Variation in developmental arrest among male orangutans: a comparison between a Sumatran and a Bornean population

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25 **Abstract**

26

Introduction

29 The presence of two sexually active male morphs with different reproductive

30 tactics in a single species is rare among mammals. The most striking case of

31 bimaturism among primates is exhibited by the orangutan (*Pongo spp*) in which

32 one adult morph, the unflanged male, irreversibly develops into another one, the

33 flanged form, but may remain arrested in the unflanged state for many years.

34 However, it has been suggested that such arrest is less common among Bornean

35 orangutans (*Pongo pygmaeus*) compared to Sumatrans (*Pongo abelii*). To

36 investigate this possible inter-specific difference we compared both the number of

37 developing males and the ratios of the two male morphs at two long-term study

38 sites, Suaq Balimbing on Sumatra and Tuanan on Borneo.

39

Results

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42 First, we observed a significantly greater number of flanged than unflanged males

43 per month in the Tuanan study area, whereas the opposite pattern held at Suaq.

44 Second, the same contrast held for the total number of identified individuals over

45 the study, with more flanged than unflanged males at Tuanan and the opposite at

46 Suaq. These differences were mainly due to transient males. For Tuanan, the

47   identification results were confirmed by detailed genetic analyses. Finally, we

48   recorded a higher proportion of unflanged males that became flanged during any

49   given year at Tuanan than at Suaq.

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Conclusion

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53   These results show that developmental arrest is far more common at Suaq than at

54   Tuanan. Preliminary comparisons suggest that this is a general contrast between

55   the island taxa of orangutans and should help efforts to identify the function and

56   proximate control of developmental arrest in orangutan males.

57   **Key words:** Arrested development; Bimaturism; Bornean orangutan; Sumatran

58   orangutan; Reproductive tactics

59

Introduction

60

61

62   Sexual selection theory attributes major differences in mating behavior to the

63   presence of alternative reproductive tactics (ART) [1-3]. ART can either be fixed

64   over the lifetime, where individuals retain a certain phenotype throughout life [3],

65   or plastic, which allows a flexible response to the environment. Fixed ART, also

66   called alternative strategies, reflect genetic polymorphism maintained by

67   frequency-dependent selection and are thus characterized by equal average fitness.

68   Examples include a marine male isopod (*Paracerceis sculpta*) with three

69   different-sized male morphs [4,5], a live-bearing fish (*Poecilia parae)* with five

70   distinct male color morphs [6] and the ruff (*Philomachus pugnax)*, a sandpiper

71   species with one conspicuous/colorful morph setting up a mating lek and an

72   inconspicuous morph acquiring matings while being a satellite on such leks [7].

73

74   The plastic tactics are adopted either in a reversible (Figure 1a) or a fixed (Figure

75   1b) sequence [1]. Irrespective of genotype, individuals adopt a tactic according to

76   the current conditions or developmental state, but the tactics usually do not have

77   equal fitness [3] as the less successful tactic is thought to make the best of a bad

78   job. For instance, large males of the Italian tree frogs (*Hyla intermedia)* adopt the

79   more successful calling tactic, whereas smaller males adopt the satellite tactic.

80   Whenever the conditions allow it, a satellite frog can also employ the calling

81   tactic, indicating that choice of tactic is reversible [8]. Among mammals,

82   reversible intrasexual bimorphism is rare [9,10], but is found in some male

83   primates. For instance, in mandrills (*Mandrillus sphinx*) the development of male

84   adornments, especially the bright face and rump coloration and the size of testes

85   are sequentially reversible, and linked to dominance rank [11]. A similar

86   phenomenon is the presence of clean and stained-chested males in Verreaux's

87   sifakas (*Propithecus verreauxi verreauxi*) [12].

88

89   Irreversible bimorphism (Figure1b) is also found in some primates. Males go

90   through a phase in which they have reached sexual maturity and are able to sire

91   offspring, but have not yet acquired the full set of secondary characteristics of

92   fully mature males [e.g. 13]. This adult phase has traditionally, but misleadingly,

93   been called 'sub-adulthood'. In many species the time spent in this 'sub-adult'

94   phase is variable. In male long-tailed macaques (*Macaca fascicularis*), for

4

95   instance, variation in the timing of the transition into the mature morph with full

96   secondary characteristics is linked to both a male's intrinsic growth rates and the

97   local social situation [14].

