLM only exhibited aggression in the presence of reproductive parous females,
207 whereas the UFM competed for access to both reproductive parous and nulliparous

208 females (Table 4).

209

210 [insert Table 3 around here]

211 [insert Table 4 around here]

212

213 *Mating interaction*

214 Forty-four copulations were documented during the study period (37 and seven
215 in the male-and female-focal observations, respectively). The FLM copulated with parous
216 females in two cases, and the UFM's also copulated with parous females in 21 cases,
217 always in the absence of the FLM. However, the FLM was not observed to make any
218 attempts to copulate with or inspect the genitals of nulliparous females, whereas the
219 UFM's were observed to copulate with the nulliparous females in 21 cases, and all of the
220 UFM's were observed to copulate with both reproductive parous and nulliparous females
221 (Table 5). We also observed 136 cases of males inspecting female genitals, either by hand
222 or mouth, and subsequent copulation occurred in 34 (25.0%) of these cases. The UFM's
223 inspected nine nulliparous females and copulated with four of them, only one of which
224 (AN) become pregnant during the study period.

225

226 [insert Table 5 around here]

227

228 **Discussion**

229 The purpose of the present study was to compare the reproductive success of
230 Bornean FLMs and UFM, and determine whether UFM sired firstborn offspring. The
231 paternity results of the present study are basically consistent with those of previous
232 paternity studies in Borneo (Table 6) and suggest that dominant FLMs might be able to
233 monopolize the fertilization of females within certain areas (Goossens et al. 2006; Banes
234 et al. 2015). Even though it is possible that the rehabilitation project influenced the
235 reproduction of the animals through interactions with the human staff and with other
236 rehabilitant orangutans, our paternity results are not different from those of previous
237 studies. Our observations that all UFM copulated with parous females when the FLM
238 was absent and that only the UFM mated with nulliparous females are also consistent
239 with the observations of previous behavioral studies (Mitani 1985; Galdikas 1985a, b;
240 Utami Atmoko et al. 2009b), which again suggests the rehabilitation project at the SORC
241 has little impact on the mating interactions or offspring paternity of the studied orangutans.

242 As in Sumatra (Utami Atmoko et al. 2009b), the UFM at the SORC sired none
243 of the offspring born to parous females, even though we observed copulation between the

244 two. A previous hormone study suggested that female Bornean orangutans might copulate
245 with the most dominant male near the time of ovulation, thereby resulting in more
246 conceptions when mating with the FLM (Knott et al. 2010). We observed that males at
247 SORC performed frequent genital inspection, which might help to estimate the
248 reproductive state of females (Knott et al. 2010). Furthermore, orangutan sperm cells have
249 better-developed acrosomes than either chimpanzee or gorilla sperm cells, which
250 facilitates conception (Fujii-Hanamoto et al. 2011). These studies may explain why the
251 dominant FLM had the highest reproductive success and the UFM did not.

252

253 [insert Table 6 around here]

254

255 The present study also provides new evidence for the siring of firstborn offspring
256 (e.g., SP) by UFM, as previously reported from Sumatra (Utami Atmoko et al. 2009b).
257 Several researchers have reported that FLMs show little interest in nulliparous females
258 (Schürmann 1981; Galdikas 1985a). Indeed, in the present study, the FLM did not attempt
259 to either copulate with or inspect the genitals of any nulliparous female, whereas all of
260 the UFM copulated with nulliparous females, and some of them competed with one
261 another for access in front of nulliparous females. In orangutans, nulliparous females are

262 regarded as less fertile than parous females, owing to adolescent sterility (Galdikas 1995;
263 Knott and Kahlenberg 2007), so the FLMs might focus their efforts on mating with parous
264 females, whereas UFM_s mate with all potentially reproductive females, including
265 nulliparous ones (Utami Atmoko et al. 2009b). The latter conclusion is also supported by
266 our observations that only the UFM_s exhibited agonistic interactions in proximity to
267 nulliparous females.

268 The tendency of subordinate males to mate with nulliparous females has also
269 been reported in other African great apes. In eastern chimpanzees (*Pan troglodytes*
270 *schweinfurthii*), for example, high-ranking males prefer to mate with older parous females
271 (Muller et al. 2006), whereas low-ranking adult and adolescent males copulate more with
272 nulliparous females (Watts 2015), which are regarded as less desirable mates
273 (Wroblewski et al. 2009). In the multi-male groups of mountain gorilla (*Gorilla beringei*
274 *beringei*), the most dominant males copulate more with parous females, whereas the
275 subordinate males copulate more with nulliparous females (6–8 years old; Stoinski et al.
276 2009), which subsequently bear offspring (Nsubuga et al. 2008). Therefore, mating with
277 nulliparous females is probably an alternative reproductive tactic.

