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1 **Title: Do non-human primates synchronise their menstrual cycles? A test in**
2 **mandrills**

3

4 **Authors:** Joanna M. Setchell^{1*}, Jeremy Kendal¹, Pola Tynieć²

5

6 **Affiliations:** ¹ Department of Anthropology, Durham University, Dawson Building, South
7 Road, Durham DH1 3LE, UK

8 ² Department of Anthropology, University of Wrocław, Kuznicza 35,
9 50-138 Wrocław, Poland

10

11

12 *** Corresponding author:** Department of Anthropology, Durham University, Dawson
13 Building, South Road, Durham DH1 3LE, UK. Tel: +44 (0)191 384 1633; email:
14 joanna.setchell@durham.ac.uk

15

16 **Running title:** Testing for cycle synchrony in mandrills

17

18 **SUMMARY**

19
20 The concept of female cycle (or estrous) synchrony has enduring popular appeal. However,
21 critical reviews of estrous synchrony studies in both humans and non-humans have found
22 that synchrony has not been demonstrated convincingly, due to methodological artifacts
23 and statistical problems. Studies of this phenomenon in animals living under naturalistic
24 conditions are rare. We used long-term records of the timing of the female menstrual cycle
25 in a semi-free-ranging population of mandrills, together with a randomisation procedure,
26 to test hypotheses relating to cycle synchrony in a naturally reproducing primate. We
27 found evidence of significant synchrony of the peri-ovulatory period in only one of ten
28 group-years – the year in which the largest number of cycles was recorded, both overall
29 and per female. However, this result was no longer significant when we corrected for
30 multiple tests of the same hypothesis. This suggests that mandrills in our study population
31 do not synchronise their cycles, possibly because they usually conceive so quickly that they
32 do not have the opportunity to synchronise. We also tested whether females in the same
33 matriline, which associate with one another more than other females, cycle significantly
34 more closely together in time than unrelated females, finding that they did so in 2 of 10
35 group-years, but that they were significantly less likely to match their cycles in another
36 group-year. Across 32 matriline-years, patterns of synchrony within individual matriline
37 (female lineages) never fell outside the distribution based on chance. Thus we found little
38 support for the pheromonal hypothesis for cycle synchrony, which predicts that females
39 that associate with one another should be more likely to cycle together. Overall, our
40 findings are in line with other studies that suggest that cycle synchrony does not occur in
41 non-human primates.

42
43 **KEYWORDS**

44
45 cycle synchrony; asynchrony; menstrual synchrony; reproductive synchrony; social
46 regulation of ovulation; pheromones; biological rhythms

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INTRODUCTION

The spatio-temporal distribution of receptive females has a major impact on male mating strategies (Ims, 1988). In particular, where receptive females are clumped in space or time, a male that tries to monopolize sexual access to one female will forfeit the opportunity to fertilize others. Cycle (or estrous) synchrony (McClintock, 1971), where females show a tendency to synchronise their receptive periods by shortening or lengthening their cycle lengths to achieve a closer match, decreases the operational sex ratio by increasing the number of females available at any one time, and increases the possibility of mating polyandrously for females, because a male that tries to monopolise one female forfeits the opportunity to fertilise others (Emlen & Oring, 1977; Clutton-Brock, 1989). This may act to confuse paternity, thereby allowing females to obtain benefits from more males (Hamilton, 1984) and/or to avoid infanticide attempts from males that do not mate (Hrdy, 1979). Conversely, asynchrony in female cycles facilitates male monopolisation (Ims, 1988), reduces inter-female competition for males and promotes indirect mate choice via male-male competition (Wiley & Poston, 1996). For example, female hamadryas baboons (*Papio hamadryas*) are more likely to conceive if they cycle asynchronously (Zinner et al., 1994).

In 1971, Martha McClintock described a social influence on the onset of menses in a study of women living in a college dormitory, who showed an increase in menstrual synchrony of two days over a period of four to six months (McClintock, 1971). A number of subsequent studies also demonstrated this phenomenon of cycle synchrony and the potential social regulation of ovulation in humans (e.g., Weller & Weller, 1993; 1995; 1997). However, the methods used to detect cycle synchrony have been criticised heavily on theoretical and statistical grounds (Wilson, 1987b; Wilson, 1992; Strassman, 1997; Arden & Dye, 1998; Schank, 2006; Yang & Schank, 2006), and other studies have failed to find statistically significant patterns of cycle synchrony in either Western populations (e.g., Jarett, 1984; Wilson et al., 1991; Trevathan et al., 1993) or in a natural-fertility population (Strassman, 1997).