98

99   Among all primates, orangutans show the most flexible time span before

100 attainment of the full set of secondary sexual characteristics, as suggested by early

101 observations of female-sized male orangutans that were skeletally mature, with

102 closed cranial sutures and mature dentition, but lacking cheek flanges, long fur,

103 large body size, and an inflatable throat sac [15,16]. Such males are called

104 unflanged, in contrast to the fully developed flanged males. This suspicion was

105 confirmed by an observation from the wild [17], in which an unflanged male

106 observed at Ketambe, Sumatra, only developed flanges twenty years after

107 [genetically confirmed: 13] siring of an offspring. Thus, he had undergone an

108 extremely prolonged phase of arrested development, and must have been well

109 over 30 years of age when developing flanges. In captivity, some Sumatran

110 orangutans are known to grow flanges at the age of 11 years [18]. However, there

111 are no known cases where a male, once flanged, reversed to the unflanged state.

112

113 The function of this unusual delay may be related to the differential mating

114 strategies of the two morphs of sexually mature orangutan males [17]. Delgado

115 and van Schaik [19] stressed the difference in social organization between

116 Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus*) orangutans (see also

117 20), which are now considered separate species [20-24], and suggested that

118 developmental arrest is more pronounced on Sumatra than on Borneo. The aim of

119 this paper is to test this proposition. A difference in arrested development between

120 the two islands would help to better understand the conditions in which this rare

121   phenomenon could have arisen and to identify the proximate triggering

122   mechanisms. Before we list our predictions we will first review the currently

123   available information on mating strategies of the two species.

124

125   Unflanged males, both Sumatran and Bornean, look very similar to females, as

126   they lack the secondary characteristics, but they have fully grown testes [25] and

127   are able to sire offspring in captivity [26-28] and in the wild [13,29]. These males

128   are highly mobile and actively search for females with whom they initiate matings

129   and try to stay in association [30]. They have relatively high copulation rates and

130   prefer to mate with fertile females [31]. However, based on the females'

131   preference for the dominant flanged male [13,32,33,34, Dunkel in prep.],

132   unflanged males often have to resort to mating attempts with females even when

133   the probability of fertilization is low [35]. Moreover, females often try to resist

134   mating attempts by unflanged males, which results in forced matings [31, 33, 36,

135   37-41]. This unusual combination of strongly resistant females and forced

136   copulations is a reflection of female preferences [31,33].

137

138   On Sumatra, the local dominant flanged male attracts fertile females by emitting

139   long calls [36]. His home range is smaller than that of other flanged males [42]. In

140   general, sexually motivated females prefer the local dominant flanged male

141   [13,32,33, Dunkel in prep.], seeking him out [43,30], and engaging with him in

142   voluntary consortships, during which both the male and the female are likely to

143   initiate mating. Flanged males never associate with each other, but when they

144   meet, behave agonistically toward each other [42]. Dominant flanged males are

145   able to sustain lengthy consortships, lasting weeks, in which they have a virtual

146   monopoly on matings with the estrous female, suggesting that the paternity rate of

147   non-dominant flanged males is virtually zero [44]. The main reason for this is

148   that if non-dominant males emit long calls they will not only attract females but

149   also the dominant male and thus are likely to be chased away. On the other hand,

150   not calling is not a promising option either, since flanged males are not as fast as

151   unflanged males [45] and thus can not employ their tactic of actively searching for

152   females who are not attracted to them.

153

154   On Sumatra, females with offspring tend to range within earshot of flanged males,

155   that is a female stays at a distance at which she can hear a vocalizing dominant

156   male, possibly to avoid harassments by unflanged males [43,46]. However,

157   tolerance of unflanged males by flanged males engaged in a consortship with

158   fertile females is commonly observed [22,25,35,47], probably because the faster

159   unflanged males can escape when attacked by flanged males. Since paternity

160   results are still scarce [13,29], it is not quite clear what the reproductive success of

161   each kind of male tactic is under various social or demographic conditions.

162   However, it has been suggested that unflanged males are more successful with the

163   less attractive nulliparous females and during periods of unstable dominance

164   relations among flanged males, when females are not effectively mate-guarded.

