DIGITAL ACCESS TO
SCHOLARSHIP AT HARVARD
DASH.HARVARD.EDU

HARVARD LIBRARY
Office for Scholarly Communication

The context of female dispersal in Kanyawara chimpanzees

The Harvard community has made this article openly available. **Please share** how this access benefits you. Your story matters

Citation	Stumpf, Wrangham, Emery Thompson, and Muller. 2009. "The Context of Female Dispersal in Kanyawara Chimpanzees." Behaviour 146 (4) (April 1): 629–656. doi:10.1163/156853909x413853.
Published Version	doi:10.1163/156853909x413853
Citable link	http://nrs.harvard.edu/urn-3:HUL.InstRepos:26372958
Terms of Use	This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Open Access Policy Articles, as set forth at http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#OAP

2
3
4
5Manuscript for *Behaviour*:
6Special Issue on Primate Dispersal (Katherine Jack and Lynne Isbell, Eds.)

7

8

9

10Title: The Context of Female Dispersal in Kanyawara Chimpanzees

11

12

13Short Title: Female Dispersal in Chimpanzees

14

15

16RM Stumpf[1], M Emery Thompson[2], MN Muller[2], & RW Wrangham[3]

17[1]Department of Anthropology, University of Illinois, [2]Department of Anthropology,

18University of New Mexico, [3]Department of Anthropology, Harvard University

19

20

21

22

23

24Corresponding Author:

25

26Rebecca M Stumpf

27Department of Anthropology

28109 Davenport Hall

29607 South Mathews Avenue

30Urbana, IL 61801

31rstumpf@uiuc.edu

32**Summary**

33

34In most social mammals, members of either one sex or both leave their natal group at sexual

35maturity. In catarrhine primates, male emigration is the predominant pattern. Female philopatry

36facilitates cooperation among kin, and female reproductive success is influenced by these

37relationships. Chimpanzees (*Pan troglodytes*) are unusual in that dispersal is almost exclusively

38by females. While plausible ultimate hypotheses can explain this dispersal pattern, the

39proximate causes of female dispersal are unknown and warrant examination due to variation in

40dispersal behavior and the associated high costs of immigration. In this study, we examine the

41behavioral and hormonal context of female dispersal in chimpanzees of Kibale National Park,

42Uganda, in order to understand variation in dispersal patterns and gain insight into functional

43explanations. Using over 10 years of behavioral, endocrinological, and demographic records, we

44examined the significance of 5 potential predictors of the timing of dispersal: (1) maturational

45state; (2) association patterns; (3) mating patterns; (4) physiological stress; and (5) feeding

46ecology. Female dispersal was not strictly predicted by chronological or gynecological age, and

47dispersal did not correlate with shifts in glucocorticoid levels. We found no evidence that

48females avoided mating in their natal group, even with known relatives, suggesting that

49inbreeding avoidance is not a sufficient proximate explanation for dispersal in chimpanzees.

50Instead, variation in social development and the availability of energy for dispersal were

51implicated and necessitate more intensive examination along with subtler variation in

52maturational trajectories.

53

54**Keywords: dispersal, adolescence, stress, inbreeding, energetics**

55

56

INTRODUCTION

58

59In most social mammals, members of one or both sexes leave their natal group at sexual maturity

60to avoid inbreeding (Pusey & Packer, 1987). For catarrhine primates, female philopatry and male

61dispersal are the predominant pattern (Pusey & Packer, 1987; Melnick & Pearl, 1987; Wrangham

621987). Philopatric females enjoy a variety of benefits from long-term cooperation with kin,

63including enhanced access to resources and reduced infant mortality (Wrangham, 1980; Silk et

64al., 2003).

65

66Chimpanzees (*Pan troglodytes*) are unusual among Old World Primates in that dispersal is

67almost exclusively by females (Goodall, 1986). Ultimate factors affecting this unusual pattern of

68dispersal include the importance of male affiliation and cooperation for defense of the

69community feeding range, the size of which affects female reproductive rates (Williams et al.,

702004). However, the proximate causes of female dispersal in chimpanzees are unclear, both

71because the timing of dispersal varies, and because some females never leave their natal

72communities (e.g., Goodall, 1986; reviewed in Stumpf, 2007).

73

74While males in various species may benefit by seeking groups with improved mating

75opportunities (Jack & Fedigan, 2004a,b; Fedigan & Jack, 2004), females receive few obvious

76benefits and face high costs of dispersal. Access to high quality food resources is critical for

77female reproductive success (Bradbury & Vehrencamp, 1977; Emlen & Oring, 1977; Trivers,

781972; for chimpanzees: Emery Thompson et al., 2007a; Emery Thompson & Wrangham, 2008).

79Food acquisition in chimpanzees is challenging because resources are patchily distributed in both

80time and space. Moreover, relative social status is a key predictor of resource access (Murray et

81al., 2006; Kahlenberg et al., 2008a). Consequently, a key cost of emigration is the loss of

82affiliative natal relationships and knowledge of food resource locations (Smuts, 1993; Alberts &

83Altmann, 1995a,b; Williams et al., 2002). In other primates, adolescents can be forcibly expelled

84from the natal group (e.g. Crockett & Pope, 1993), increasing the relative cost of philopatry

85(Pusey & Packer, 1987; Moore, 1984). However, this does not occur in chimpanzees. Instead,

86females leave without being coerced, enter a new group at the bottom of the social hierarchy,

87receive considerable aggression from resident females, and must fight to establish a residential

88core area: these are costly activities associated with elevations in stress hormone production

89(Townsend et al., 2007; Kahlenberg et al., 2008a,b; Pusey et al., 2008). One major benefit of

90dispersal is avoidance of the negative effects on reproductive fitness caused by breeding with

91close kin (Moore & Ali, 1984). However, while inbreeding avoidance provides a plausible

92ultimate explanation for sex-biased dispersal in primates generally, and male cooperative

93territoriality presents a reasonable explanation for male philopatry in chimpanzees specifically,

94the proximate behavioral and biological mechanisms underlying female dispersal in chimpanzees

95are poorly understood.

96

97The purpose of this study was to document behavioral and physiological changes in adolescent

98female chimpanzees so as to test potential proximate mechanisms for the timing of their dispersal

99to a new community. We tested 5 non-mutually exclusive hypotheses:

100   (1) Dispersal is consistently related to sexual maturation, such that (a) female emigration

101   corresponds to the onset of sexual cycling, or (b) females who reach sexual maturity

102   earlier emigrate at an earlier age. Female emigration is frequently coincident with sexual

103   receptivity in chimpanzees (Nishida, 1979; Pusey, 1979, 1980; Boesch and Boesch-

104   Achermann, 2000) as in some other primates (Jolly et al., 1982; Moore, 1984), but it is

105   not known how the timing of female chimpanzee dispersal is related to the onset of

106   sexual maturity.

107   (2) Dispersal is correlated with the risk of inbreeding, such that females avoid mating with

108   related males in their natal community. Females were reported to avoid mating with close

109   kin (Pusey, 1980; Wrangham, pers. comm.), but the proximate role of inbreeding

110   avoidance in influencing individual dispersal decisions is unknown.

111   (3) Dispersal is predicted by social relationships, such that (a) shifts in association patterns

112   precede emigration, and/or (b) association patterns differ between females who emigrate

113   early, late or not at all. In adolescent Gombe chimpanzees, female sexual maturation is

114   associated with a shift from exclusive association with the mother to association with

115   adolescent and adult males that precedes emigration (Pusey, 1990; Goodall, 1986). The

116   quality of female social relationships (e.g. aggression from adult females) might also

117   influence the relative costs and benefits of dispersal.

118   (4) Dispersal is correlated with stress, as measured by urinary cortisol levels, such that (a)

119   females emigrate when experiencing greater stress, and/or (b) adolescents with generally

120   higher stress levels emigrate earlier.   Increased stress hormones could be associated with

121   any of the previously-described predictors and might mediate detachment from the natal

122   community, as in willow tits (*Parus montanus*: Silverin, 1997) or winged insects (e.g.

123   *Cardiocondyla obscurior*: Cremer & Heinze, 2003).

124   (5) Dispersal corresponds with changes in resource availability in the natal habitat. There are

125   two opposing predictions. Females may emigrate only during periods of high fruit

126   consumption when they have sufficient energy reserves to face a period of resource

127   uncertainty (e.g., screech-owls (*Otus kennicottii*), Belthoff & Dufty, 1998).

128   Alternatively, low dietary quality may lead young females to seek improved foraging

129   opportunities in other habitats (e.g. Lurz, et al., 1997; Nunes et al., 1999).

130.

131**METHODS**

133*Study site*

134We studied wild chimpanzees (*P.t. schweinfurthii*) of the Kanyawara community in Kibale

135National Park, western Uganda (0°34′N and 30°21′E). The Kanyawara chimpanzees range over

136approximately 32 km^2 of medium altitude habitat, comprising areas of moist evergreen primary

137forest, logged regenerating forest, grassland, swamp, and agriculture (Chapman & Wrangham,

1381993). R. Wrangham established the Kibale Chimpanzee Project in 1987, following earlier work

139by Isabirye-Basuta (1988, 1989), and research has been continuous since then (Wrangham et al.,

1401996). Individual chimpanzees are well habituated to human observers, and have never been

141provisioned.

142

143*Study subjects and age estimation*

144The Kanyawara chimpanzee community currently consists of 10 adult males, 16 adult females

145and 23 immature males and females. We extracted relevant data on reproductive parameters and

146dispersal events from long-term behavioral records collected over a fourteen year period between

1471994 and 2007. During this period, we studied 22 nulliparous females, including 8 immigrants

148aged at least 10 years and 14 natal Kanyawara females aged at least 5 years (Table I). Of the

149natal females studied, 10 had birthdates known to within one month. Four natal females born in

150the 1980s and 8 immigrant females have birthdate estimates based on observer estimations of

151their body size at first sighting relative to individuals of known age.

152

153Females who were last observed in healthy condition between the ages of about 9-15 are

154assumed in these data to have emigrated, or attempted emigration. However, we do not have

155records from neighboring chimpanzee communities to confirm dispersal, nor do we often recover

156the remains of dead chimpanzees. We present these data with the caveat that some assumed

157emigrants may have died in the natal community. In one case (JK), dispersal was confirmed by

158her revisiting the Kanyawara community briefly, several years after her initial departure.

159

160*Reproductive data*

161We used Kaplan-Meier survival analyses to calculate time interval data, such as the age of

162emigration or the interval between first maximal sexual swelling (defined as the first

163unambiguous observation of tumescence of both vaginal and perianal tissue without occurrence

164of wrinkling (Dahl et al., 1991) and emigration. This method increases statistical power by

165including censored datapoints (e.g., females who had experienced a swelling but had not yet

166emigrated). We provide the mean and standard error from the Kaplan-Meier analysis, the

167number of uncensored (Nu) and censored (Nc) datapoints, and the range of uncensored events.

168For age of emigration, we performed each analysis for the set of females with known dates of

169birth (to within one month) and again with the larger sample that includes females with estimated

170birthdates.

171

172Two sources of bias might impact behavioral observations of new community members.