80 This controversy extends to non-human species, principally rodents and non-human
81 primates. Among rodents, estrous synchrony has been reported for Norway rats (*Rattus*
82 *norvegicus*) (McClintock, 1978) and golden hamsters (*Mesocricetus auratus*) (Handelmann
83 et al., 1980), but in each case the study has been criticised on methodological grounds, with
84 the conclusion being that there was no statistical evidence for synchrony (Schank, 2000b;
85 2001a; d). A later study found evidence for asynchrony in golden hamsters (Gattermann et
86 al., 2002), while a study of another hamster species (Djungarian hamsters, *Phodopus*
87 *campbelli*) found no evidence of synchrony (Erb et al., 1993). In non-human primates cycle
88 synchrony has been reported for captive chimpanzees (*Pan troglodytes*) (Wallis, 1985) and
89 golden lion tamarins (*Leontopithecus rosalia*) (French & Stribley, 1987). However, again,
90 these studies have been criticised for employing statistics which violated the assumption of
91 independence of observations, meaning that results were likely to be due to chance,
92 (Strassman, 1997; Schank, 2000b; 2001a; b) and a subsequent study of golden lion
93 tamarins found no evidence of cycle synchrony (Monfort et al., 1996). Conversely, ring-
94 tailed lemurs (*Lemur catta*) have been shown to cycle asynchronously, with two females
95 rarely coming into oestrous on the same day (Pereira, 1991), and grey mouse lemurs
96 (*Microcebus murinus*) show increased synchrony between spatially clustered related
97 females, with the difference in oestrus timing in females that share a sleeping site being
98 shorter than that for members of different sleeping groups, within strict seasonality
99 (Eberle & Kappeler, 2004). In both cases this is despite a very short breeding season. A
100 recent study of chimpanzees also found evidence for cycle asynchrony (Matsumoto-Oda et
101 al., 2007) in this non-seasonally breeding species.

102

103 Investigations of the potential proximate mechanisms underlying synchrony suggested that
104 the timing of ovulation may be under pheromonal control (Russell et al., 1980; Preti et al.,
105 1986; Stern & McClintock, 1998). Building on observations in rats, in which the odour of
106 follicular phase females shortened the ovarian cycle, while that of ovulatory females
107 lengthened it (McClintock, 1984), Stern & McClintock (1998) reported that exposure to
108 axillary compounds changed female cycle length in human females in a similar way, with
109 two opposing pheromones: axillary secretions from women in the follicular phase shorten
110 the length of the recipient's cycle, accelerating menses, while secretions from woman near

111 ovulation delay menses. However, the statistics and methods used in these studies have
112 also been heavily criticised (Doty, 1981; Wilson, 1987a; Wilson, 1992; Weller & Weller,
113 1993; Strassmann, 1999; Schank, 2000a).

114
115 Thus, critical reviews of estrous synchrony studies in both humans and non-humans have
116 shown that synchrony has not been demonstrated convincingly and evidence in support of
117 the pheremonal hypothesis is similarly contentious (Schank, 2001c; Graham, 2002; Schank,
118 2002; Weller & Weller, 2002). However, cycle synchrony remains both a common belief
119 (Arden et al., 1999) and a popular subject of inquiry (Schank, 2006; Yang & Schank, 2006;
120 Ziomkiewicz, 2006; Jahanfar et al., 2007; Matsumoto-Oda et al., 2007; Weissenböck et al.,
121 2009). Studies of animals in the wild, or even under naturalistic conditions are rare,
122 probably because most long-term studies lack the daily records of female cycle necessary
123 to investigate patterns of cycle synchrony. In light of this ongoing controversy, we make
124 use of a large dataset comprising daily records of the timing of the female menstrual cycle
125 in a semi-free-ranging colony of mandrills to test hypotheses relating to cycle synchrony in
126 a naturally reproducing primate species.

127
128 Mandrills are catarrhine primates, in which females are philopatric and associate primarily
129 with maternal relatives, forming stable matriline (Setchell, 1999). Females develop large
130 sexual swellings during the menstrual cycle, providing a convenient indicator of female
131 cycle status (Setchell & Wickings, 2004). Females in our study population have a median
132 menstrual cycle length of 38 days, and display a great deal of variation in cycle length (18-
133 108 days, n=57), particularly in the length of the follicular phase (median 24 days, range 6-
134 96 days) (Setchell & Wickings, 2004), suggesting that social regulation of ovulation may be
135 possible in this species via changes in the length of the follicular phase. Mandrills show a
136 seasonal peak in female swelling cycles, with 63 % (187 of 296) occurring between July and
137 September, and only 6 % from December to April (Setchell & Wickings, 2004). Females
138 undergo 1-8 cycles before conceiving, although 60 % conceive during their first, cycle, and
139 87 % conceive within two cycles (Setchell & Wickings, 2004). Males show the greatest
140 sexual interest in females that advertise impending ovulation with maximal sexual swelling

141 size (Setchell, 1999; Setchell et al., 2005), and the alpha male attempts to monopolise such
142 females by mate-guarding them.