165   [13,48]

166

167   As a possible explanation for the potentially long developmental arrest of

168   unflanged male Sumatran orangutans, Utami et al. [48] therefore suggested that

169   the highly mobile unflanged males are at least somewhat reproductively

170   successful when females are not in association with the dominant flanged male,

171   whereas subordinate flanged males' reproductive success is expected to be close

172   to zero [19]. Thus, unflanged males probably have lower per capita success than

173 the dominant flanged male, but higher success than subordinate flanged males

174 [48]. Therefore, males may benefit from remaining unflanged until they can

175 become the locally dominant flanged male.

176

177 On Borneo, flanged males seem to be more escalation-prone [42, Dunkel in

178 prep.], and dominance relations among them appear less stable compared to

179 Sumatra [38,49, Dunkel in prep.]. Bornean flanged males, even dominant ones,

180 engage in shorter consortships with females than the Sumatrans [32,38], and also

181 force matings. Moreover, females have been observed to copulate with multiple

182 flanged males within a period of several weeks [35,38, Dunkel in prep.]. On the

183 other hand, Bornean males tend to travel much more on the ground, which make

184 all of them more mobile and able to displace unflanged males from females.

185 Bornean females, unlike Sumatran ones, do not engage in earshot association with

186 flanged males [50]. However, they have been shown to approach long-calling

187 males when they were harassed by another male [51].

188

189 The proposal that arrested development may be more pronounced on Sumatra

190 than on Borneo [19] has never been tested in detail. To test it we will examine the

191 following predictions. First, we expect relatively more flanged males in a Bornean

192 population if males are less likely to arrest their development on Borneo than on

193 Sumatra (alternative explanations for different morph ratios will be examined in

194 the discussion section). Second, if this difference in male morph ratios is due to

195 differences in developmental arrest, we expect that the probability that a male

196 grows flanges during a certain period will be higher on Borneo than on Sumatra

197 [44].

198

199   The third prediction concerns the behavioral differences between resident and

200   transient males [36,37,41,52]. Transients largely include individuals who use the

201   area to pass through one time only, and never come back, or individuals with very

202   large home ranges, who occasionally appear, during periods of local food

203   abundance or during periods when local females are reproductively attractive [38].

204   On Sumatra, the males able to break the monopoly of the dominant flanged males

205   during such periods are the unflanged ones [42], whereas on Borneo multiple

206   flanged males but few unflanged males mate with fertile females [Dunkel in

207   prep]. Thus, we predict a higher number of transient unflanged males on Sumatra

208   and a higher number of transient flanged males on Borneo.

209

210   In this study, we took great care to identify individual males to obtain the most

211   accurate estimate of their number in the population, by using careful descriptions,

212   photographic records and genetic confirmation of identity, at least for one site.

213

214   **Results**

215

216   Numbers of flanged versus unflanged males

217

218   **Monthly male presence**

219

220   At Suaq (Sumatra), the mean number of males recorded in the study area in any

221   given month during the 59-month observation period was 2.5 for flanged males

222 and 4.5 for unflanged males (Figure 2); this difference was significant (Mann-

223 Whitney U= 996.5; N=59 months; P<0.001, 1-tailed). At Tuanan (Borneo),

224 however, we found the opposite as significantly more flanged than unflanged

225 males were recorded (3.2 flanged versus 2.3 unflanged males, Mann-Whitney U=

226 1894.5 N=72 months; P=0.002, 1-tailed).

227

228 **Total number of identified individuals**

229

230 The total number of flanged versus unflanged males in Suaq identified in the field

231 was 14 vs. 30, while in Tuanan it was 21 vs. 11 (Figure 3a). Thus, we found,

232 based on comparisons of detailed descriptions and photographs, that the Suaq

233 population was biased toward unflanged males, whereas the Tuanan population

234 was biased toward flanged males. This difference between the male proportions at

235 the two sites was highly significant (Pearson's Chi-Square Exact Sig. 1-sided:

236 X^2=8.523, df=1, N=76, P=0.003).

237

238 For the Tuanan population we could use genetic analysis to evaluate the accuracy

239 of the procedure applied at both Suaq and Tuanan. There were three categories of

240 potential errors (Table 1). First, in the field animals were split conservatively.