173Unhabituated individuals may be wary of human observers or of group members, and it may take

174time for the field staff to reliably identify individual immigrants. We do not believe these biases

175have affected our findings. First, observers note identifying characteristics of unidentified

176females and record their presence and all behaviors involving them as they would with a known

177individual. Once a female is established and named, which typically takes less than one month,

178we are able to update records of her presence from her initial sighting onwards. For example,

179when we note the interval between immigration and first copulation, we have verified this

180against copulation records of 'unidentified' females. Thus, we believe that our behavioral records

181for each immigrant female are complete from the time of her first being seen in Kanyawara

182parties. Second, observation rates of the immigrant females during their first six months in the

183community were higher than those of natal adolescents overall (mean ± S.E.: natal: 345 ± 165

184hrs/month, immigrants 447 ± 114 hr/month) and during estrus, specifically (natal: 125 ± 67

185hrs/month, immigrants: 232 ± 78 hrs/month). In fact, our ability to observe immigrants is

186enhanced by their tendency to affiliate with large groups of males as a counterstrategy to the

187aggression they receive from resident females (Kahlenberg et al., 2008b).

188

189*Association Patterns*

190Association data were recorded as a part of continuous data collection. KCP field staff conduct

191daily observations, following one chimpanzee party, when possible, from nest to nest, recording

192the identities of all individuals in the party every 15 minutes.   We analyzed the association

193patterns of target females with a) juvenile males and females (5-8 years of age) excluding the

194target's dependent siblings, b) adolescent females (9-15 years of age), c) adolescent males (9-14

195years of age), d) adult females (>15 years of age, excluding each target's mother), e) adult males

196($\geq$15 years) and f) each target's mother.

197

198Association rates were determined by obtaining a simple ratio association index for each

199adolescent female with each individual in the community (Cairns & Schwager, 1987; Ginsberg

200& Young, 1992). The simple index is calculated for each dyad as $X/(X+Y_{AB}+Y_A+Y_B)$, where X is

201the number of scans during which A and B were observed together, Y_{AB} is the number of scans

202during which A and B were both observed in separate groups, Y_A is the number of scans during

203which only A was observed, and Y_B is the number of scans during which only B was observed.

204This ratio was calculated for each year (age 9-15 or until emigration or parturition) of the target

205female. These ratios for each female were then averaged by age class (all juvenile males and

206females, adolescent males and females, adult males and females and mothers) for each year and

207then a final association index for each age class was obtained for each female by averaging

208across all years she was aged 9-15 (or until emigration or parturition). Individuals (from any age

209class) present for fewer than 25 observations per year were excluded from analyses.

210

211We used the simple index (Cairns & Schwager, 1987) because, relative to other association

212indices (e.g. half-weight or twice-weight indices (Cairns & Schwager, 1987), the simple index is

213statistically unbiased (Ginsberg & Young, 1992) and is more appropriate in situations where

214associations are determined by membership in the same group (Whitehead & Dufault, 1999).

215Nevertheless, we did compare the patterns in our results from the simple index to two other

216association indices, the half-weight index and another dyadic association index, calculated as the

217number of scans an individual was present with the female of interest divided by the total

218number of scans the female was present.   All three indices supported the same association

219patterns.

220

221*Sexual behavior*

222The KCP field staff recorded all attempted and completed copulations during daily observations.

223We analyzed the copulation patterns of adolescent females with adult males (≥ 15 years of age)

224as a rate per hour of observation while in maximal swelling. Rates were calculated for each four

225month period beginning with the first observation of maximal sexual swelling in the community

226and ending with emigration, conception, or last available data (Dec. 2006); periods with fewer

227than 20 estrous observation hours were excluded. This left us with copulation data for 12

228females: 7 immigrants and 5 natal females.

229

230Whenever possible, the initiator of the copulation was noted. The male was considered to have

231initiated the copulation if he approached the female for intromission or performed a clear

232solicitation behavior (e.g., penis-flicking, branch-shaking) to the female. Female-initiation was

233defined by female approach without solicitation by the male, leading to copulation. In 65% of

234the adolescent female copulations there was one clear initiator, and 10 females had at least 10

235such copulations. For each of these females, we calculated the number of copulations she

236initiated as a proportion of all her copulations with a single clear initiator.

237

238Finally, we looked at mating partner diversity by calculating the percentage of potential adult

239male partners with which each female mated and the variance in copulation frequency across all

240males, each plotted against the total number of copulations observed for the female.

241

242*Glucocorticoid data*

243Routine collection of chimpanzee urine was initiated at Kanyawara in November 1997, and has

244continued through the present day. Detailed information on collection and storage methods is

245presented by Muller & Wrangham (2004a, b) and Emery Thompson (2005). Samples were ana-

246lyzed for cortisol using enzyme-immunoassay reagents provided by C.J. Munro at the University

247of California at Davis and protocols previously described for use with chimpanzees (Muller et

248al., 2007; Kahlenberg et al., 2008b). Interassay coefficients of variation for this assay were 11.5

249and 14.4% (N = 94) for high and low pools, respectively. Intra-assay coefficients of variation for

25012 replicates were 5.4 and 9.5% for high and low pools, respectively. To correct for variation in

251urine concentration, cortisol values were indexed to creatinine, which was quantified colorimetri-

252cally. Samples with creatinine measurements below 0.05 mg/ml were excluded from all analyses.

253

254

255Cortisol shows a distinct circadian pattern in chimpanzee urine, with levels peaking in the early

256morning, and subsequently declining throughout the day (Muller & Lipson, 2003). To correct

257for this, we first calculated a regression equation of hour of the day versus cortisol (in ng/mg-Cr)

258for each of 14 Kanyawara females from whom we have collected 50 or more samples (mean =

25982 samples), then we averaged the slopes (-11.3 ± 1.2 S.E.) and intercepts (253.5 ± 16.0). This

260circadian pattern was consistent across age groups. Following previous analyses (Kahlenberg et

261al., 2008a), we calculated cortisol values as the time-adjusted residual of this average regression

262line. These values provide an intuitive gauge of relative cortisol elevation: the "expected"

263cortisol residual of any female sample is zero (mean of 3064 female samples = 4.2), with positive

264or negative values representing titers greater or less than expected. To place cortisol fluctuations

265of adolescents in perspective with other females, we present plots with a y-axis that represents ±

2661 standard deviation (168, N = 3064) of all Kanyawara female cortisol titers assayed to date. To

267further correct for uneven sampling, we calculated a single daily average when multiple samples

268had been taken and then derived a monthly average for each individual for use in the final

269analyses.

270

271We calculated age patterns of cortisol for natal females only, as our research group has

272previously documented significant elevations in the cortisol levels of new immigrants

273(Kahlenberg et al., 2008b). We analyzed samples from females beginning at the age of 5 and

274ending with death, dispersal, or conception. One female (JK) received a severe wire snare injury

275at age 13 which was accompanied by elevated cortisol levels. For this female, we examined only

276samples collected prior to the injury. We calculated the female mean at each age (by year) and,

277excluding age classes represented by a single subject, computed a linear regression to test for

278trends. We considered both chronological age (time since birth) and gynecological age (time

279since first maximal sexual swelling). For emigrants, we conducted a similar analysis using 6

280month intervals during the three years prior to emigration.

281

282*Diet*

283We quantified changes in energy availability in Kanyawara by examining variation in the

284monthly consumption of fruit (see Emery Thompson & Wrangham, 2008). During daily

285observations, feeding behavior of the chimpanzee party was recorded every 15 minutes. We

286calculated the percentage of observations in which chimpanzees ate fruit as a proportion of all

287observations in which chimpanzees fed. At Kanyawara, this measure of dietary quality is

288significantly correlated with fruit availability estimates obtained from phenological transects

289(Wrangham et al., 1991, 1996; Sherry, 2002) and with biomarkers of chimpanzee energetic

290condition (C-peptide of insulin, Emery Thompson et al., 2009).

291

292**RESULTS**

293

294**Timing of Dispersal**

295Females of known age who emigrated from Kanyawara did so at an average age of 12.6 years

296(SE = 1.0, Nu = 4, Nc = 5, range: 10.4 – 15.1). Adding natal females of estimated age gives us a

297slightly higher figure of 12.9 years (SE = 0.7, Nu = 8, Nc = 5, range: 10.4 – 15.7). This is

298consistent with the average age estimates of 13 years that we assigned to 8 new immigrants. The

299interval between sexual maturity, as defined by the first maximal swelling, and emigration was

300highly variable. Two of eight emigrating females were not observed with a maximal swelling

301prior to their disappearance. The interval to emigration for the six females who experienced

302prior maximal swellings was an average of 15.5 months (SE = 3.4, range = 1.2 - 22.7). One natal

303female remained in Kanyawara to breed. Because first swellings typically preceded emigration,

304females who matured at a later age also dispersed at a later age (r_s = 0.83, N = 8, p = 0.027).

305However, there was no significant relationship between a female's age at sexual maturity and her

306subsequent latency to dispersal (r_s = 0.26, N = 8, p = 0.5). With one exception, immigrants were

307sexually mature when first identified. The one exception was not observed with a swelling for

308approximately 1 year.

309

310**Mating Behavior and Inbreeding Risk**

311Five of seven natal females copulated with an adult male during their first maximal swelling

312cycle. Natal females were first seen to copulate with adult males an average of 0.7 months after

313their first sexual swelling (SE = 0.5, Nu = 7, Nc = 0, range: 0 – 3.7), whereas immigrants first

314copulated with an adult Kanyawara male an average of 2 months after their first swelling in the

315community (SE = 0.9, Nu = 7, Nc = 0, range: 0 – 4.8). The only natal female to give birth (LR)

316did so 37.0 months after her first sexual swelling. Immigrants experienced an average delay of

31726.9 months before birth (SE = 3.3, Nu = 5, Nc = 3, range: 10.6 – 36.8; n.b., gestation length in

318chimpanzees is approximately 230 days, Wallis 1997; Shimizu et al. 2003).

319

320There was a significant positive relationship between gynecological age (defined here as the time

321since first observed maximal sexual swelling in the Kanyawara community), and copulation rate

322with adult males (R^2 = 0.51, df = 7, p = 0.047, Figure 1).   There was no significant difference

323between natal females and immigrants in their rates of copulation, matched for gynecological age

324group (Wilcoxon matched-pairs test, z = -1.69, $N_1 = N_2$ = 7 age groups, p = 0.09).   One natal

325female (LR) maintained consistently higher copulation rates than all other adolescent females.

326This individual was the sole natal female who did not emigrate from the community. Comparing

327immigrant females with only the natal females who later emigrated, we did find a significant

328difference, with immigrant females copulating at moderately higher rates in each age group (z =

13 13

329-2.032, $N_1 = N_2 = 5$, $p = 0.042$). However, even these differences were small when considered

330against the high copulation rates generally achieved by chimpanzees (Watts, 2007; Wrangham,

3312002): during the first 2 years of sexual cycling in the community, immigrants had an average

332rate of 0.15 copulations/hour, while natal emigrants had copulation rates of 0.11

333copulations/hour.