143

144 Early observations of the same mandrill population noted a tendency of females within the
145 same matriline to 'exhibit closer coupling of their ovarian cycles' (Fig. 14.17 in Dixson,
146 1998), but offered no statistical tests of this phenomenon against chance. Here, we use a
147 simulation procedure to determine whether female cycles within the mating period are
148 significantly more or less synchronous than expected by chance, and if so, under what
149 conditions these phenomena occur. Our use of a large dataset (10 group-years) for a
150 species closely related to humans, under naturalistic conditions, with long-term detailed
151 records of female reproductive status furnishes a good test of the ability of female primates
152 to synchronise their cycles. If female cycles are synchronised in mandrills, to decrease male
153 monopolisation potential, then we predict that the observed pattern of cycles will be more
154 synchronous than expected from a random distribution of female cycles. Conversely, if
155 female cycles are asynchronous, to increase the chance of mating with the dominant male,
156 then we predict the opposite, that the observed pattern will be more asynchronous than
157 expected from a random distribution. If mandrill cycles are neither synchronous nor
158 asynchronous, then we predict that the observed pattern of cycles will not differ from a
159 random distribution. Finally, if social regulation of ovulation is achieved via a pheromonal
160 mechanism (Stern & McClintock, 1998), then we predict that the effect (synchrony or
161 asynchrony) will be stronger in females of the same matriline when compared with females
162 in different matriline, because matriline associate with one another more often than with
163 other females, and would therefore be more exposed to any pheromones more often than
164 with other females.

165

166

METHODS

167

168 The mandrill colony at the Centre International de Recherches Médicales in Franceville,
169 Gabon (CIRMF), was established in 1983/4, when 15 animals (7 males, 8 females,
170 originating from the wild) were released into a 6.5 ha naturally rain-forested enclosure

171 (Enclosure 1). All further additions to the group, subsequent to 1984, are due to
172 reproduction of the founder animals; some animals have been removed. A second semi-
173 free-ranging group was established in 1994 (in Enclosure 2, 3.5 ha) by transferring 17
174 mandrills (including 4 adult males and 6 adult females) from the first enclosure. In 2001
175 there were 111 animals in Enclosure 1, and 49 in Enclosure 2. The animals forage freely in
176 the enclosure, and receive daily supplements of monkey chow and seasonal fruits; water is
177 available *ad libitum*. CIRMF record the date of birth for all individuals born into the colony,
178 and estimated the age of founder females using dental estimates of age when the animals
179 arrived at CIRMF and their previous history.

180

181 While hypotheses regarding the evolution of cycle synchrony generally model the
182 advantages and disadvantages of synchronised ovulation, empirical studies rely on
183 different proxies for the female hormonal cycle. Studies of human females generally use the
184 onset of menstruation (e.g. McClintock, 1971; Weller & Weller, 1993; Weller & Weller,
185 1997), but this is difficult to detect in non-human primates. Fortunately, the brief receptive
186 periods of strepsirhines (one night in mouse lemurs (Eberle & Kappeler, 2004), 4-12 hours
187 in ring-tailed lemurs (Pereira, 1991)) and the sexual swellings of some Old World primates,
188 including chimpanzees (Matsumoto-Oda et al., 2007) and mandrills, provide alternative
189 indicators of the peri-ovulatory period. An increase in sexual swelling size co-occurs with
190 increased estrogen levels during the follicular phase of the menstrual cycle and ovulation is
191 presumed to occur during the last few days of maximal tumescence, although it may not be
192 limited to this period (reviewed by Dixson, 1998; Nunn, 1999). A rapid decrease in sexual
193 swelling size ('break-down'), followed by detumescence, coincides with a post-ovulatory
194 rise in progesterone. For the purposes of this study, we used records of female swellings
195 kept from 1990 to 2004, and defined the peri-ovulatory period as the five days preceding
196 break-down of the sexual swelling, based on data for baboons (Wildt et al., 1977; Shaikh et
197 al., 1982). Because we were unable to determine the exact day of ovulation using endocrine
198 analyses, we also re-ran our simulation analyses (see below) assuming a seven day peri-
199 ovulatory period (data not shown). These results supported the intuition that increasing
200 the length of the peri-ovulatory period increases overlap of peri-ovulatory periods in both
201 the observed and the simulated variance distributions. Using a seven-day peri-ovulatory

202 period increased the position of the observed value relative to the simulated distribution
203 for some years, and decreased it in others, but only changed the significance of the results
204 in one case (in 2004/E1, see Results).

205
206 We excluded five group-years where less than three months of records were available
207 during the mating season, to achieve adequate representation of each mating season. We
208 also excluded one group-year because several females were removed during the mating
209 season, which is likely to have disrupted the pattern of female cycles, as well as meaning
210 that the removed females were not present for the entire mating season.

211
212 A total of 57 females, in seven matriline derived from the founder females (one founder
213 female never reproduced successfully), contributed to the study, with a total of 218
214 swelling cycles recorded (see ESM for details of female contributions). For some analyses,
215 we exclude adolescent females undergoing their first cycles, as cycles in these females may
216 be constrained by their physiology more than more mature females (Dixson, 1998).

217
218 We defined the mating season as the period from the start of the first peri-ovulatory period
219 to the end of the last peri-ovulatory period in a year, excluding 13 cycles that occurred
220 more than one month away from any other female's cycle, because these females had no
221 possibility of synchronising their cycles with other females. These unusual cycles were due
222 to females that resumed cycling outside the normal mating season because their infant that
223 died, and one female who was still cycling but no longer reproducing, due to old age.