241 Without genetic analysis they would have been lumped again in the final tally.

242 Genetic analysis confirmed all six to be the same individual, thus confirming the

243 normal procedure. Second, genetic analysis showed that three of the individuals

244 split in the field were actually of the same individual. Thus, we had overestimated

245 the total number of males by three. Third, on the other hand we had wrongly

246 lumped two individuals in the field that upon genetic analysis turned out to be

247   distinct individuals. In total, then, we had overestimated the number of unflanged

248   males by two and underestimated the number of flanged males by one (Figure 3b).

249   Because the errors revealed by genetic analysis showed that the estimated

250   flanged/unflanged male ratio at Tuanan was conservative relative to the difference

251   with Suaq as estimated through normal descriptions, our earlier conclusion was

252   confirmed by this analysis.

253

254   In addition, we collected several samples of unnamed individuals that would not

255   have been included in a normal tally. Among the numerous unknowns (over 20)

256   we found three more new unnamed individuals, one flanged and two unflanged.

257   This indicates that a certain proportion of unidentified individuals in the field are

258   indeed novel individuals. However, since they remained unknown these are

259   probably vagrant individuals.

260

261   **Numbers of resident and transient males based on their monthly presence**

262

263   The total numbers of true residents (defined as being present > 50% of the

264   months) and partial residents (with a 10-49% monthly presence) among the

265   flanged and unflanged males during the study period (72 months for Tuanan and

266   59 for Suaq) did not significantly differ between the two study sites (sample size

267   for true residents too small for statistics; for partial residents: Pearson's Chi-

268   Square exact 2 sided: $X^2 = 0.427$, df=1, N=32, P=0.720) (Figure 4). However, for

269   the number of transients (males seen less than 10% of the months) we found

270   significantly more transient unflanged males in Suaq and more transient flanged

271   males in Tuanan (Pearson's Chi-Square exact 2 sided: $X^2 = 13.065$, df=1, N=44, P

272   =0.001).

273

Rates of flange development at Suaq and Tuanan

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276 At Suaq, 16 different unflanged males were included in the sample, accounting for

277 a total of 58 unflanged male years. In this dataset, we recorded only a single male

278 developing flanges resulting in an estimated annual probability of 0.017, or

279 approximately once every 58 years. At Tuanan, 8 different unflanged males were

280 included in the sample, totaling 35 unflanged male years. We recorded 4 cases of

281 flange development, for an estimated annual probability of 0.114, or once every 9

282 years. The males concerned had been encountered both as unflanged and

283 subsequently as flanged males, and their identities were genetically confirmed.

284 Despite the small sample size, the difference between the two proportions (1/58,

285 4/35) approaches significance (Fisher's exact test P=0.08; but see discussion). The

286 nearly seven-fold difference observed strongly suggests that there is a large

287 between-site difference in the probability that an unflanged male grows flanges

288 and other secondary sexual characteristics in a particular year.

289

Discussion

291

292 All three basic sets of results (the monthly presence in study area, the total

293 number of males identified, and the observed rate of flange development) strongly

294 suggest that males at Tuanan (Borneo) experience far less developmental arrest

295   then males at Suaq (Sumatra). The consistency of these results suggests that errors

296   are not responsible for this pattern.

297

298   One may of course question the accuracy of our estimate of 0.017 flanging events

299   per year for Suaq. However, in contrast to Tuanan, there is also only one known

300   record of a male with partial flanges in Suaq, despite comparable observation

301   effort. This single record mirrors that made at Ketambe, also on Sumatra, by te

302   Boekhorst et al. [53]. In their study, no flanging events were recorded in 61

303   unflanged male years (the flanging event reported by Utami et al. [48,54] occurred

304   later). In contrast, the Tuanan flanging events were striking, and would also have

305   been noted without genetic analysis. We encountered 5 partially flanged males in

306   Tuanan, who could easily be distinguished from males with shriveled flanges due

307   to old age or poor body condition in the event of food scarcity (although we

308   cannot exclude that some males may go through flange development very slowly).