334

335We expected that natal females would be unlikely to solicit matings with adult males if they were

336motivated to avoid inbreeding. However, for those copulations with one clear initiator, just over

337half were initiated by the female (54.9% ± 0.1 S.E., 10 females). Females varied greatly in the

338percentage of copulations they initiated (7-77%, $N = 10$), but there was no significant difference

339between natal females and immigrant females in this measure (Mann-Whitney U test, $z = -0.801$,

340$N_I = 5$, $N_N = 5$, $p = 0.49$).

341

342Similarly, we expected that if natal females were avoiding inbreeding, they would differ from

343immigrants in the distribution of their matings among male partners, avoiding known kin or

344males of the same age cohort. We calculated regressions of number of matings (log-

345transformed) versus the percentage of available partners mated. The slopes of these regressions

346did not differ for natal and immigrant females ($t = 0.711$, $df = 10$, $p = 0.49$, Figure 2a).

347Similarly, when we compared the number of matings with the variance in copulation frequency

348across partners, we found no significant difference between slopes for natal and immigrant

349females ($t = -1.718$, $df = 10$, $p = 0.12$, Figure 2b). Thus, there was no evidence that natal females

350consistently avoided mating with certain partners.

351

352There was only one female who had known adult male kin, two elder brothers, in the group. This

353was LR, the female who remained to breed in her natal community. She mated with her brothers

354at rates of 0.06 and 0.05 copulations/hour of maximal swelling, which is similar to the median

355rate of 0.05 copulations/hour (range 0.03-0.13) for other adult partners.

356

357**Association Patterns**

358As expected, adolescence was associated with decreased association of a female with her mother

359and increased association with adolescent and adult males. For the 5 natal females with living

360mothers and association data through the time of emigration, there tended to be a marked

361decrease in maternal association in the 1-2 years prior to dispersal (Figure 3).

362There were substantial differences in association indices of adolescent females with various age-

363sex classes (Figure 4). Adolescent females associated most often with adolescent and adult

364males and least often with juvenile males and adult females (Friedman, N=20; X^2=60.3, df=5,

365p<0.001). Association patterns of natal females and immigrants were similarly distributed across

366age-sex classes (Friedman, N_N =12; X^2=37.0, df=5, p<0.001; N_I =8; X^2=27.9, df=5, p<0.001),

367except that immigrant females associated significantly more frequently with adolescent and adult

368males than did natal females (Mann-Whitney U, N_N= 12, N_I = 8 Z=-2.006, p=0.047; N_N = 12, N_I

369= 8, Z= -2.237, p=0.025).

370

371There was a non-significant trend for females who dispersed at a younger-than-average age

372(N=4) to have lower association indices across age-sex classes, particularly with adolescent and

373adult males, than late dispersing females (N=4) (Figure 5a). In line with this tendency, LR (who

374stayed to breed in her natal group) had association indices similar to females who emigrated late.

375Early emigrating females also demonstrated a trend toward lower association indices with their

376mothers than females who emigrated late or not at all (data standardized by age; Mann Whitney

377U test z=-1.879 p=0.06; Figure 5b).

378

379Physiological Stress

380Urinary cortisol levels were remarkably stable during adolescence. There was a marginally

381significant trend toward decreasing cortisol with age between 5 and 12 years ($R^2 = 0.51$, df $= 7$

382age groups, N= 3-9 females/year, p $= 0.05$). However, this actually represented a very low range

383of variation (time-adjusted residuals: -25.7 to -58.6), equivalent to 0.2 standard deviations of the

384mean for all Kanyawara females. Because females matured on different reproductive schedules,

385an analysis based on chronological age might mask underlying variation with regard to

386gynecological age. However, cortisol profiles aligned relative to gynecological age also showed

387little variation ($R^2 = 0.30$, df $= 5$, N $= 4$-5 females per year, p $= 0.26$. Figure 6a). In general, the

388time-adjusted cortisol residuals for natal adolescent females were negative, indicating that stress

389hormone levels were lower than average for immigrant and adult Kanyawara females (c.f.,

390Kahlenberg et al., 2008b).

391

392To examine whether social stress could act as a trigger for dispersal, we examined cortisol titers

393of females aligned relative to the time of emigration. We found no indication that either an

394abrupt or gradual increase in cortisol preceded emigration ($R^2 = 0.55$, df $= 5$, N $= 2$-5 females per

395year, p $= 0.09$; Figure 6b). Within the constraints of our small sample size, we also asked

396whether females with relatively high cortisol during adolescence were more likely to disperse

397early. There was no evidence for this. In fact, females who emigrated before the average age

398had slightly lower cortisol titers on average (-95.0 ± 18.2 SE, N $= 3$) than females who emigrated

399late or not at all (-51.2 ± 23.1, N $= 4$). Similarly, females who emigrated soon after sexual

400cycling had slightly lower cortisol levels (-85.8 ± 27.2, N $= 2$) than females who had not

401emigrated within a year of cycling (-63.6 ± 21.8, N $= 5$).

402

403Ecological Variation

16   16

404We predicted that changes in energy availability might affect the timing of dispersal if females

405choose times of positive energy balance to undertake the potential costs of emigration or,

406alternatively, if resource pressure leads them to look elsewhere for new foraging grounds.

407Among transfer events with available dietary data, there was a tendency for both emigrations

408(6/8) and immigrations (5/7) to occur in months of above average fruit consumption by

409Kanyawara chimpanzees (% fruit composition in diet, reference data from Emery Thompson &

410Wrangham, 2008). However, fruit consumption in these months was not significantly different

411from the set of months in which no transfer event occurred ($69.3\% \pm 4.0$ SE vs. $64.8\% \pm 1.4$,

412Mann-Whitney U, $z = -0.937$, $NT = 15$, $N0 = 154$, $p = 0.35$). Nevertheless, two additional

413findings support the hypothesis that energetic condition impacts emigration timing. First, there

414was a strong negative correlation between latency to emigrate (in months) and average fruit

415consumption in the three month period leading up to and including the month of first maximal

416sexual swelling (Figure 7a, $rs = -0.75$, $N = 8$, $p = 0.031$). Three females that matured during

417periods of above average fruit consumption emigrated within 2 months. Second, among the

418remaining five females with delayed dispersal, emigration coincided with periods when fruit

419consumption in Kanyawara increased significantly (Figure 7b, $rs = 0.829$, $N = 6$ months, p=

4200.042). Because our dietary measures do not incorporate individual differences in feeding

421behavior, a larger sample and more sensitive measures of individual energetic condition are

422needed to confirm this finding.

423

424**DISCUSSION**

425

426At Kanyawara, we observed considerable variation in female dispersal behavior. This is

427consistent with observations at other chimpanzee study sites (Pusey, 1979; Nishida et al., 2003).

428We thus examined several hypotheses for proximate mechanisms affecting female dispersal.

429

430We expected that, regardless of the ultimate reason for female dispersal in chimpanzees,
431increased stress might be a proximate mechanism associated with this event.   Stress could be
432hypothesized to result from decreased association with the mother, greater involvement in
433feeding competition and the need to establish a feeding range, or as a response to new mating
434attention from males. Elevated cortisol might also be expected from increased ranging resulting
435from females travelling more with males and less with mothers. We were surprised to find that
436both before and after sexual cycling began, female adolescents showed very low and stable
437levels of urinary cortisol.   We found no evidence that increased physiological stress either
438preceded dispersal or determined which females dispersed quickly.   In theory changes in body
439size might mask increases in cortisol levels, because of the use of creatinine to correct for urinary
440concentration.   However, such masking seems unlikely because a significant cortisol elevation
441was observed in immigrants, relative to same-aged natal females, corresponding to high levels of
442aggression (Kahlenberg et al. 2008b). Although it is possible that abrupt rises in stress levels
443influenced dispersal without being captured in our sample, we found no evidence that negative
444aspects of the social environment triggered emigration. Our results therefore contrast with the
445patterns of coerced emigration in some primates (Pusey & Packer 1987) or elevated
446glucocorticoids in dispersing birds (Silverin 1997). Our cortisol data support the hypothesis that,
447at least over the short-term, the relative costs of dispersal are low.

448

449Female reproductive maturation did not reliably predict emigration. Some females emigrated
450immediately after menarche, some did so years later, and one stayed to breed in the natal
451community. The "swelling passport" hypothesis predicts that females use their attractiveness as
452a tool to integrate into a new community (Pusey, 1979; Nishida, 1979). Males are expected to be
453welcoming to new mates, as evidenced by their low rates of aggression to immigrant females as

454well as policing aggression directed at immigrants by resident females (Townsend et al., 2007;

455Kahlenberg et al., 2008b). In support of the passport hypothesis, females were generally cycling

456at the time of emigration. However, contrary to the hypothesis, at least two females left

457Kanyawara without having shown signs of swelling. It is possible that these females left

458immediately upon experiencing their first swelling, or had one by the time they contacted a new

459community, but this seems unlikely given that one had never shown even partial tumescence, and

460the other had shown only slight signs of swelling the day before her disappearance.

461Additionally, copulation rates and latency to first copulations do not support a strong attraction

462of Kanyawara males to immigrants. This is particularly unexpected because, assuming that

463immigrants followed similar growth trajectories as Kanyawara females, immigrant females

464should have been both older and more reproductively mature than natal adolescents, having

465experienced nearly 1 year of cycling on average before dispersal. These patterns at Kanyawara

466support a general link between sexual attractivity and dispersal, but it appears that swellings are

467not a prerequisite for acceptance into a new group, and males do not show strong mating interest

468in new cycling immigrants.

469

470We found little support for the hypothesis that inbreeding avoidance was a proximate

471determinant of female dispersal. First, prior to leaving the community natal females reduced

472their association time with their mothers and increased association time with potential sexual

473partners (see also Pusey 1990). Second, most Kanyawara females mated within the community

474before emigrating, some for well over 1 year. Third, natal females usually copulated with adult

475male community members on their first maximal swelling cycle. Fourth, there was only a small

476difference between the copulation rates of immigrants and future emigrants, and the female who

477did not emigrate maintained the highest copulation rates. Fifth, the female who did not emigrate

478had two known maternal brothers in the community and was observed mating with them. Sixth,

479females initiated the majority of their copulations, and natal females were no less likely to do so

480than immigrants. Finally, given the high level of reproductive skew in chimpanzees (Constable

481et al. 2001; Boesch et al., 2006) many of the males that natal females mate with are likely to

482share paternally related genes. However, there was no significant difference in the number of, or

483variance among, sexual partners for natal and immigrant females, suggesting that natal females

484did not display strong aversion to certain partners or were ineffective at exerting these

485preferences. This is consistent with other primate studies, including of Gombe chimpanzees, in

486which natal adolescent females are highly proceptive toward adult males (Rasmussen, 1983;

487Goodall, 1986; Perry & Manson, 1995), with males often showing relatively little interest in

488return (Pusey, 1978; Wrangham, 2000; Muller et al., 2007). These findings do not imply that

489inbreeding avoidance has been unimportant in the evolution of sex-biased dispersal in this

490species. Rather, they suggest that proximate dispersal decisions are not predicated on a female's

491relative risk of mating with potential relatives.