224

225 **Synchrony index**

226

227 To test the null hypothesis that females neither synchronise nor de-synchronise their peri-
228 ovulatory periods, we adapted a randomisation test devised by Matsumoto-Oda et al.
229 (2007). This test is based on the premise that if the degree of synchronisation is high, then
230 females are more likely to be peri-ovulatory on the same day. This would result in a higher
231 proportion of peri-ovulatory females on some days and a lower proportion on other days,
232 and thus high variation in the proportion of peri-ovulatory females among days. In

233 contrast, where females avoid cycling together, variation in the proportion of peri-
234 ovulatory females among days will be small. When there is neither synchrony nor
235 asynchrony, variation will be intermediate.

236

237 Matsumoda-Oda et al (2007) defined the 'estrous synchrony index' (ESI) as the variance in
238 the proportion of females (in their case chimpanzees) that showed maximum swelling to
239 cycling females observed per day, normalised by the variance of frequencies from the
240 binomial distribution. Values of ESI are large when females synchronise their peri-
241 ovulatory periods, and small when they avoid doing so. We simplified this to consider the
242 variance in the number of peri-ovulatory female mandrills available per day during the
243 mating period. Like ESI, this simplified index ('overall synchrony index') is large when
244 females synchronise their peri-ovulatory periods, and small when they avoid doing so. To
245 test the significance of our simplified index, we compared it with an expected distribution
246 derived as follows:

247

248 We used the same number of individuals and cycles per individual as found in the observed
249 data for each run of the simulation for each year. We allowed females to undergo their peri-
250 ovulatory period at any time during the mating season, giving the maximum opportunity
251 for synchrony or asynchrony. We determined the start of a simulated peri-ovulatory period
252 by randomly selecting a day in the mating season. Where females underwent more than
253 one peri-ovulatory period during a mating season, we constrained the peri-ovulatory
254 periods to be at least 18 days apart (i.e., a peri-ovulatory period could not start until the
255 18th day after the start of a previous peri-ovulatory period) because this is the minimum
256 refractory period between cycles in the observed dataset (Setchell & Wickings, 2004).

257

258 We ran 10,000 simulations to produce a distribution of the test statistic, against which we
259 compared the observed test statistic to determine whether the variance in the number of
260 observed synchronous female peri-ovulatory periods across the season was significantly
261 different from the simulated distribution of variance scores (i.e., in the 2.5% tails of the
262 distribution). Our null hypothesis was that the observed distribution could have been

263 obtained by random timing of the female cycles. Thus, the results of the test reveal whether
264 female mandrills cycle more synchronously (or asynchronously) than expected by chance.

265

266 **Influence of matrilineal relatedness**

267

268 To investigate the influence of matrilineal relatedness on female cycle synchrony, we
269 calculated the difference between the start date of each peri-ovulatory period for each
270 female and that of peri-ovulatory periods for every other female. We matched this to a
271 variable that described the matrilineal relatedness of the females, scoring females in the
272 same matriline 1, and those in different matriline 0. We calculated a test statistic,
273 'matriline synchrony index', as the difference between the mean start date differences for
274 related females and the mean start date differences for unrelated females and tested the
275 significance of this value using a randomisation procedure.

276

277 In each simulation, we used the start dates of each peri-ovulatory period observed for each
278 female and randomised the relatedness scores between dyads, keeping the number of
279 related individuals the same as that found in the observed data. We calculated the 'related
280 vs. non-related index' for 10,000 simulations to generate the null distribution against
281 which we compared the observed index score. In the observed data, there was more than
282 one start date distance for the same dyad if one or both females cycled more than once. We
283 controlled for this in the randomisation procedure by forcing the same relatedness for
284 multiple start date distances belonging to the same original dyad (i.e., if the relatedness
285 was randomly assigned to 1 for any one of a dyad's start date distances, the same
286 relatedness score was assigned to all other start date distances for the same dyad).

287

288 Our null hypothesis was that the observed relationship between distance and matrilineal
289 relatedness could have been obtained by any random arrangement in time of the female
290 cycles. Thus, the results of the test reveal whether members of the same matriline cycled
291 more synchronously (or asynchronously) than members of different matrilineal lines.

292

293 Studies of the influence of genetic relatedness on social behaviour in cercopithecine
294 primates suggest that they may be able to recognise true genetic relatedness (r), including
295 relatedness through the paternal line (Widdig et al., 2001; Smith et al., 2003; Charpentier et
296 al., 2007), meaning that a simple measure of matrilineal kinship may not capture all social
297 behaviour relevant to the pheromone hypothesis, if paternal kin also preferentially
298 associate with one another. However, replacing our 1/0 score of matrilineal relatedness
299 membership with a measure of genetic relatedness ($r > 0.5$ vs. $r < 0.5$) gave results that did
300 not differ qualitatively from those for matrilineal relatedness, and we do not report them
301 here.