309   Thus, the rate of flange development at Tuanan was many times higher than at

310   Suaq and Ketambe.

311

312   The extremely low rate observed at Suaq and Ketambe may indicate that many

313   unflanged males on Sumatra may never grow flanges at all, and in fact may

314   remain arrested for their entire life. Alternatively, it could indicate that flange

315   development occurs in synchronized bursts. However, both known cases, one at

316   Suaq and one at Ketambe, were isolated cases. At Ketambe, for instance, the

317   unflanged male grew flanges after the take-over of the dominant male by an

318   intruding male, and subsequently challenged the intruder when he had become

319   flanged [54].

320

321   The consistency of our results could be questioned because of discrepancies

322   between the flanged / unflanged proportions in the monthly presence data and the

323   total number of identified individuals. The monthly presence data could have been

324   biased. For Suaq the flanged / unflanged ratio in the monthly presence records of

325   0.6 is quite close to the proportion of their total identified numbers. For Tuanan,

326   in contrast, the ratio for the number of total identified individuals (1.9) is higher

327   than the monthly presence ratio (1.4). This discrepancy can be explained by the

328   fact that most of the flanged males at Tuanan are transients, that is, males without

329   a fixed home range but roving around. In contrast, unflanged males made up the

330   highest number of transients in Suaq (Figure 4).

331

332   This study was the first to incorporate genetic analyses to identify all wild

333   orangutans in the study area at Tuanan. The total numbers of flanged and

334   unflanged males estimated through field observations and genetic identity

335   analyses did not vary substantially. Possible errors of identification in the field,

336   like unintentionally lumping of two different individuals into one or splitting of a

337   single individual into two, could be detected in Tuanan with genetic analyses.

338   The results however, revealed that such errors were minor (see table 1). Thus,

339   although the application of genetic techniques did improve the accuracy of

340   identification procedures at Tuanan, the differences were so minor that they do

341   not compel us to revise the conclusion that there are major differences between

342   Suaq and Tuanan in male developmental arrest. Nevertheless, orangutan

343   researchers should be aware of these problems and put efforts into correct field

344   identification.

345

346   Alternative explanations

347

348 As this was an observational study, we should not rule out other possible

349 explanations for the different male morph ratios at the two study sites. There are

350 two issues here: Estimated rates of flange development and morph ratios. The

351 rates of flange development for two Sumatran sites, Suaq and Ketambe [53] were

352 made in different periods and covered multiple years. They are therefore likely to

353 be reliable. The one for Tuanan is only based on one site and a relatively short

354 period compared to adult male lifespan. It could be artificially high, but we could

355 not construct a realistic scenario that could bring this about. The island differences

356 in morph ratios are found across many sites and at Ketambe, for instance, have

357 remained stable over decades. Moreover the observations at both study sites of

358 this project here, continued beyond the periods compared here (even though

359 observations in Suaq were only resumed in 2007), allowing us to compare the

360 numbers for the more recent situation. Data collected in Suaq 2007 until 2011 (E.

361 Meulman, pers. comm.) and the additional data from Tuanan after 2009

362 (B.Spillmann, pers. comm.) show the same pattern as the larger dataset analysed

363 here.

364

365 Another cause of modified morph ratios could be selective mortality of one age

366 class due to external disturbance, especially logging. In general, mortality among

367 orangutans is extremely low [55]. In Ketambe and Suaq no logging was

368 performed in the study area during decades leading up the study. Some logging

369 elsewhere could have led to male influxes, but there is no reason to expect flanged

370 and unflanged males to differ. Tuanan has indeed been subject to selective

371 logging in the late 80s-early 90s. If logging causes high infant mortality this

372 would have led to a gap in the cohort that was born before and during the logging

373   period, which would account for the relatively low number of unflanged males.

374   However, Bornean orangutans seem to be less affected by logging than Sumatrans

375   [56-58]. Moreover, morph ratios biased toward flanged males have also been

376   recorded in study areas that were never logged, or in the 70s before logging

377   [36,38,39,59]. Finally past logging would not explain the higher rates of flanged

378   development in Tuanan compared to Suaq. We can therefore exclude logging as a

379   general cause for possible island differences in morph ratios. Furthermore we can

380   exclude differences in dispersal between populations of the two islands as recent

381   studies convincingly showed that males are the dispersing sex, whereas females

382   are philopatric on both islands [24,29,60-62].