492

493We found two patterns that suggest plausible proximate models for variation in dispersal

494behavior. First, dispersal was associated with dietary quality, such that females experiencing

495conditions of high fruit consumption emigrated soon after menarche and others emigrated during

496periods of increasing fruit consumption. This may explain disparities in emigration timing, if

497females wait until they have sufficient energy reserves to afford the high costs of dispersal,

498which could include long travel distances, lack of knowledge about new foraging areas,

499increased feeding competition, and aggression by resident females in the new community, and

500time spent in more than one community. However, it is possible that the emigration patterns we

501observed were directly related not to dietary quality, but to a correlated variable such as the

502changing size or composition of social parties (Chapman et al., 1994; Hashimoto et al., 2003;

503Emery Thompson & Wrangham, 2006) or an increase in fecundity or the presence of other

504estrous females (Anderson et al., 2006; Emery Thompson & Wrangham, 2008). While we found

505a strong significant pattern, we hope in the future to corroborate these data with a more sensitive

506measure of individual energetic condition (Emery Thompson et al., 2009).

507

508Second, there was a trend for decreasing levels of association across all age/sex classes for

509females who emigrated early versus those who emigrated later or not at all. Females who retain

510longer or stronger relationships with natal group members, particularly their mothers, may delay

511dispersal. These females might be in a better position to exploit high-quality core foraging areas

512(e.g., Emery Thompson et al., 2007a; Kahlenberg et al., 2008a), which could affect their

513emigration decisions. However, core area location could also indirectly affect their rates of

514contact with other group members or bias their ease of observation in larger or smaller groups.

515

516Our hypotheses, given the available data, are not exhaustive. Here, we briefly discuss some

517alternatives that warrant future examination. Reproductive success in female chimpanzees is

518critically sensitive to seasonal and inter-individual variation in the availability of high quality

519food resources (Emery Thompson et al., 2007b; Emery Thompson & Wrangham, 2008), and

520relative social status is an important predictor of resource access (Pusey et al., 1997; Murray et

521al., 2006; Kahlenberg et al., 2008a). It appears that a key challenge during adolescence, perhaps

522one of the most critical in a female chimpanzee's life, is establishing long-term access to a core

523foraging area, the best of which will be subject to intense competition (Williams et al., 2002;

524Townsend et al., 2007; Kahlenberg et al., 2008a,b; Pusey, 1980; Pusey et al., 2008). In

525Kanyawara, in particular, females occupying lower quality foraging areas have significant

526deficits in reproductive rates and offspring survivorship (Emery Thompson et al., 2007a).

527Therefore, the dispersal decisions of individual females might be expected to hinge on the

528quality of foraging opportunities and the degree of female competition in the natal group versus

529nearby communities (Pusey et al., 1997). This hypothesis is difficult to examine without detailed

530knowledge of neighboring chimpanzee groups and habitats. Furthermore, the reproductive

531advantage of dispersing vs. remaining may differ across sites, given that studies in different

532chimpanzee communities suggest that the age at first birth may be comparatively delayed

533(Boesch & Boesch-Achermann, 2000) or advanced (Nishida et al., 2003) in natal vs. dispersing

534individuals, and that in some populations a high proportion of natal females fails to disperse

535(Pusey et al. 1997). Nonetheless, the importance of this decision may explain observations like

536those at Gombe, where nulliparous females sometimes spend time visiting one or more

537neighboring communities before returning temporarily or permanently to their natal group

538(Pusey, 1979). Without access to habituated neighboring communities, we cannot be certain

539how frequently this happens at Kanyawara, but unusual periods of absence by adolescent females

540make it likely. Our sample of adolescent females, however, is overwhelmingly comprised of the

541daughters of females in the high-quality foraging ranges, thus we cannot easily explain

542disparities in dispersal behaviors by social status alone. It is interesting that LR, who did not

543emigrate, was the daughter of the alpha female, was high-ranking compared to other nulliparous

544females, and inherited her mother's high-quality foraging range (Kahlenberg et al., 2008a).

545

546Relative morphological (skeletal) maturation could also be an important variable influencing

547dispersal timing, if it influences female competitive success and access to high-quality feeding

548areas in the new community. Alternately, as adolescent subfecundity in chimpanzees is lengthy

549and highly variable (1.2 – 4.1 years at Mahale, Nishida et al., 2003; 0.7 – 4.9 years at Gombe,

550Wallis, 1997), differences in the development of ovulatory function among females may better

551predict timing of dispersal. An appropriate test of this hypothesis would incorporate measures of

552ovarian hormone production in both emigrants and immigrants.

553

554This and other hypotheses arise from and highlight two significant questions. First, why do

555females cycle and mate in their natal community prior to emigration? Because ovulatory function

556takes time to develop in anthropoids (Lunenfield et al., 1978; Resko et al., 1982; Zehr et al.,

5572004), an extended period of subfecundity permits females to cycle several times prior to

558emigration with little inbreeding risk, providing opportunity to obtain social, sexual and foraging

559knowledge in a context when they are among familiar individuals but semi-independent of their

560mothers (Shepher, 1983; Strier, 1997). A second question is why females experience such a long

561delay between dispersal and reproduction. This may simply reflect the long duration of

562adolescent subfecundity, though our data and those from Mahale (Nishida et al., 2003) suggest

563that immigrants have delays in reproduction relative to natal females. Similarly, even females

564who changed foraging areas within the community at Gombe had disrupted reproduction

565(Williams et al., 2002). Such a delay could occur as a consequence of social and energetic

566stresses of the dispersal process. Reproductive delay would also diminish infanticide risk

567through increasing the probably of paternity within the new community's male cohort by

568establishing a mating history and forging social bonds.

 569

570While there has been considerable theoretical inquiry regarding the evolution of sex-biased

571dispersal, and models have been proposed to explain the advantages of male versus female

572dispersal in various species, few primate studies have examined the proximate mechanisms

573influencing dispersal. For chimpanzees, in which dispersal is almost exclusively by females,

574dispersal is not strictly predicted by the physiological events of puberty nor by stress in the natal

575community. Our data from Kanyawara suggests that individual variation in sociality, temporal

576variation in energy availability, and perhaps subtle variation in developmental trajectories, play

577roles in female decisions to seek new communities.

 578

592**Bibliography**
593
594Alberts, S.C. & Altmann, J. (1995a). Balancing costs and opportunities: Dispersal in male
595   baboons. – Amer. Nat. 145: 279-306.
596
597Alberts, S.C. & Altmann, J. (1995b). Preparation and activation: Determinants of age at
598   reproductive maturity in male baboons. – Behav. Ecol. Sociobiol. 36: 397-406.
599
600Anderson, D.P., Nordheim, E.V., Boesch, C. (2006). Environmental factors influencing the
601   seasonality of estrus in chimpanzees. - Primates 47: 43-50.
602
603Belthoff, J.R. & Dufty Jr., A.M. (1998). Corticosterone, body condition and locomotor activity: a
604   model for dispersal in screech-owls. - Anim. Behav. 55: 405–415.
605
606Boesch, C. & Boesch-Achermann, H. (2000). The chimpanzees of the Taï Forest: Behavioural
607   ecology and evolution. - Oxford University Press, Oxford.
608
609Boesch, C., Kohou, G., Néné, H. & Vigilant, L. (2006). Male competition and paternity in wild
610   chimpanzees of the Taï Forest. – Amer. J. Phys. Anthro. 130: 103-115.
611
612Bradbury, J.W. & Vehrencamp, S.L. (1977). Social organization and foraging in emballonurid
613   bats II. Mating systems. – Behav. Ecol. Sociobiol. 2: 1–17.
614

615 Cairns, S.J. & Schwager, S.J. (1987). A comparison of association indices. – Anim. Behav. 35:
616   1454-1469.
617
618 Chapman, C.A. & Wrangham, R.W. (1993). Range use of the chimpanzees of Kibale:
619   Implications for the evolution of chimpanzee social organization. – Am. J. Primatol. 31:
620   263−273.
621
622 Chapman, C.A., White, F.J., Wrangham, R.W. (1994). Party size in chimpanzees and bonobos: a
623   reevaluation of theory based on two similarly forested sites. In: Chimpanzee cultures
624   (Wrangham, R.W., McGrew, W.C., de Waal, F.B. & Heltne, P., eds). Harvard University
625   Press, Cambridge, p. 41-58.
626
627 Constable, J.L., Ashley, M.V., Goodall, J. & Pusey, A.E. (2001). Noninvasive paternity
628   assignment in Gombe chimpanzees. – Mol. Ecol. 10: 1279-1300.
629
630 Cremer, S. & Heinze, J. (2003). Stress grows wings. Environmental induction of winged
631   dispersal males in *Cardiocondyla* ants. - Curr. Biol. 13: 219–223.
632
633 Crockett, C.M., & Pope, T.R. (1993). Consequences of sex differences in dispersal for juvenile
634   red howler monkeys. - In: Juvenile primates: Life history, development, and behavior
635   (Pereira, M.E. & Fairbanks, L.A. eds). Oxford University Press, Oxford, p. 454–565.
636
637 Dahl, J.F., Nadler, R.D. & Collins, D.C. (1991). Monitoring the ovarian cycles of *Pan
638   troglodytes* and *P. paniscus*: a comparative approach. - Am. J. Primatol. 24: 195-209.
639
640 Emery Thompson, M. (2005) Reproductive endocrinology of wild female chimpanzees (*Pan
641   troglodytes schweinfurthii*): Methodological considerations and the role of hormones in sex
642   and conception. – Am. J. of Primat. 67: 137-158.
643
644 Emery Thompson, M., Kahlenberg, S.M., Gilby, I.C. & Wrangham, R.W. (2007a). Core area
645   quality is associated with variance in reproductive success in chimpanzees at Kanyawara,
646   Kibale National Park. – Anim. Behav. 73: 501-512.
647
648 Emery Thompson, M., Jones, J.H., Pusey, A.E., Brewer-Marsden, S., Goodall, J., Marsden, D.,
649   Matsuzawa, T., Nishida, T., Reynolds, V., Sugiyama, Y. & Wrangham, R.W. (2007b). Aging
650   and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. –
651   Curr. Bio. 17: 2150-2156.
652
653 Emery Thompson, M. & Wrangham, RW. (2008). Diet and reproductive function in wild female
654   chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. – Am. J. of
655   Phys.Anthro. 135: 171-181.
656
657 Emery Thompson, M. & Wrangham, R.W. (2006). Comparison of sex differences in
658   gregariousness in fission-fusion species: reducing bias by standardizing for party size. - In:
659   Primates of Western Uganda (Newton-Fisher, N.E., Notman, H., Reynolds, V., Paterson, J.,
660   eds). Springer, New York, p. 209-226.
661
662 Emery Thompson, M., Muller, M., Wrangham, R, Lwanga, J. & Potts, K. (2009). Urinary C-
663   peptide tracks seasonal and individual variation in energy balance in wild chimpanzees. –
664   Hormon. & Behav. 55: tba.

