The context of female dispersal in Kanyawara chimpanzees

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10**Title: The Context of Female Dispersal in Kanyawara Chimpanzees**

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13**Short Title: Female Dispersal in Chimpanzees**

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32Summary

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

57INTRODUCTION

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.

- (2) Dispersal is correlated with the risk of inbreeding, such that females avoid mating with related males in their natal community. Females were reported to avoid mating with close kin (Pusey, 1980; Wrangham, pers. comm.), but the proximate role of inbreeding avoidance in influencing individual dispersal decisions is unknown.
- (3) Dispersal is predicted by social relationships, such that (a) shifts in association patterns precede emigration, and/or (b) association patterns differ between females who emigrate early, late or not at all. In adolescent Gombe chimpanzees, female sexual maturation is associated with a shift from exclusive association with the mother to association with adolescent and adult males that precedes emigration (Pusey, 1990; Goodall, 1986). The quality of female social relationships (e.g. aggression from adult females) might also influence the relative costs and benefits of dispersal.
- (4) Dispersal is correlated with stress, as measured by urinary cortisol levels, such that (a) females emigrate when experiencing greater stress, and/or (b) adolescents with generally higher stress levels emigrate earlier. Increased stress hormones could be associated with any of the previously-described predictors and might mediate detachment from the natal community, as in willow tits (*Parus montanus*: Silverin, 1997) or winged insects (e.g. *Cardiocondyla obscurior*: Cremer & Heinze, 2003).
- (5) Dispersal corresponds with changes in resource availability in the natal habitat. There are two opposing predictions. Females may emigrate only during periods of high fruit consumption when they have sufficient energy reserves to face a period of resource uncertainty (e.g., screech-owls (*Otus kennicottii*), Belthoff & Dufty, 1998). Alternatively, low dietary quality may lead young females to seek improved foraging opportunities in other habitats (e.g. Lurz, et al., 1997; Nunes et al., 1999).

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 km² 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 $\pm$ 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(≥ 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 $\pm$
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 ($SE = 0.5$, $N_u = 7$, $N_c = 0$, 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 ($SE = 0.9$, $N_u = 7$, $N_c = 0$, 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 ($SE = 3.3$, $N_u = 5$, $N_c = 3$, 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 ($z =$

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 ($54.9\% \pm 0.1$ 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 $N_1 = 5$, $N_N = 5$, $p = 0.49$).

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

357Association 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, $N=20$; $X^2=60.3$, $df=5$,
365 $p<0.001$). 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

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, $z = -0.937$, $NT = 15$, $N_0 = 154$, $p = 0.35$). 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, $r_s = -0.75$, $N = 8$, $p = 0.031$). 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, $r_s = 0.829$, $N = 6$ 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

424DISCUSSION

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.

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

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

well as policing aggression directed at immigrants by resident females (Townsend et al., 2007; Kahlenberg et al., 2008b). In support of the passport hypothesis, females were generally cycling at the time of emigration. However, contrary to the hypothesis, at least two females left Kanyawara without having shown signs of swelling. It is possible that these females left immediately upon experiencing their first swelling, or had one by the time they contacted a new community, but this seems unlikely given that one had never shown even partial tumescence, and the other had shown only slight signs of swelling the day before her disappearance. Additionally, copulation rates and latency to first copulations do not support a strong attraction of Kanyawara males to immigrants. This is particularly unexpected because, assuming that immigrants followed similar growth trajectories as Kanyawara females, immigrant females should have been both older and more reproductively mature than natal adolescents, having experienced nearly 1 year of cycling on average before dispersal. These patterns at Kanyawara support a general link between sexual attractivity and dispersal, but it appears that swellings are not a prerequisite for acceptance into a new group, and males do not show strong mating interest in new cycling immigrants.