383

384   Finally, we can exclude hunting as the cause of the higher proportion of flanged

385   males in Tuanan. Hunting is absent in the region of Suaq and Ketambe [63], but is

386   found patchily on Borneo. However, because flanged males are bolder and more

387   likely to come close to humans, especially as crop-raiders, they are more likely to

388   get killed. Thus, differential hunting can also not account for the differences in

389   morph ratios.

390

391   ## Inter-site differences or inter-island differences?

392

393   Does the difference in flanged /unflanged male ratios found in this study

394   generalize to a difference between Sumatra and Borneo? A previous review [19]

395   suggested this based on the number of flanged and unflanged males reported in

396   papers on orangutan behavior. More flanged than unflanged males are mentioned

397   in reports for the Bornean study sites Mentoko [40], Tanjung Puting [38,39],

398   Kinabatangan [29] and Gunung Palung [64], and fewer flanged than unflanged

399   males for the Sumatran site Ketambe, which is about 70 km from Suaq [53], and

400   the Bornean site Sabangau [49]. These reports provide the numbers included for

401   particular analyses and not necessarily the total number of identified individuals,

402   let alone the total number of males visiting a study site. It should be noted that the

403   largest inter-morph difference occurs among transient males, which may not

404   always have been equally recorded in all studies. Nevertheless, it is unlikely that

405   the overall difference between the Sumatran and Bornean sites is completely due

406   to methodological details across sites. Moreover, the average monthly number of

407   the two male morphs at Ketambe showed the same trend as Suaq [42]. Finally, te

408   Boekhorst et al. [53] also found very low rates of flange development at Ketambe

409   (none in 61 unflanged male years involving 13 different males over a 12-year

410   period). If the males at Ketambe and Suaq follow the same developmental tactic

411   we can lump the data on flanging rates. The difference in flanging rate between

412   Tuanan and the two Sumatran sites Ketambe and Suaq combined becomes

413   significant (Fisher's exact test P=0.013). Overall, these data suggest that the

414   Tuanan-Suaq difference reflects a more general island difference but more

415   detailed future work at other Bornean sites is needed.

416

417   The outcome of this study may have implications for our understanding of the

418   proximate function and the regulation of developmental arrest in orangutan males.

419   As to the ultimate reasons for the differences between the two orangutan species,

420   Pradhan et al. [65] developed a model that points to the sexual monopolization

421   potential of dominant males as the key factor for differences in arrested

422   development. Several studies already found that on Sumatra consortships between

423   flanged males and females last longer than on Borneo [32,38,44], suggesting a

424 much higher monopolization by dominant flanged males on Sumatra at the

425 expense of all other flanged males. Therefore, subordinate flanged males' access

426 to females is near-zero and lower than that of unflanged males, who do

427 occasionally get matings with fertile females and mate frequently with nulliparous

428 females [48]. On Sumatra therefore, the prolonged arrested development may be

429 adaptive. On Borneo however, the monopolization potential of a single dominant

430 flanged male is low and other less dominant flanged males also have access to

431 females. But because flanged males are always dominant to unflanged males, the

432 latter can be displaced easily and probably have lower reproductive success. In

433 future work, we will test this hypothesis in more detail with data from Suaq and

434 Tuanan.

435

436 As to the proximate regulation, studies in captivity and in the field have shown

437 that arrested males have lower testosterone and dihydro-testosterone levels than

438 developing and flanged males, but they have enough testicular steroids to support

439 sexual function and fertility [26,66, Marty et al.in prep.). However, the conditions

440 that elicit the rise in testosterone in developing males remain unclear. Some

441 captive studies suggested that the presence of a flanged male, and therefore socio-

442 endocrine effects of social interactions, could be the proximate reason for the

443 arrest of unflanged males [26-28,67,68]. However, this is unlikely in the wild

444 because multiple flanged males are always present at a site [48]. Moreover,

445 because less pronounced or absent developmental arrest, as in Tuanan, produces

446 higher absolute numbers of flanged males, the proposed mechanism is unlikely to

447 explain developmental arrest. Instead we suggest that the increased access to

448 potentially fertile females by unflanged males, especially during periods of

449 unstable dominance relations, may trigger the development of secondary

450 characteristics [54].On Borneo however, dominance ranks are unstable most of

451 the time, which allows less dominant flanged males access to females. As yet

452 however, this hypothesis remains untested.