665

666 Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating
667   systems. – Science 197: 215-223.
668

669 Fedigan, L.M. & Jack, K. (2004). The demographic and reproductive context of male
670   replacements in *Cebus capucinus*: How, when and why do male white-faced capuchins
671   take over groups? - Behav. 141: 755-775.
672

673 Ginsberg, J.R. & Young, T.P. (1992). Measuring association between individuals or groups in
674   behavioural studies. – Anim. Behav. 44: 377-379.
675

676 Goodall, J. (1986). The chimpanzees of Gombe: Patterns of behavior. – Belknap Press,
677   Cambridge.
678

679 Hashimoto, C., Suzuki, S., Takenoshita, Y., Yamagiwa, J., Basabose, A.K., Furuichi, T. (2003).
680   How fruit abundance affects the chimpanzee party size: a comparison between four study
681   sites. - Primates 44: 77-81.
682

683 Isabirye-Basuta, G. (1988). Food competition among individuals in a free-ranging chimpanzee
684   community in Kibale Forest, Uganda. – Behav. 105: 135-147.
685

686 Isabirye-Basuta, G. (1989). Feeding ecology of chimpanzees in the Kibale Forest, Uganda. – In:
687   Understanding chimpanzees (Heltne, P.N. & Marquardt, L., eds). Harvard University Press,
688   Cambridge: p. 116-127.
689

690 Jack, K. & Fedigan, L.M. (2004a). Male dispersal patterns in white-faced capuchins (*Cebus
691   capucinus*) Part 1: Patterns and causes of natal emigration. - Anim. Behav. 67(4):761-769.
692

693 Jack K and Fedigan LM. 2004b. Male dispersal patterns in white-faced capuchins, *Cebus
694   capucinus* Part 2: Patterns and causes of secondary dispersal. - Anim. Behav. 67(4):771-782.
695

696 Jolly, A., Gustafson, H., Oliver, W.L.R. & O'Connor, S. M. (1982).*Propithecus verreauxi*
697   population and ranging at Berenty, Madagascar, 1975 and 1980.- Folia primatol. 39: 124–
698   144.
699

700 Kahlenberg, S.M., Emery Thompson, M., Wrangham, R.W. (2008a). Female competition over
701   core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. – Int. J.
702   Primatol. 29: 931-947.
703

704 Kahlenberg, S.M., Emery Thompson, M., Muller, M.N. & Wrangham, R.W. (2008b).
705   Immigration costs for female chimpanzees and male protection as an immigrant
706   counterstrategy to intrasexual aggression. – Anim. Behav. 76: 1497-1509.
707

708 Lunenfeld, F., Kraiem, Z., Eshkol, A. & Werner-Zodrow, I. (1978). The ovary learns to ovulate.
709   - J. Biosocial Sci. Supp. 5: 43-62.
710

711 Lurz, P.W.W., Garson, P.J. & Wauters, L.A. (1997). Effects of temporal and spatial variation in
712   habitat quality on red squirrel dispersal behavior. Anim. Behav. 54: 427-435.
713

714 Melnick, D. & Pearl, M. (1987). Cercopithecines in multimale groups: Genetic diversity and
715   population structure. - In: Primate Societies. (Smuts, B.B., Cheney, D.L. , Seyfarth, R.M.,
716   Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago, Chicago, p. 121-134.
717
718 Moore, J. (1984). Female transfer in primates. - Int. J. Primatol. 5: 537–589.
719
720 Moore, J. & Ali, R. (1984). Are dispersal and inbreeding avoidance related? - Anim. Behav. 32:
721   94-112.
722
723 Muller, M.N. & Lipson, S.F. (2003). Diurnal patterns of urinary steroid excretion in wild
724   chimpanzees. – Am. J. Primatol. 60:161-166.
725
726 Muller, M.N. & Wrangham, R.W. (2004a). Dominance, aggression and testosterone in wild
727   chimpanzees: a test of the 'challenge hypotheses'. – Anim. Behav. 67:113-123.
728
729 Muller, M.N. & Wrangham, R.W. (2004b). Dominance, cortisol and stress in wild chimpanzees
730   (*Pan troglodytes schweinfurthii*). – Behav. Ecol. and Sociobiol. 55: 332-340.
731
732 Muller, M.N., Kahlenberg, S.K., Emery Thompson, M. & Wrangham, R.W. (2007). Male
733   coercion and the costs of promiscuous mating in chimpanzees. – Proc. Roy. Soc. B: Bio. Sci.
734   274: 1009-1014.
735
736 Murray, C.M., Eberly, L.E. & Pusey, A.E. (2006). Foraging strategies as a function of season
737   and rank among wild female chimpanzees. (*Pan troglodytes*). – Behav. Ecol. 17:1020-1028.
738
739 Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. – In: The
740   great apes (Hamburg, D.A. & McCown, E.R., eds). Benjamin/Cummings, Menlo Park.
741
742 Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt,
743   K.D., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J.C., Nakamura, M., Norikoshi,
744   K., Sakamaki, T., Turner, L., Uehara, S. & Zamma, K. (2003). Demography, female life
745   history, and reproductive profiles among the chimpanzees of Mahale. – Am. J. Primatol. 59:
746   99-121.
747
748 Nunes, S., Duniec, T.R., Schweppe, S.A & Holekamp, K.E. (1999). Energetic and endocrine
749   mediation of natal dispersal behavior in Belding's ground squirrels. Hormon. & Behav. 335:
750   113-124.

751 Perry, S. & Manson, J.H. (1995). A comparison of the mating behavior of adolescent and adult
752   female rhesus macaques (*Macaca mulatta*). – Primates. 36: 27-39.

753 Pusey, A.E. (1978). The physical and social development. of wild adolescent chimpanzees (*Pan
754   troglodytes schweinfurthii*). Ph.D., Stanford University.
755
756 Pusey, A.E. (1979). Inter-community transfer of chimpanzees in Gombe National Park. - In: The
757   great apes. (Hamburg, D. & McCown, E., eds). Benjamin/Cummings, Menlo Park, p. 465-
758   479.
759
760 Pusey, A.E. (1980). Inbreeding avoidance in chimpanzees. –Anim. Behav. 28: 543–552.
761

762 Pusey, A.E. & Packer, C. (1987). Dispersal and philopatry. - In: Primate Societies, (Smuts, B.B.,
763   Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of
764   Chicago Press, Chicago, p. 250–266.
765

766 Pusey, A.E. (1990). Behavioural changes at adolescence in chimpanzees. – Behav. 115: 203-246.
767

768 Pusey, A.E., Williams, J. & Goodall, J. (1997). The influence of dominance rank on the
769   reproductive success of female chimpanzees. - Science 277: 828-831.
770

771 Pusey A., Murray C., Wallauer W., Wilson M., Wroblewski E. & Goodall J. (2008). Severe
772   aggression among female chimpanzees at Gombe National Park, Tanzania. –Int. J. Primatol.
773   29: 949-973.
774

775 Rasmussen, K.L.R. (1983). Age-related variation in interactions of yellow baboons. - In: Primate
776   social relationships: An integrated approach. (Hinde, R.A., ed.). Blackwell, Oxford, p. 47–52.
777

778 Resko, J.A., Goy, R.W., Robinson, J.A. & Norman, R.L. (1982). The pubescent rhesus monkey –
779   Some characteristics of the menstrual cycle. – Biol. Reprod. 27:354-361.
780

781 Shimizu, K., Douke, C., Fujita, S., Matsuzawa, T., Tomonaga, M., Tanaka, M., Matsubayashi, K.
782   & Hayashi, M. (2003). Urinary steroids, FSH and CG measurements for monitoring the
783   ovarian cycle and pregnancy in the chimpanzee. – J. Med. Primatol. 32: 15-22.
784

785 Shepher, J. (1983). Incest: A biosocial view. - Academic, New York.
786

787 Silk, J.B., Alberts, S.C; & Altmann, J. (2003). Social bonds of female baboons enhance infant
788   survival. – Science 302:1331–1334.
789

790 Silverin, B. (1997). The stress response and autumn dispersal behaviour in willow tits. - Anim.
791   Behav. 53: 451–459.
792

793 Smuts, B.B. (1993). Male aggression and sexual coercion of females in nonhuman primates and
794   other mammals: evidence and theoretical implications. – Advan. Stud. Behav. 22: 1-63.
795

796 Strier, K.B. (1997). Mate preferences in wild muriqui monkeys (*Brachyteles arachnoides*):
797   reproductive and social correlates. - Folia Primatol. 68: 120-133.
798

799 Stumpf, R.M. (2007). Chimpanzees and bonobos: Diversity within and between species. - In:
800   Primates in Perspective (Campbell, C., Fuentes, A., MacKinnon, K., Panger, M. & Bearder,
801   S., eds). Oxford University Press, Oxford, p. 321-344.
802

803 Townsend, S.W., Slocombe, K.E., Emery Thompson, M. & Zuberbühler, K. (2007). Female-led
804   infanticide in wild chimpanzees. – Curr. Biol. 17: 365-366.
805

806 Trivers, R.L. (1972). Parental investment and sexual selection. – In: Sexual selection and the
807   descent of man. (Campbell B., ed.). Aldine-Atherton, Chicago, p. 136-79.
808

809 Wallis J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe
810   National Park. – J. Reprod. Fertil. 109: 297-307.
811

812 Watts, DP. (2007). Effects of male group size, parity, and cycle stage on female chimpanzee
813   copulation rates at Ngogo, Kibale National Park, Uganda. - Primates 48: 222-231.
814
815 Whitehead, H. & Dufault, S. (1999). Techniques for analyzing vertebrate social structure using
816   identified individuals: review and recommendations. – Adv. Stud. Behav. 28: 33-74.
817
818 Widholm, O. & Kantero, R. (1971). A statistical analysis of the menstrual patterns of 8,000
819   Finnish girls and their mothers. - Acta Obstet Gynecol Scand. 14:1-36.
820
821 Williams, J.M., Pusey, A.E., Carlis, J.V., Farm, B.P. & Goodall, J. (2002). Female competition
822   and male territorial behaviour influence female chimpanzees' ranging patterns. – Anim.
823   Behav. 63: 347-360.
824
825 Williams, J.M., Oehlert, G.W., Carlis, J.V. & Pusey, A.E. (2004). Why do male chimpanzees
826   defend a group range? – Anim. Behav. 68: 523-532.
827
828 Wrangham, R. (1980). An ecological model of female-bonded primate groups. – Behav. 75:
829   262–300.
830
831 Wrangham, R.W. (1987). Evolution of social structure. – In: Primate societies. (Smuts, B.B.,
832   Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of
833   Chicago Press, Chicago, p. 282–296.
834
835 Wrangham, R,W,, Conklin, N,L,, Chapman, C.A., Hunt, K.D. (1991). The significance of fibrous
836   foods for Kibale Forest chimpanzees. – Phil. Trans. Roy. Soc. Lond. B. 334: 171-178.
837
838 Wrangham, R.W., Chapman, C.A., Clark, A.P. & Isabirye-Basuta, G. (1996). Social ecology of
839   Kanyawara chimpanzees; Implications for understanding the costs of great ape groups. - In:
840   Great ape societies. (McGrew, W., Marchant, L.F. & Nishida, T., eds). Cambridge University
841   Press, Cambridge, p. 45−57.
842
843 Wrangham, R.W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble
844   competition hypothesis. - In: Male primates (Kappeler, P., ed.). Cambridge University Press,
845   Cambridge, p. 248-258.
846
847 Wrangham, R.W. (2002). The cost of sexual attraction: Is there a trade-off in female *Pan* between sex
848   appeal and received coercion? -In: Behavioural diversity in chimpanzees and bonobos (Boesch,
849   C., Hohmann, G. & Marchant, L., eds). Cambridge University Press, Cambridge, p. 204-215.
850
851 Zehr, J.L., Van Meter, P.E. and Wallen, K. (2004). Factors regulating the timing of puberty onset
852   in female rhesus monkeys (*Macaca mulatta*): Role of prenatal androgens, social rank, and
853   adolescent body weight, *Biol. Reprod.* 72, 1087–1094.

