The context of female dispersal in Kanyawara chimpanzees

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Title: The Context of Female Dispersal in Kanyawara Chimpanzees

Short Title: Female Dispersal in Chimpanzees

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Summary

In most social mammals, members of either one sex or both leave their natal group at sexual maturity. In catarrhine primates, male emigration is the predominant pattern. Female philopatry facilitates cooperation among kin, and female reproductive success is influenced by these relationships. Chimpanzees (Pan troglodytes) are unusual in that dispersal is almost exclusively by females. While plausible ultimate hypotheses can explain this dispersal pattern, the proximate causes of female dispersal are unknown and warrant examination due to variation in dispersal behavior and the associated high costs of immigration. In this study, we examine the behavioral and hormonal context of female dispersal in chimpanzees of Kibale National Park, Uganda, in order to understand variation in dispersal patterns and gain insight into functional explanations. Using over 10 years of behavioral, endocrinological, and demographic records, we examined the significance of 5 potential predictors of the timing of dispersal: (1) maturational state; (2) association patterns; (3) mating patterns; (4) physiological stress; and (5) feeding ecology. Female dispersal was not strictly predicted by chronological or gynecological age, and dispersal did not correlate with shifts in glucocorticoid levels. We found no evidence that females avoided mating in their natal group, even with known relatives, suggesting that inbreeding avoidance is not a sufficient proximate explanation for dispersal in chimpanzees. Instead, variation in social development and the availability of energy for dispersal were implicated and necessitate more intensive examination along with subtler variation in maturational trajectories.

Keywords: dispersal, adolescence, stress, inbreeding, energetics
In most social mammals, members of one or both sexes leave their natal group at sexual maturity to avoid inbreeding (Pusey & Packer, 1987). For catarrhine primates, female philopatry and male dispersal are the predominant pattern (Pusey & Packer, 1987; Melnick & Pearl, 1987; Wrangham, 1987). Philopatric females enjoy a variety of benefits from long-term cooperation with kin, including enhanced access to resources and reduced infant mortality (Wrangham, 1980; Silk et al., 2003).

Chimpanzees (Pan troglodytes) are unusual among Old World Primates in that dispersal is almost exclusively by females (Goodall, 1986). Ultimate factors affecting this unusual pattern of dispersal include the importance of male affiliation and cooperation for defense of the community feeding range, the size of which affects female reproductive rates (Williams et al., 2004). However, the proximate causes of female dispersal in chimpanzees are unclear, both because the timing of dispersal varies, and because some females never leave their natal communities (e.g., Goodall, 1986; reviewed in Stumpf, 2007).

While males in various species may benefit by seeking groups with improved mating opportunities (Jack & Fedigan, 2004a,b; Fedigan & Jack, 2004), females receive few obvious benefits and face high costs of dispersal. Access to high quality food resources is critical for female reproductive success (Bradbury & Vehrencamp, 1977; Emlen & Oring, 1977; Trivers, 1972; for chimpanzees: Emery Thompson et al., 2007a; Emery Thompson & Wrangham, 2008). Food acquisition in chimpanzees is challenging because resources are patchily distributed in both time and space. Moreover, relative social status is a key predictor of resource access (Murray et al., 2006; Kahlenberg et al., 2008a). Consequently, a key cost of emigration is the loss of...
affiliative natal relationships and knowledge of food resource locations (Smuts, 1993; Alberts & Altmann, 1995a,b; Williams et al., 2002). In other primates, adolescents can be forcibly expelled from the natal group (e.g. Crockett & Pope, 1993), increasing the relative cost of philopatry (Pusey & Packer, 1987; Moore, 1984). However, this does not occur in chimpanzees. Instead, females leave without being coerced, enter a new group at the bottom of the social hierarchy, receive considerable aggression from resident females, and must fight to establish a residential core area: these are costly activities associated with elevations in stress hormone production (Townsend et al., 2007; Kahlenberg et al., 2008a,b; Pusey et al., 2008). One major benefit of dispersal is avoidance of the negative effects on reproductive fitness caused by breeding with close kin (Moore & Ali, 1984). However, while inbreeding avoidance provides a plausible ultimate explanation for sex-biased dispersal in primates generally, and male cooperative territoriality presents a reasonable explanation for male philopatry in chimpanzees specifically, the proximate behavioral and biological mechanisms underlying female dispersal in chimpanzees are poorly understood.