453

454 ## Conclusion

455

456 Male developmental arrest is quite rare among mammals. The unexpected inter-

457 island differences in orangutans documented here provide us with an

458 unprecedented opportunity to examine both the conditions in which this

459 adaptation could evolve and identify the proximate triggering mechanisms. It

460 would be especially interesting to examine the flexibility in developmental arrest

461 among Bornean males in more detail to assess whether some males are capable of

462 showing long-term arrest, as on Sumatra.

463

464 ## Material and Methods

465

466 **Study sites and animal sampling methods**

467

468 Data were used from two study sites: Suaq Balimbing on Sumatra and Tuanan on

469 Borneo. The Sumatran data were collected over 59 months from 1993-1998 at the

470 Suaq Balimbing research station (ca 5.5 km^2; 3°04'N, 97° 26'E), Gunung Leuser

471 National Park. The local orangutan population density was 6.9 ind/km^2 [69]. This

472 site is located at near-sea level and primarily consists of swamp forest on shallow

473 peat. Most of the study area was pristine, but nearby areas were subject to

474 selective logging.

475

476 The data on Bornean orangutans were collected over 72 months from June 2003

477 until mid 2010 at the field station Tuanan (ca. 7.5 km^2, 2° 09' S; 114° 26' E)

478 inside the Mawas Reserve in Central Kalimantan. The area supports an average

479 orangutan density of 4.25 ind/km^2 [70], and consists of peat swamp forest on

480 shallow peat, also at near sea-level. It had been subject to selective commercial

481 logging in the late 80s and early 90s, followed by additional opportunistic

482 logging.

483

484 Orangutans at both study sites were followed from morning nest to evening nest

485 using standardized focal animal sampling techniques described in detail at the

486 orangutan network website [71] of the Anthropological institute and museum,

487 University of Zurich. Individuals on which behavioral data were collected were

488 called focal animals, whereas individuals spotted in the forest, but without taking

489 data on them were the non-focals.

490

491 To estimate the exact number of individual males in an area is not a trivial task

492 since the total number of individuals encountered in an orangutan study site is

493 subject to continuous change, for two reasons. First, unlike virtually all other

494 primates, orangutans do not live in distinct groups or communities [52,72].

495 Second, both unflanged and flanged males usually range widely and because

496 study areas are necessarily less than 1000 hectares, therefore come and go [42].

497 As a result, new individuals may appear at all times, and orangutan identification

498   is not straightforward. Because the new ones are usually unhabituated, it may be

499   difficult to visually identify them.

500

501   The main method for identifying individuals was based on comparisons of verbal

502   descriptions and standardized sketches complemented by lists of peculiarities,

503   such as stiff fingers and scars, and photographs. However, this method is subject

504   to errors, especially for males, due to incorrectly splitting identical males or

505   incorrectly lumping different males. Most studies applied the following

506   procedure: When in doubt males were given distinct names to be able at some

507   later moment to either keep them separate or lump them again depending on

508   further evidence. Without further evidence, however, such provisionally separate

509   males would be lumped again at the end of the study.

510

511   During the last decade, one additional technique has become available that for the

512   first time makes it possible to estimate the magnitude of these errors. Genetic

513   analysis of individual identities based on non-invasively collected fecal samples

514   became the tool of choice for individual identification in situations where field

515   methods did not give unambiguous answers. For both field sites identification was

516   done with help of descriptions and photography comparisons, but for only Tuanan

517   we additionally collected fecal samples for later genetic analyses.

518

519   We followed two procedures to identify the ratio of flanged to unflanged males in

520   the population. First, we counted the number of each class observed in the study

521   area each month, either as focal animals or in association with focal individuals,

522   or encountered during other activities in the forest. This monthly number probably

523 depends on the hours spent in the forest, yet there is no reason to assume a bias

524 toward flanged or unflanged males with differential research effort.

525

526 A bias could arise when one class of adult males is far more likely to be transient.

527 Hence, second we also counted the total number of identified individuals of each

528 class (In Tuanan three developing males were included as unflanged males and

529 one as flanged and in Suaq one as flanged, depending on the timing of their flange

530 development). The latter is also reported by most other studies.