854**Table 1. Kanyawara Chimpanzee Subjects**

855

Female	Date of Birth[1]	Immigration Status	Age of Emigration	Association data	Copulation data	Cortisol data (N days)
WR	7/2/1982	Emigrated 1997	14	Y	N	0
NE	7/2/1983	Emigrated 1999	16	Y	Y	12
BW[2]	7/2/1985	Emigrated 1997	12	Y	N	0
BR	7/2/1989	Emigrated 2000	11	Y	Y	7
AS	11/2/1990	Emigrated 2002	12	Y	Y	44
GA	1/15/1991	Emigrated 2001	10	Y	N	8
JK	11/15/1992	Emigrated 2007	15	Y	N	58
OK	11/15/1994	Emigrated 2007	13	Y	Y	198
LR	5/15/1989	Natal, bred in Kanyawara	n/a	Y	Y	143
FN	5/30/1989	Juvenile (died 1998)	*	Y	n/a	1
LS	11/10/1996	Juvenile	**	Y	n/a	67
BU	12/28/1997	Juvenile	**	Y	n/a	17
OT	2/13/1998	Juvenile	**	Y	n/a	106
NP	2/9/2000	Juvenile	**	Y	n/a	67
TG	7/2/1980	Immigrated 1993	n/a	Y	N	n/a
UM	7/2/1981	Immigrated 1995	n/a	Y	Y	n/a
AL	7/2/1982	Immigrated 1994	n/a	Y	Y	n/a
NL	7/2/1982	Immigrated 1997	n/a	Y	Y	n/a
WA	7/2/1991	Immigrated 2004	n/a	Y	Y	n/a
HH	7/2/1992	Immigrated 2005	n/a	Y	Y	n/a
QT	7/2/1992	Immigrated 2005	n/a	Y	Y	n/a
WL	7/2/1992	Immigrated 2005	n/a	Y	Y	n/a

856[1] Dates of birth given as July 2 are estimated to the nearest year. Others are known to within one
857month.

858[2] It is unclear whether BW was a natal female or a previous immigrant who subsequently left the
859community.

860* Died prior to emigration; ** had not emigrated by time of publication; Y =yes; N=No; n/a=
861data type was not applicable.

862

863

864

865

866

867

868

870**Figure Legends**

871

872Figure 1. Copulation rates (mean ± standard error) of adolescent females relative to their first
873maximal sexual swelling in the community.

874

875Figure 2. Sexual partner variety in immigrant and natal females: (a) proportion of adult males in
876the community mated in relation to total copulations, (b) variance in copulation frequency across
877partners. Natal females are designated by solid circles with a solid black logarithmic trend line;
878immigrant females are designated by open squares and a dotted trend line.

879

880Figure 3.Association indices between natal adolescent female chimpanzees and their mothers
881(N=5) decreased abruptly in the year prior to transfer, and corresponded to increased association
882indices with natal adolescent and adult males.

883

884Figure 4. Adolescent female association times with each age/sex class (box: median ±
885interquartile range; whiskers:range). Adolescent females (N=20) associated significantly more
886with adolescent and adult males and least with juvenile males and adult females. Mothers and
887maternal siblings are excluded from analyses.

888

889Figure 5a. Association indices (mean ± standard error) for early (N=4), late (N=4) and non-
890transferring (N=1) adolescent females. (a) Early transferring females demonstrated lower
891association indices across the majority of age/sex classes, particularly with adolescent and adult
892males, than late or non-transferring females, though these differences were not significant. (b).
893Association indices for early vs late/non–transferring females with their mothers. Data
894standardized by age.

895

896Figure 6. Longitudinal patterns of urinary cortisol in adolescent chimpanzees females (mean ±
897standard error of individuals) aligned (a) relative to gynecological age [first maximal swelling =
8980], and (b) relative to time of emigration. Y-axis is set to ± 1 standard deviation of cortisol
899concentrations in all female samples of this population.

900

901Figure 7. Relationship between fruit consumption and emigration timing. (a) Latency to
902emigration (Y-axis) correlated negatively with fruit consumption in the 3-month window up to
903and including the month of first maximal swelling. (b) Among females with delayed emigration
904(>2 months after maturity), timing of emigration was associated with increasing fruit
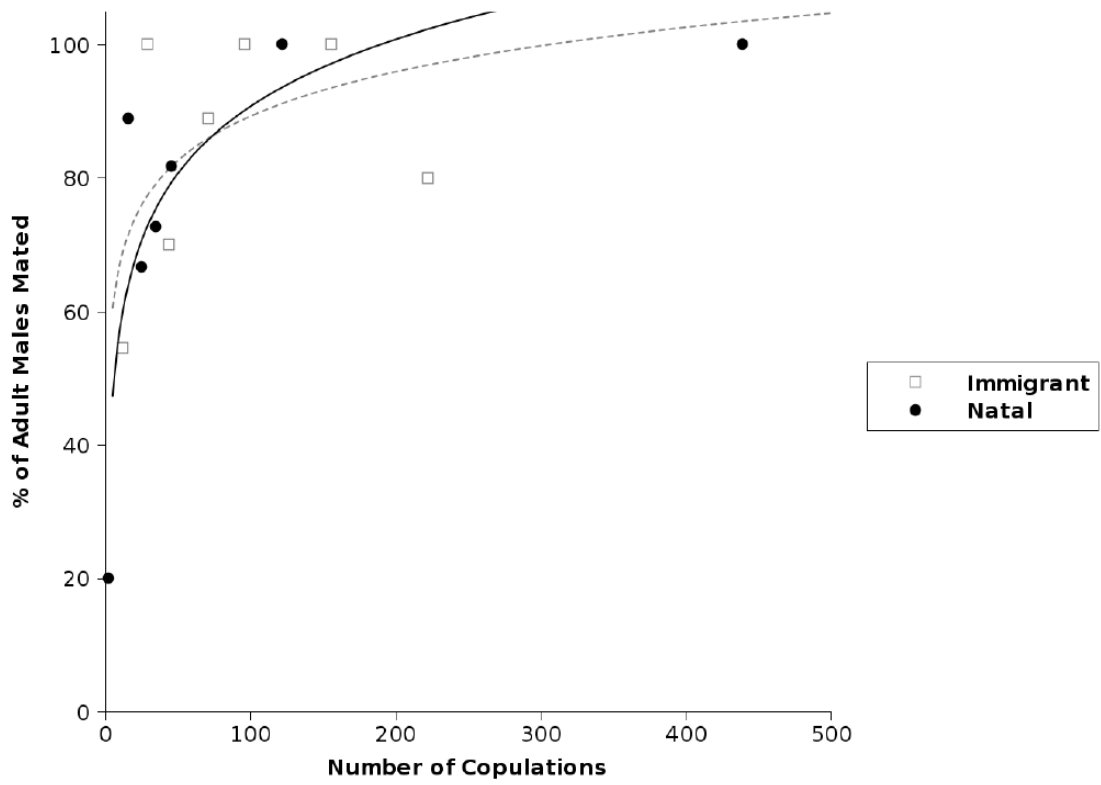905consumption. Dotted lines indicate mean fruit consumption at Kanyawara from 1994-2007.
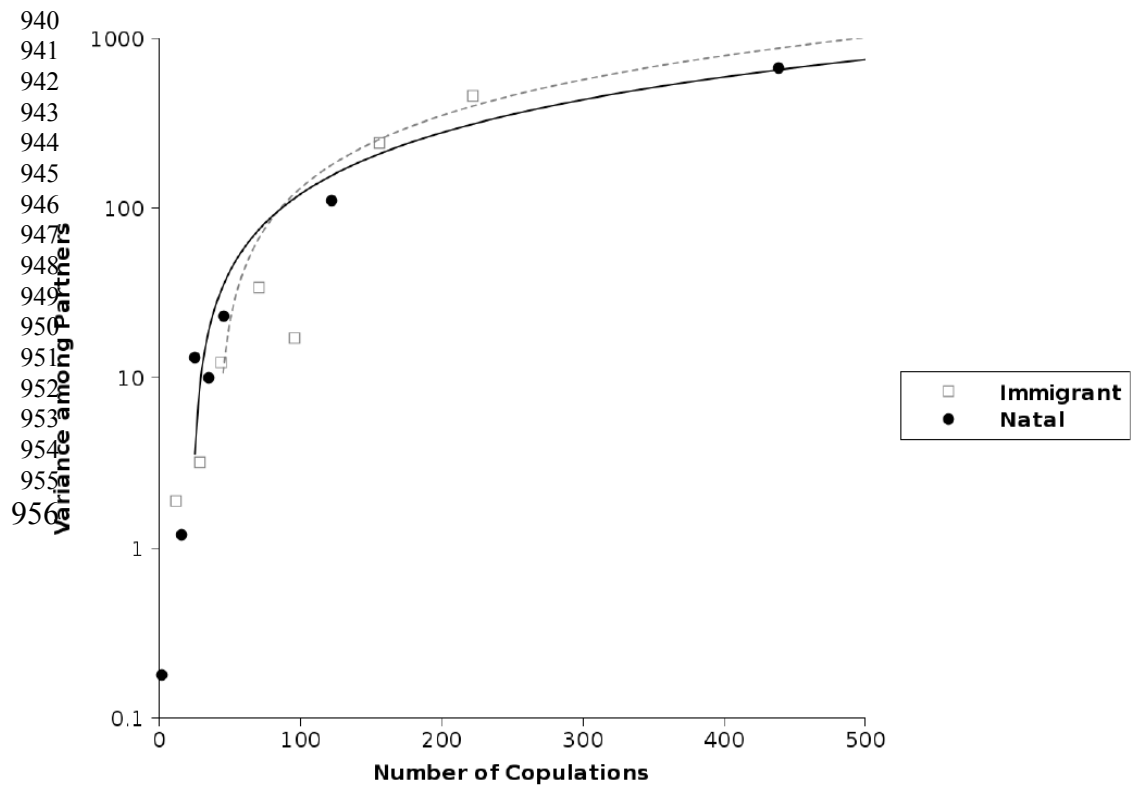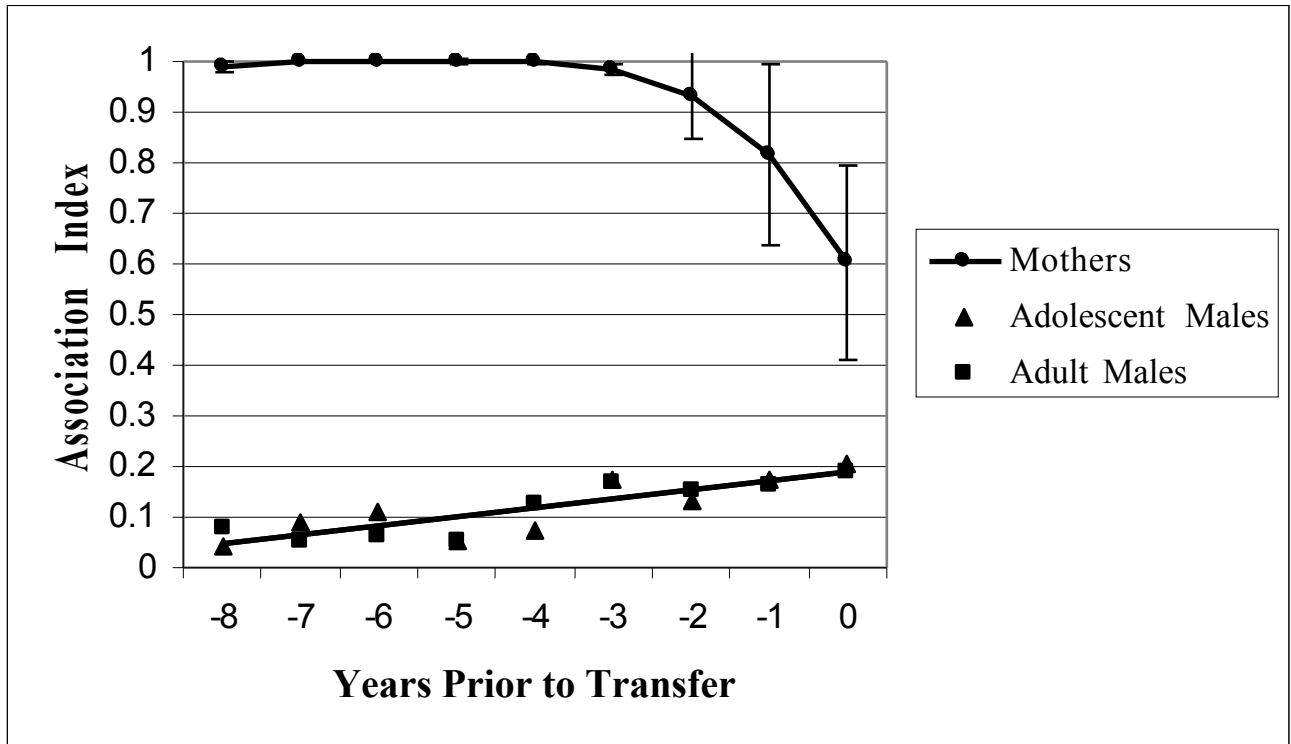
906
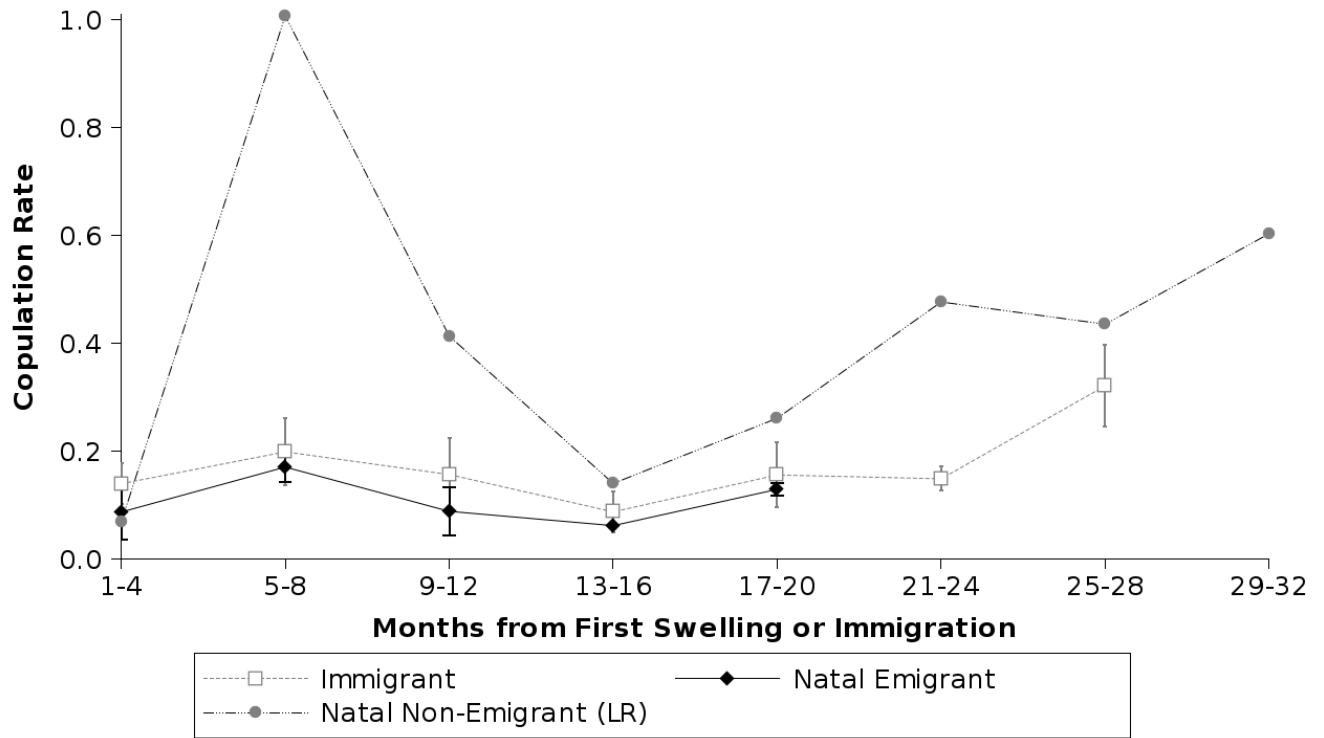
Figure 1