302

303 Each of our simulations was based on data for the individuals contributing to the observed
304 dataset. This means that we cannot combine them to create one overall test of each
305 hypothesis because it would be inappropriate to compare the observed value for one
306 enclosure-year (or matriline) against the simulated distribution for another enclosure-year
307 (or matriline). Instead, therefore, we corrected for multiple (10 group-years) tests of each
308 hypothesis using the Bonferroni correction.

309

310 **Cycle synchrony within matriline**

311

312 Finally, we also investigated patterns of cycle synchrony within matriline, using the
313 synchrony index for data for each individual matriline in each year (32 matriline-years).
314 Due to the large number of tests of the same hypothesis (that matriline synchronise their
315 cycles more or less than expected by chance) we did not rely on tests of the significance of
316 the observed patterns, but simply examined the overall pattern of the results (the area of
317 the simulated distribution in which the observed data fell).

318

319 Where we obtained results that were close to significance, we repeated the simulation
320 using 100,000 simulations, and obtained the same results in each case.

321

322

RESULTS

When we investigated overall patterns of cycle synchrony in the mandrill colony we found that only one of the ten group-years tested (2004/E1) exhibited a degree of synchrony expected by chance with a probability of less than 0.025 (Table 1, Fig. 1). This result approached significance when we corrected for multiple tests (Table 1), and was significant when we used a seven day (rather than a five day) peri-ovulatory period ($p = 0.0008 < 0.0025$). No other years showed a significant departure from random distribution of cycles.

<Insert Table 1 about here>

<Insert Figure 1 about here>

Females belonging to the same matriline were more synchronised than females in different matriline than expected by chance, with a probability of less than 0.025, in 2 of 10 group-years (1993/E1 and 2004/E1, Table 2, Fig 1). Conversely, related females in 2000/E1 were more asynchronous than unrelated females than expected by chance, with a probability of less than 0.025, but this finding was not significant once we applied the Bonferroni correction, and is likely to be due to multiple testing (Table 2). Inspection of the data for this year suggested that this asynchrony was due to two adolescent females that both cycled for the first time very late in the season (107 and 119 days after the start of the mating season), and who may have physiologically incapable of cycling earlier. Removing all such nulliparous, adolescent females from the dataset for 2000/E1 resulted in an observed value which was not significantly different from that expected by chance (38.57%). Excluding such females did not alter the significance of results for other group-years.

<Insert Table 2 about here>

351 When we examined the 'cycle synchrony index' within individual matriline-years, we found
352 that the observed value for a matriline did not fall outside the 95 % limits of the simulated
353 distribution in any of 32 matriline-years (Table 3).

354

355 <Insert Table 3 about here>

356

357

DISCUSSION

358

359 The concept of female cycle synchrony has enduring popular appeal, perhaps due to
360 misconceptions concerning statistical probability, the psychological appeal of the idea that
361 friends synchronise (Strassman, 1997; Arden et al., 1999), and an evolved human tendency
362 to detect patterns in meaningless noise (Shermer, 1998). However, the only studies
363 showing synchrony in non-human primates (Wallis, 1985; French & Stribley, 1987) have
364 been shown to be statistically flawed (Strassman, 1997; Schank, 2000b; 2001a; b), while
365 other studies report significant patterns of asynchrony (Pereira, 1991; Eberle & Kappeler,
366 2004; Matsumoto-Oda et al., 2007). We used 10 group-years of data to examine whether
367 females in a naturally reproducing primate population either synchronise or asynchronise
368 their peri-ovulatory period more often than expected from a random distribution of cycles.
369 Overall, only one of ten group-years (2004/E1) approached significance for synchrony,
370 assuming a 5 day peri-ovulatory period. This group-year was neither the year with the
371 smallest, nor the largest group, and was not exceptional in the number of related vs.
372 unrelated females present. However, it was the year in which the largest number of cycles
373 was recorded, both overall (43, Table 1), and per female (mean 1.7 cycles per female, ESM).
374 Thus, our results that female mandrills generally do not show cycle synchrony or
375 asynchrony, but they also suggest that cycle synchrony may occur under certain conditions.

376

377 Unlike most human populations in which cycle synchrony has been studied (Strassman,
378 1997), the semi-free-ranging mandrills we studied live together permanently and
379 reproduce naturally. However, they conceive very quickly once they begin to cycle, with
380 87% conceiving within two cycles (Setchell & Wickings, 2004). No comparative data are
381 available for wild, un-provisioned mandrills, but provisioning is known to enhance female

382 reproduction (Mori et al., 1997), and wild baboons undergo an average of four cycles
383 before conceiving (Altmann et al., 1977), suggesting that wild mandrills may undergo more
384 cycles to conception than our study population. If cycle synchrony increases with the
385 number of cycles (i.e., over time), due to mutual entrainment (McClintock, 1971), then it
386 may be that our study animals have little opportunity to synchronise their menstrual cycles
387 during a mating season before they conceive. Post-partum amenorrhea is variable in length
388 (Setchell & Wickings, 2004), and it may be that this precludes synchrony if females begin to
389 cycle at very different times during the mating season, then conceive quickly. This
390 possibility is reinforced by the fact that individual females cycled more often in the only
391 year in which we detected significant synchrony.