278 Our observations of male agonistic interactions suggest that clear dominance
279 relationships occur among the three UFM_s, a finding which has not been reported by

280 previous studies (e.g., Utami Atmoko et al. 2009a). It is possible that long-term
281 interactions between ex-rehabilitants might influence the relationships among UFM.
282 However, owing to our study's small sample size, we were unable to determine whether
283 dominance rank affected the siring of firstborn offspring. Therefore, future studies should
284 focus on the dominance relationships of UFM, as well as the possible effects of such
285 relationships on reproductive success.

286

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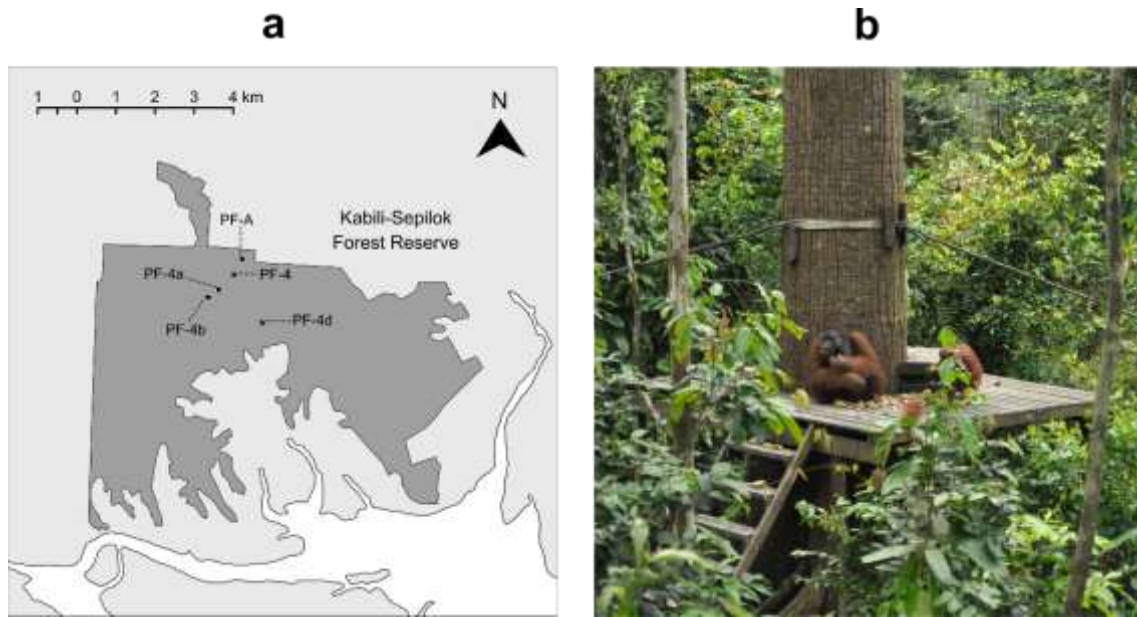
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Fig. 1 Kabili Sepilok Forest Reserve. (a) Location, (b) Feeding platform in the reserve