908 **Figure 2.**
909
910 **(a)**

912
913
914
915
916
917
918
919
920
921
922
923
924
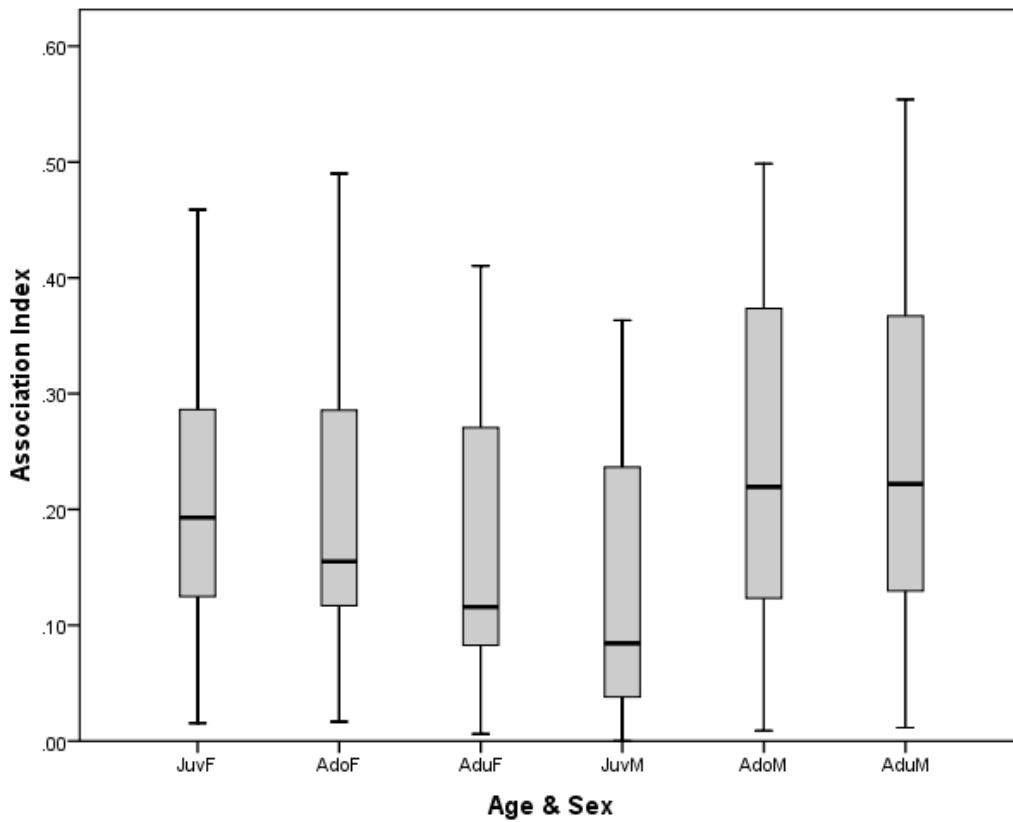925
926
927
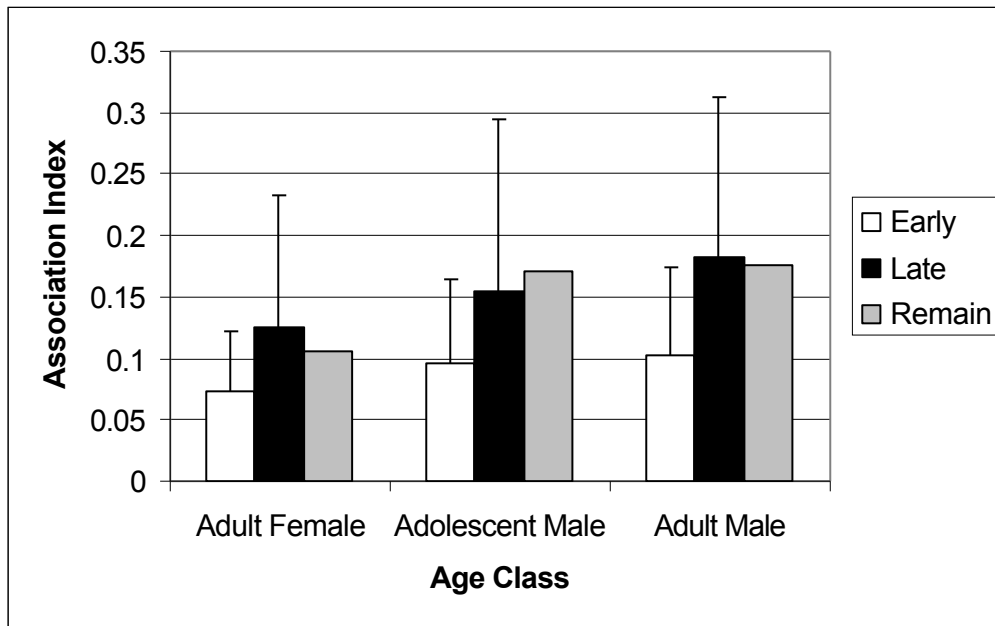928
929
930
931
932
933
934
935
936
937
938 **(b)**
939