392

393 Thus the possibility exists that wild, unprovisioned mandrills may have more opportunity
394 to synchronise, if they experience more cycles to conception. However, the question
395 remains of how biologically relevant cycle synchrony is in mandrills. Like other catarrhine
396 primates, female mandrills have various other strategies to achieve the paternity confusion
397 goals that cycle synchrony might achieve, such as infanticide avoidance (van Schaik et al.,
398 2000). For example, they have a long and variable follicular phase (Setchell & Wickings,
399 2004), during which they show a sexual swelling that increases in size to a maximum
400 around the time of ovulation. The exact timing of ovulation within this period is unknown,
401 but it is likely to vary, as in other species with sexual swellings (Wildt et al., 1977; Deschner
402 et al., 2003; Engelhardt et al., 2005; Higham et al., 2008). This long, variable signal of
403 receptivity may allow females to confuse males sufficiently as to who sires the eventual
404 offspring, meaning that synchrony is not necessary.

405

406 In contrast to studies of ring-tailed and mouse lemurs, which are highly seasonal breeders
407 (Pereira, 1991; Eberle & Kappeler, 2004) and wild chimpanzees, which are not seasonal
408 (Matsumoto-Oda et al., 2007), we found little substantial evidence for significant overall
409 patterns of cycle asynchrony in our study population, which breeds moderately seasonally
410 (Setchell & Wickings, 2004). The main hypothesis to explain cycle asynchrony is to
411 decrease female–female competition for mates, and ensure conception (Pereira, 1991;
412 Matsumoto-Oda et al., 2007). However, there is no influence of number of simultaneously

413 cycling females on the probability of conception in our study population (Setchell &
414 Wickings, 2004), suggesting that there may be no need for asynchrony to ensure
415 conception. Nevertheless, asynchrony could promote fertilisation by the most desired male,
416 if there is competition for particular mates, and female choice converges on particular
417 males (dominant and/or brightly coloured males, Setchell, 2005).

418

419 If females synchronise in response to olfactory cues, as suggested by the pheromone
420 hypothesis (Russell et al., 1980; Preti et al., 1986; Stern & McClintock, 1998), then females
421 of the same matriline, who associate with one another more often than with other females,
422 should show increased synchrony because they would be more exposed to any
423 pheromones more often than other females. We found that related females were more
424 likely to synchronise with one another than with unrelated females, but only in two of ten
425 group-years (2004/E1 and 1993/E1). While this might offer some support for the
426 pheromone hypothesis, we also found the opposite pattern in another group-year, when
427 related females were more asynchronous than unrelated females. Most importantly, no
428 individual matriline showed any departure from chance patterns of cycle synchrony in
429 these group-years. In fact, in all but one of 32 matriline-years the pattern of cycling fell well
430 within the expected distribution, based on chance. Our data, therefore, suggest that females
431 within matriline do not synchronise their cycles. Similarly, in the only other study of the
432 influence of proximity on cycle synchrony in non-human primates, researchers found no
433 difference in cycle synchrony between two pairs of cycling females in a wild chimpanzee
434 community that spent a large amount of time together (the chimpanzee equivalent of
435 room-mates in human studies) and other females (Matsumoto-Oda & Kasuya, 2005). Thus,
436 there is as yet no support for the pheromone hypothesis from studies of non-human
437 primates.

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595

596 **Table 1. Overall patterns of cycle synchrony. Observed and simulated values of the distribution of variance in the**
 597 **number of peri-ovulatory female mandrills available per day during the mating period ('overall synchrony index')**

Year/ Enclosure	Days observed ^a	No. females (No. cycles)	Observed ^b			Simulated values			Conclusion ^c
			value	%	0%	2.5%	97.5%	100%	
1991/E1	91	15 (19)	0.87	40.58	0.34	0.56	1.51	2.71	Cannot reject Ho
1992/E1	111	11 (15)	0.47	9.85	0.27	0.40	0.98	1.84	Cannot reject Ho
1993/E1	172	15 (26)	0.92	93.29	0.31	0.49	1.01	1.46	Cannot reject Ho
1994/E1	125	9 (15)	0.51	38.70	0.24	0.37	0.82	1.44	Cannot reject Ho
1998/E1	172	18 (24)	0.68	20.07	0.35	0.54	1.20	1.87	Cannot reject Ho
1998/E2	112	7 (13)	0.44	25.62	0.24	0.33	0.81	1.30	Cannot reject Ho
2000/E1	153	21 (33)	1.04	58.38	0.48	0.69	1.50	2.07	Cannot reject Ho
2000/E2	208	9 (11)	0.28	20.56	0.23	0.24	0.50	0.85	Cannot reject Ho
2002/E2	98	13 (18)	0.75	32.04	0.32	0.50	1.36	2.36	Cannot reject Ho
2004/E1	154	25 (43)	2.24	99.64	0.56	0.89	1.93	2.68	Cannot reject Ho

598 ^a Days observed = days from beginning of first peri-ovulatory period to end of last peri-ovulatory period in mating period (see
 599 methods for definition of mating period)

600 ^b Observed % represents the proportion of simulated variance values that are smaller than the observed variance.