449 Table 1 Information of subject individuals (N=26)

Category	Studbook ID	Name ID	Sex	Year of age ^a	Date of birth ^b	Origin ^c	Focal hour	DNA analyzed
FLM	-	CD	M	21 ^a	-	Unknown, identified in 2010	43	Yes
UFM	PP412	MK	M	18	18-Dec-1994	Rehabilitated	150	Yes
	-	RG	M	15 ^a	-	Unknown, identified in 2007	204	Yes
	-	TK	M	15 ^a	-	Unknown, identified in 2010	41	Yes
Parous	PP249	MR	F	22	03-Feb-1990	Offspring of rehabilitated mother	265	Yes
	PP505	MM	F	18	28-Nov-1996	Wild-born, rehabilitated	329	Yes
	PP483	CL	F	14	19-Sep-1996	Offspring of rehabilitated mother	300	Yes
	PP617	BR	F	12	27-Nov-1999	Wild-born, rehabilitated	151	Yes
Offspring	PP688	RN	M	6	07-Oct-2004	Firstborn offspring of MM	-	Yes
	PP739	SL	F	0	01-Jun-2010	Offspring of MR	-	Yes
	PP740	CH	M	0	10-Jun-2010	Offspring of BR	-	Yes
	PP748	MM3	F	-	04-Dec-2011	Offspring of MM	-	Yes
	PP749	CL3	F	-	13-Mar-2012	Offspring of CL	-	Yes
	PP753	MO	M	-	13-Jan-2013	Offspring of MR	-	Yes
	PP756	AW	M	-	27-Jul-2013	Offspring of CL	-	Yes
	PP758	SP	M	-	20-Feb-2014	Offspring of AN	-	Yes
Nulliparous	PP655	TP	F	10	24-May-2002	Wild-born, rehabilitated	-	-
	PP660	RS	F	9	27-Nov-2002	Wild-born, rehabilitated	-	Yes
	PP658	HP	F	9	30-Aug-2002	Wild-born, rehabilitated	-	Yes
	PP665	AN	F	8	25-Jan-2003	Wild-born, rehabilitated	-	Yes
	PP725	OT	F	8	16-Oct-2007	Wild-born, rehabilitated	-	-
	PP663	RSL	F	7	15-Dec-2002	Offspring of rehabilitated mother	-	-
	PP677	CT	F	7	16-Dec-2003	Wild-born, rehabilitated	-	Yes
	PP691	KR	F	7	28-Feb-2005	Wild-born, rehabilitated	-	Yes
	PP719	GN	F	7	08-May-2007	Wild-born, rehabilitated	-	Yes
	PP689	SG	F	6	23-Jan-2005	Wild-born, rehabilitated	-	-

450 ^aAge was estimated based on the definition provided by Wich et al. (2004). ^bDate of birth was estimated by SORC at

451 the first appearance. ^cData was derived from the studbook of SORC.

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Table 2 Results of paternity assignment at 12 microsatellite loci (N=8)

Offspring	Date of birth	Birth order	Mother	Father	Morph	Number of mismatches with the next best male	Level of confidence (%)	Number of paternal candidates (Number of sampled males)	
								FLM	UFM
RN	07-Oct-04	1st	MM	CD	unknown	4	99	1 (0) ^a	2 (0) ^b
SL	01-Jun-10	3rd	MR	-	unknown	3	-	1 (0) ^b	2 (2)
CH	10-Jun-10	2nd	BR	-	unknown	2	-	1 (0) ^b	2 (2)
MM3	04-Dec-11	3rd	MM	CD	FLM	3	99	1 (1)	3 (3)
CL3	13-Mar-12	3rd	CL	CD	FLM	2	99	1 (1)	3 (3)
MO	13-Jan-13	4th	MR	CD	FLM	5	99	1 (1)	2 (2)
AW	27-Jul-13	4th	CL	CD	FLM	5	99	1 (1)	2 (2)
SP	20-Feb-14	1st	AN	RG	UFM	4	99	1 (1)	2 (2)

^aOne FLM and two UFM were observed but samples could not be collected in 2004 (Kuze 2005). ^bOne FLM occasionally appeared but samples could not be collected in 2009.

Table 3 Results of agonistic interactions among males

		Looser				Total
		CD	MK	RG	TK	
Winner	CD (FLM)	-	5	3	3	11
	MK (UFM)		-	4	2	6
	RG (UFM)			-	5	5
	TK (UFM)				-	0
	Total	0	5	7	10	22

Table 4 Number of male-male aggression by reproductive status of females in proximity

Opponents	Status of females in proximity	
	Reproductive parous	Nulliparous ^a
FLM-UFM (10)	10	0
UFM-UFM (12)	10	2

^a No reproductive parous female was observed.

Table 5 Number of successful copulations for each male and the partners' parity

Male ID	Focal hour	Female parity	
		Parous	Nulliparous
CD (FLM)	43	2 (1)	0 (0)
MK (UFM)	150	4 (3)	7 (4)
RG (UFM)	204	14 (11)	13 (9)
TK (UFM)	41	3 (1)	1 (1)

Number in parentheses indicates forced copulation.

1 Table 6 Comparison with previous paternity studies

Site	Species	Number of analyzed offspring ^a	Morph of father			References
			FLM	UFM	Unknown ^b	
Ketambe	<i>P. abelii</i>	10	4	6	–	Utami et al. 2002
Kinabatangan	<i>P. pygmaeus</i>	6	5	1	–	Goossens et al. 2006
	<i>morio</i>					
Tanjung Puting	<i>P. pygmaeus</i>	14	10	3	1	Banes et al. 2015
	<i>wurmbii</i>					
Sepilok	<i>P. pygmaeus</i>	6	4	1	1	This study
	<i>morio</i>					

 2 ^a Criterion for paternity assignment is different among studies. ^b Paternity could be assigned, but morph at the time of the offspring's conception was unknown.

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