940
941
942
943
944
945
946
947
948
949
950
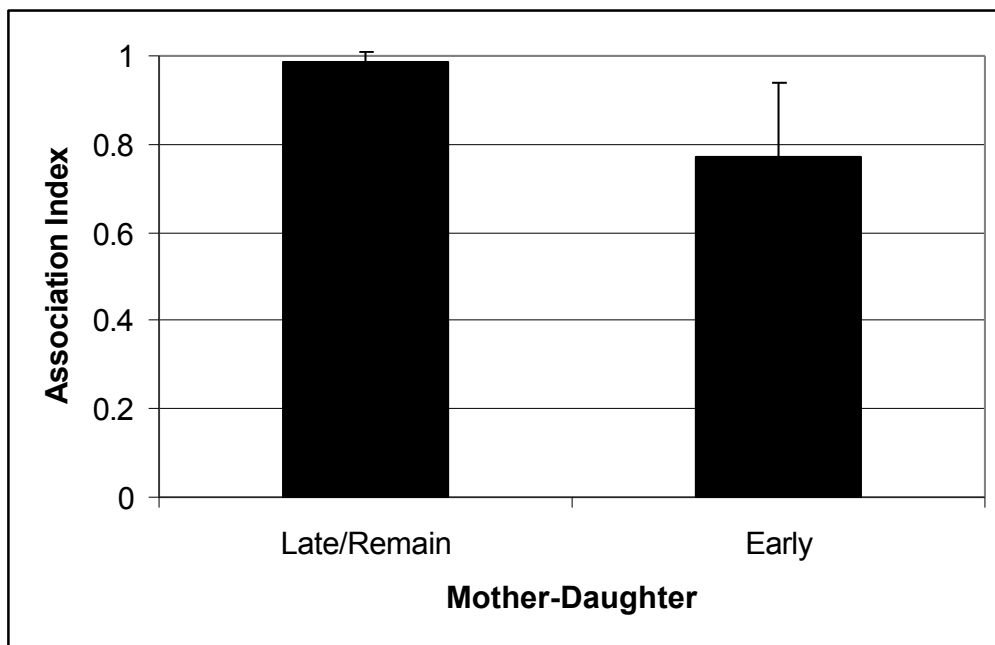951
952
953
954
955
956

957 **Figure 3.**

958
959 **Figure 4.**

960
961

962
963

Figure 5a
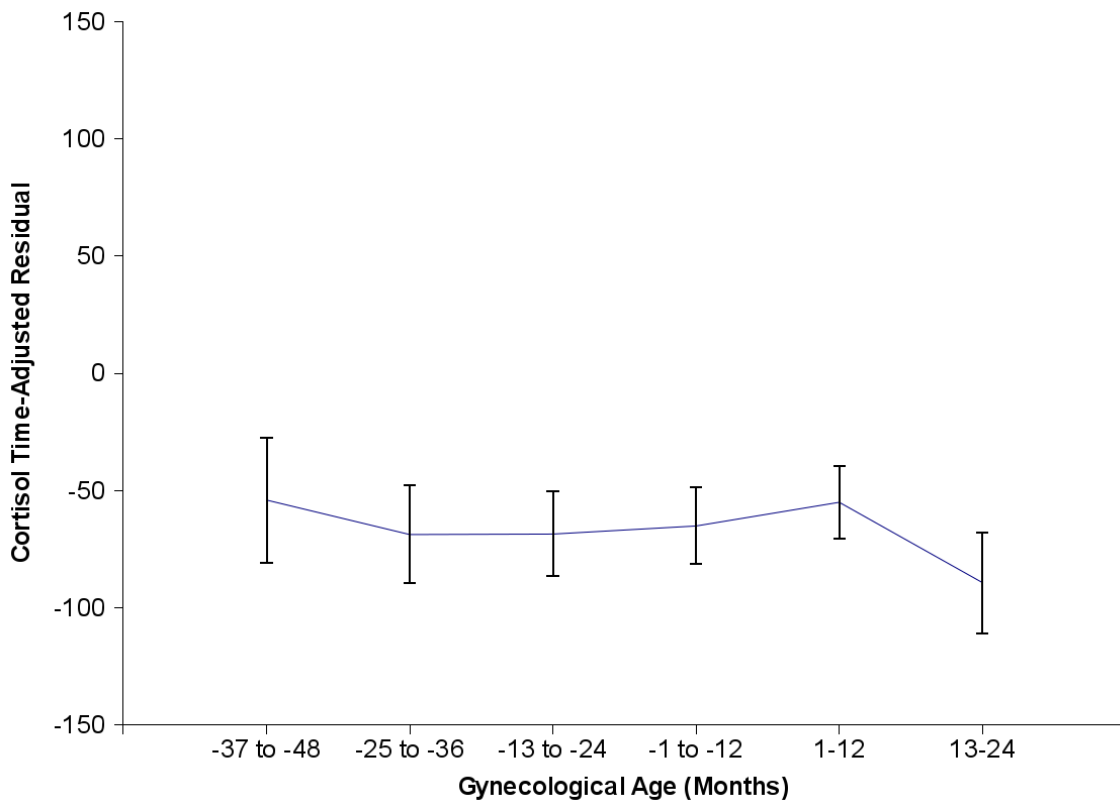
Figure 5b.

Figure 6.
(a)

972
973
974
975
976
977
978
979
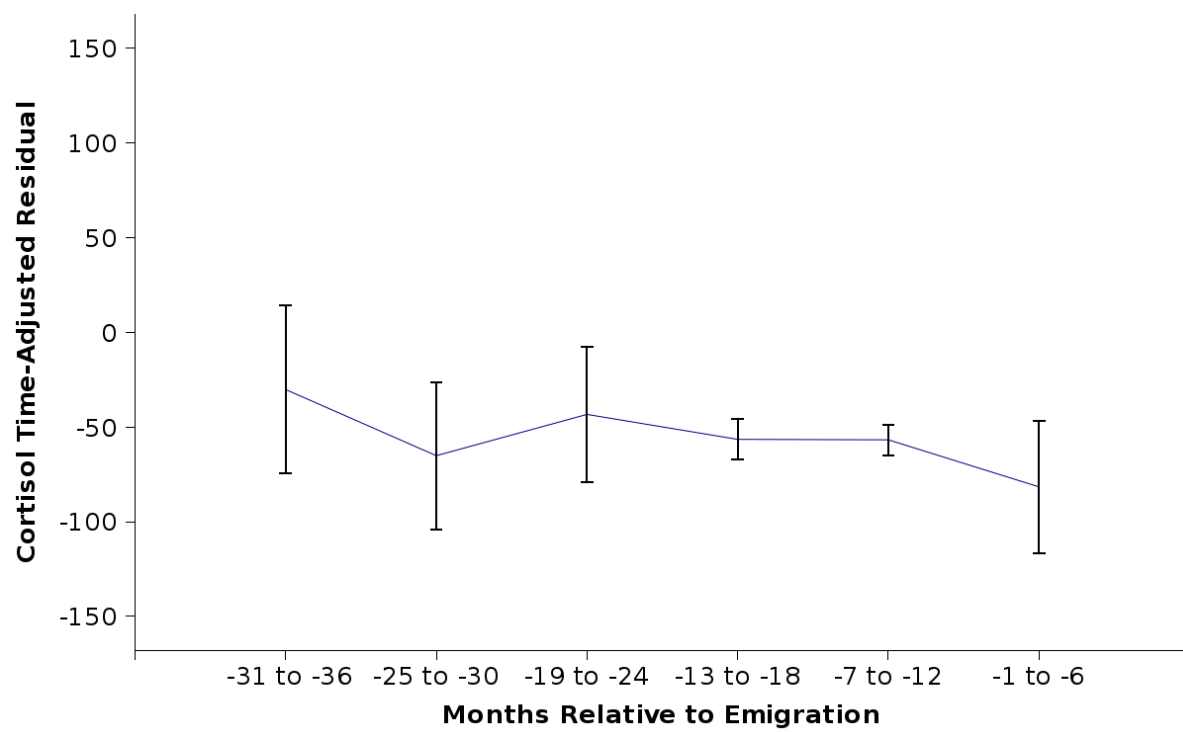980
981
982
983
984
985
986
987
988
989
990
991
992
993
994
995
996
997
998

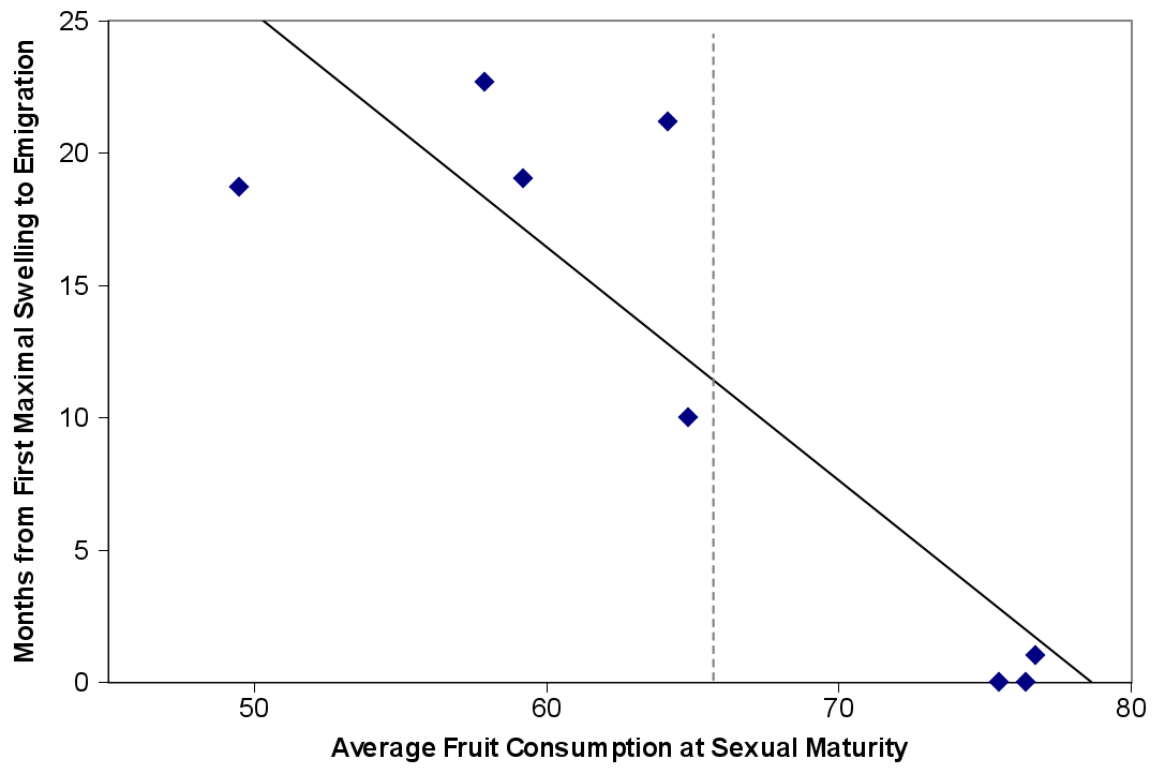**Figure 7a.**