601 ^c Following Bonferroni correction (alpha/n) for 10 tests of the same hypotheses, the significance level for the two-tailed test is
 602 $p < 0.0025$, such that a significant level of synchrony requires the observed value to exceed 99.75% of the simulated
 603 distribution.

604 Bold indicates a value expected < 2.5 % by chance, before application of the Bonferroni correction.

605

606 **Table 2. Comparing cycle synchrony within and among matriline. Observed and simulated values of the difference**
 607 **between the mean start date differences for related females and the mean start date differences for unrelated females**
 608 **('related vs. non-related index').**

Year/Enclosure	Related/unrelated dyads (n)	Observed		Simulated values				Conclusion ^a
		value	%	0%	2.5%	97.5%	100%	
1991/E1	0.11 (12/93)	-5.92	11.34	-19.96	-10.07	10.46	17.37	Cannot reject Ho
1992/E1	0.13 (7/48)	12.47	95.90	-24.34	-11.73	13.75	23.99	Cannot reject Ho
1993/E1	0.17 (18/87)	15.93	99.96	-24.37	-13.54	8.40	20.82	Related more synchronous
1994/E1	0.16 (9/46)	-7.77	8.16	-27.39	-12.03	14.32	24.76	Cannot reject Ho
1998/E1	0.19 (33/138)	7.71	96.70	-31.26	-18.98	8.68	23.59	Cannot reject Ho
1998/E2	0.48 (10/11)	13.27	97.08	-29.43	-18.21	13.88	23.30	Cannot reject Ho
2000/E1	0.22 (47/163)	-10.83	<u>1.94</u>	-16.62	-10.25	7.92	17.55	Cannot reject Ho
2000/E2	0.48 (21/23)	-2.55	75.23	-59.20	-34.83	13.71	35.04	Cannot reject Ho
2002/E2	0.60 (30/105)	3.49	89.49	-16.09	-8.97	6.46	16.69	Cannot reject Ho
2004/E1	0.25 (74/225)	10.11	100.00	-23.72	-16.82	-0.372	6.429	Related more synchronous

609
 610 Numbers of females, cycles and days in the mating season are the same as for Table 1

611 Bold and underline indicate synchronous and asynchronous results, respectively, that are expected < 2.5 % by chance.

612 ^a After application of the Bonferroni correction for multiple (10) tests of the same hypothesis both findings of synchrony
 613 remain significant, but the finding of asynchrony is no longer significant.

614

615 **Table 3. Patterns of cycle synchrony within individual matriline. Observed and simulated values of the distribution**
616 **of variance in the number of peri-ovulatory female mandrills available per day during the mating period ('overall**
617 **synchrony index').**

Year/Enclosure	Matriline	Number of females	Observed		Simulated values			
			value	% ^a	0%	2.5%	97.5%	100%
1991/E1	m2	2	0.14	79.86	0.14	0.14	0.23	0.25
1991/E1	m5	2	0.10	0-89.8	0.10	0.10	0.19	0.21
1991/E1	m10	2	0.17	0-62.4	0.17	0.17	0.28	0.39
1991/E1	m12	4	0.26	89.11	0.17	0.17	0.33	0.61
1991/E1	m17	3	0.14	72.90	0.14	0.14	0.25	0.42
1992/E1	m2	2	0.08	0-91.8	0.08	0.08	0.15	0.17
1992/E1	m12	3	0.19	78.33	0.15	0.15	0.24	0.42
1992/E1	m17	3	0.18	46.98	0.17	0.17	0.30	0.48
1993/E1	m5	2	0.10	0-79.1	0.10	0.10	0.16	0.22
1993/E1	m10	2	0.10	0-84.0	0.10	0.10	0.15	0.16
1993/E1	m12	6	0.18	39.75	0.16	0.16	0.28	0.49
1993/E1	m16	2	0.14	0-73.7	0.14	0.14	0.20	0.20
1994/E1	m2	2	0.14	78.07	0.13	0.13	0.20	0.21
1994/E1	m5	2	0.16	0-71.1	0.16	0.16	0.24	0.24
1994/E1	m12	3	0.14	88.42	0.11	0.11	0.19	0.31
1998/E1	m2	4	0.17	61.40	0.15	0.15	0.25	0.45