531

532 Although the second measure is intuitively obvious, there are various reasons to

533 prefer the first one. First, it is less sensitive to uncertainties in identification (a

534 male is added as present even if he remains unidentified), and it is less likely that

535 multiple unidentified males of the same morph visit a study area during a single

536 month than in a period covering multiple years. Moreover, these numbers are a

537 direct reflection of the actual number of males of each morph competing at one

538 time.

539

540 To estimate male presence in the area we determined the monthly presence for all

541 individuals. Thus, each identified male recorded in the study area during a

542 particular month was included into the monthly presence file. Subsequently, the

543 males were placed into one of three different presence categories. True residents

544 were defined to be present at least 50% of the months, and thought to include the

545 study site in their core area. Males with lower presence scores were divided into

546 two classes. Partial residents were males with a monthly presence of 10 to 50%.

547 They were probably nearby residents, who had their core area outside but near the

548 study site and were attracted either by periods of high food abundance or by

549   sexually attractive females. We defined transients as males with a monthly

550   presence of less than 10%. They were observed to visit the study area only once or

551   rarely, and were generally seen to pass through.

552

553   To estimate the likelihood that a male grows flanges, we determined the number

554   of "unflanged male months". Males entered the sample in the year of their first

555   observation in the study area and were eliminated from it upon the time they grew

556   flanges or after the year of their last recorded presence. Only males with more

557   than 10% monthly presence and sighted in at least two different years were

558   included into the sample.

559

560   All statistical analyses were done in SPSS 14.0.

561

562   **Genetic sampling and analysis for Tuanan**

563

564   When possible, one or more fecal samples were collected whenever an orangutan

565   with uncertain identification was encountered. Sample collection was carried out

566   as described in the Genetic Sampling Protocol from the Anthropological Institute

567   and Museum, University of Zurich [73]. For details on the genetic analyses of

568   these samples see [60].

569

570   Individuals were genotyped at 6 nuclear microsatellite markers and subjected to

571   identity analyses using Cervus 3.0 [74]. The six markers had a combined non-

572   exclusion probability of 1.36×10^{-5} and 8.90×10^{-3} for unrelated individuals and

573 full siblings, respectively, suggesting that samples with different genotypes were

574 indeed from different individuals.

575

Competing interests

577

578 The authors declare that they have no competing interests.

579

Authors' contributions

581

582 LPD collected data on wild orangutans for a total of 32 months at the Tuanan

583 station including fecal samples in Central Kalimantan, analyzed data and drafted

584 the paper. NA and MK performed the genetic analyses. APP assisted in data

585 collection. CPvS and MAvN conceived the study. CPvS, SSUA and MAvN

586 coordinated data collection and management in Suaq and Tuanan. LPD and CPvS

587 wrote, and all authors read and approved, the manuscript.

588

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590

24

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927 **Table 1 Identification errors made in the field affecting the total number of**

928 **individuals in Tuanan**

	Flanged males	Unflanged males
Visually identified and confirmed by genetic analysis	20	9
Conservatively split in the field, genetically confirmed one individual	4	2
Incorrectly split in the field, genetically shown to be the same individual	1	2
Wrongly lumped in the field, genetically shown to be separate individuals	2	0
Total balance	Underestimated by 1	Overestimated by 2

929

930

931 **Figure legends**

932

933 **Figure 1 Plastic alternative reproductive tactics.**

934 (a) An individual reversibly develops into morph A or B (e.g. mandrills); (b) or an

935 individual develops into morph A and then can irreversibly continue toward

936 morph B, or remain in state A, as in orangutans.

937

938 **Figure 2 Monthly male presence.**

939 The average monthly number of identified flanged (black) and unflanged (white)

940 males in Suaq (Sumatra) and Tuanan (Borneo).

941

942 **Figure 3 Total number of identified individuals.**

943   (a) The total number of identified flanged males (black bars) in Suaq Balimbing

944   and Tuanan, as compared with the total number of unflanged males at the same

945   sites (white bars), based on field identifications. (b) The total number of

946   genetically identified flanged (black bar) and unflanged (white bar) males, for

947   Tuanan only (unknowns genetically identified as new individuals are not

948   included).

949

950   **Figure 4 Numbers of resident and transient males based on their monthly**

951   **presence**.

952   The number of individuals included into three different monthly presence

953   categories. Black: monthly presence < 50%, grey: monthly presence 10 until 49%

954   and white: monthly presence < 10%.