469

We found little support for the hypothesis that inbreeding avoidance was a proximate determinant of female dispersal. First, prior to leaving the community natal females reduced their association time with their mothers and increased association time with potential sexual partners (see also Pusey 1990). Second, most Kanyawara females mated within the community before emigrating, some for well over 1 year. Third, natal females usually copulated with adult male community members on their first maximal swelling cycle. Fourth, there was only a small difference between the copulation rates of immigrants and future emigrants, and the female who did not emigrate maintained the highest copulation rates. Fifth, the female who did not emigrate had two known maternal brothers in the community and was observed mating with them. Sixth,

479 females initiated the majority of their copulations, and natal females were no less likely to do so
480 than immigrants. Finally, given the high level of reproductive skew in chimpanzees (Constable
481 et al. 2001; Boesch et al., 2006) many of the males that natal females mate with are likely to
482 share paternally related genes. However, there was no significant difference in the number of, or
483 variance among, sexual partners for natal and immigrant females, suggesting that natal females
484 did not display strong aversion to certain partners or were ineffective at exerting these
485 preferences. This is consistent with other primate studies, including of Gombe chimpanzees, in
486 which natal adolescent females are highly proceptive toward adult males (Rasmussen, 1983;
487 Goodall, 1986; Perry & Manson, 1995), with males often showing relatively little interest in
488 return (Pusey, 1978; Wrangham, 2000; Muller et al., 2007). These findings do not imply that
489 inbreeding avoidance has been unimportant in the evolution of sex-biased dispersal in this
490 species. Rather, they suggest that proximate dispersal decisions are not predicated on a female's
491 relative risk of mating with potential relatives.

492
493 We found two patterns that suggest plausible proximate models for variation in dispersal
494 behavior. First, dispersal was associated with dietary quality, such that females experiencing
495 conditions of high fruit consumption emigrated soon after menarche and others emigrated during
496 periods of increasing fruit consumption. This may explain disparities in emigration timing, if
497 females wait until they have sufficient energy reserves to afford the high costs of dispersal,
498 which could include long travel distances, lack of knowledge about new foraging areas,
499 increased feeding competition, and aggression by resident females in the new community, and
500 time spent in more than one community. However, it is possible that the emigration patterns we
501 observed were directly related not to dietary quality, but to a correlated variable such as the
502 changing size or composition of social parties (Chapman et al., 1994; Hashimoto et al., 2003;
503 Emery 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

554 This and other hypotheses arise from and highlight two significant questions. First, why do
555 females cycle and mate in their natal community prior to emigration? Because ovulatory function
556 takes time to develop in anthropoids (Lunenfield et al., 1978; Resko et al., 1982; Zehr et al.,
557 2004), an extended period of subfecundity permits females to cycle several times prior to
558 emigration with little inbreeding risk, providing opportunity to obtain social, sexual and foraging
559 knowledge in a context when they are among familiar individuals but semi-independent of their
560 mothers (Shepher, 1983; Strier, 1997). A second question is why females experience such a long
561 delay between dispersal and reproduction. This may simply reflect the long duration of
562 adolescent subfecundity, though our data and those from Mahale (Nishida et al., 2003) suggest
563 that immigrants have delays in reproduction relative to natal females. Similarly, even females
564 who 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
566 stresses of the dispersal process. Reproductive delay would also diminish infanticide risk
567 through increasing the probability of paternity within the new community's male cohort by
568 establishing a mating history and forging social bonds.

569

570 While there has been considerable theoretical inquiry regarding the evolution of sex-biased
571 dispersal, and models have been proposed to explain the advantages of male versus female
572 dispersal in various species, few primate studies have examined the proximate mechanisms
573 influencing dispersal. For chimpanzees, in which dispersal is almost exclusively by females,
574 dispersal is not strictly predicted by the physiological events of puberty nor by stress in the natal
575 community. Our data from Kanyawara suggests that individual variation in sociality, temporal
576 variation in energy availability, and perhaps subtle variation in developmental trajectories, play
577 roles in female decisions to seek new communities.

578

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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

8561 Dates of birth given as July 2 are estimated to the nearest year. Others are known to within one
857month.

8582 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.

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870Figure Legends

871

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

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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.

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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.

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884Figure 4. Adolescent female association times with each age/sex class (box: median $\pm$
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 $\pm$ 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 $\pm$
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 $\pm$ 1 standard deviation of cortisol
899concentrations in all female samples of this population.

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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.

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907Figure 1

908**Figure 2.**

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910**(a)**

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957Figure 3.

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959Figure 4.

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964 **Figure 5a**

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966 **Figure 5b.**

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968**Figure 6.**
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970(a)

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1000Figure 7a.

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