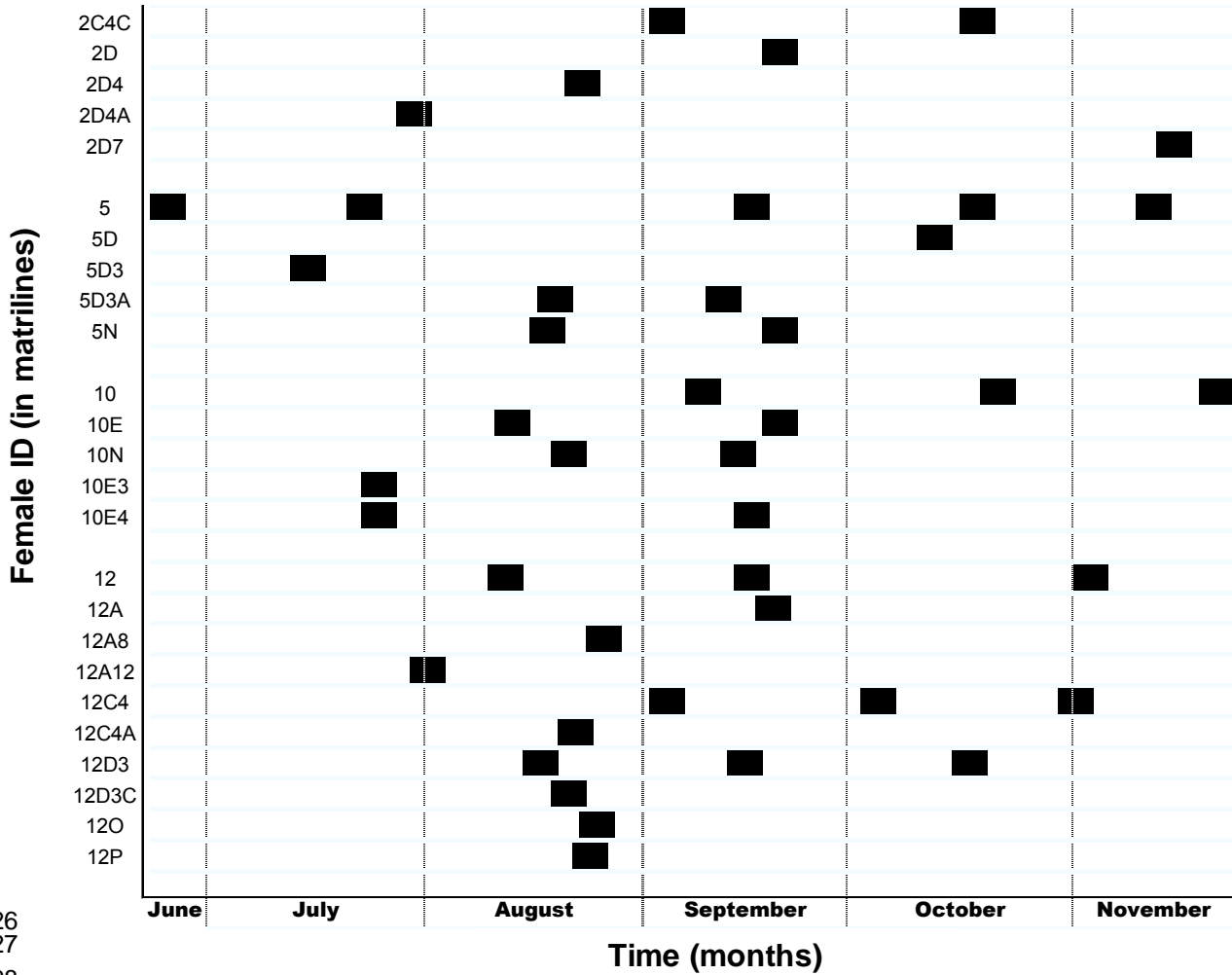
1998/E1	m5	4	0.21	89.09	0.15	0.15	0.25	0.48
1998/E1	m10	3	0.15	0-56.0	0.15	0.15	0.25	0.36
1998/E1	m12	6	0.20	52.84	0.17	0.17	0.33	0.51
1998/E2	m17	5	0.32	55.72	0.23	0.23	0.52	0.87
2000/E1	m2	5	0.16	39.78	0.16	0.16	0.28	0.43
2000/E1	m5	3	0.20	93.81	0.14	0.14	0.20	0.31
2000/E1	m10	4	0.16	42.51	0.16	0.16	0.28	0.46
2000/E1	m12	8	0.39	53.85	0.24	0.28	0.57	0.91
2000/E2	m16	2	0.09	0-88.3	0.09	0.09	0.14	0.15
2000/E2	m17	6	0.19	57.31	0.16	0.16	0.27	0.49
2002/E2	m16	2	0.19	79.16	0.16	0.16	0.26	0.26
2002/E2	m17	10	0.71	84.21	0.24	0.36	0.91	1.52
2004/E1	m2	5	0.16	39.56	0.16	0.16	0.27	0.47
2004/E1	m5	5	0.31	49.66	0.23	0.23	0.45	0.70
2004/E1	m10	5	0.34	79.62	0.22	0.22	0.43	0.65
2004/E1	m12	10	0.68	96.41	0.25	0.33	0.70	1.30

618

619 ^a We present ranges where the distribution lies flat from 0 to the given % (where there is a long mating season and only a few
620 cycles, there are many ways of getting non-overlapping cycles, which fall in this range).

621 **Figure 1: Female cycles in 2004/E1, the only group-year (of 10) in which we detected**
 622 **significant overall patterns of cycle synchrony. Females are arranged in matriline**
 623 **on the y-axis. Black bars indicate the peri-ovulatory period for each female cycle.**

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