The purpose of this study was to document behavioral and physiological changes in adolescent female chimpanzees so as to test potential proximate mechanisms for the timing of their dispersal to a new community. We tested 5 non-mutually exclusive hypotheses:

1. Dispersal is consistently related to sexual maturation, such that (a) female emigration corresponds to the onset of sexual cycling, or (b) females who reach sexual maturity earlier emigrate at an earlier age. Female emigration is frequently coincident with sexual receptivity in chimpanzees (Nishida, 1979; Pusey, 1979, 1980; Boesch and Boesch-Achermann, 2000) as in some other primates (Jolly et al., 1982; Moore, 1984), but it is not known how the timing of female chimpanzee dispersal is related to the onset of sexual maturity.
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.

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.

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).

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).
METHODS

Study site
We studied wild chimpanzees (*P. t. schweinfurthii*) of the Kanyawara community in Kibale National Park, western Uganda (0°34′N and 30°21′E). The Kanyawara chimpanzees range over approximately 32 km$^2$ of medium altitude habitat, comprising areas of moist evergreen primary forest, logged regenerating forest, grassland, swamp, and agriculture (Chapman & Wrangham, 1993). R. Wrangham established the Kibale Chimpanzee Project in 1987, following earlier work by Isabirye-Basuta (1988, 1989), and research has been continuous since then (Wrangham et al., 1996). Individual chimpanzees are well habituated to human observers, and have never been provisioned.

Study subjects and age estimation
The Kanyawara chimpanzee community currently consists of 10 adult males, 16 adult females and 23 immature males and females. We extracted relevant data on reproductive parameters and dispersal events from long-term behavioral records collected over a fourteen year period between 1994 and 2007. During this period, we studied 22 nulliparous females, including 8 immigrants aged at least 10 years and 14 natal Kanyawara females aged at least 5 years (Table I). Of the natal females studied, 10 had birthdates known to within one month. Four natal females born in the 1980s and 8 immigrant females have birthdate estimates based on observer estimations of their body size at first sighting relative to individuals of known age.

Females who were last observed in healthy condition between the ages of about 9-15 are assumed in these data to have emigrated, or attempted emigration. However, we do not have records from neighboring chimpanzee communities to confirm dispersal, nor do we often recover
the remains of dead chimpanzees. We present these data with the caveat that some assumed
emigrants may have died in the natal community. In one case (JK), dispersal was confirmed by
her revisiting the Kanyawara community briefly, several years after her initial departure.

Reproductive data

We used Kaplan-Meier survival analyses to calculate time interval data, such as the age of
emigration or the interval between first maximal sexual swelling (defined as the first
unambiguous observation of tumescence of both vaginal and perianal tissue without occurrence
of wrinkling (Dahl et al., 1991) and emigration. This method increases statistical power by
including censored datapoints (e.g., females who had experienced a swelling but had not yet
emigrated). We provide the mean and standard error from the Kaplan-Meier analysis, the
number of uncensored (Nu) and censored (Nc) datapoints, and the range of uncensored events.

For age of emigration, we performed each analysis for the set of females with known dates of
birth (to within one month) and again with the larger sample that includes females with estimated
birthdates.

Two sources of bias might impact behavioral observations of new community members.
Unhabituated individuals may be wary of human observers or of group members, and it may take
time for the field staff to reliably identify individual immigrants. We do not believe these biases
have affected our findings. First, observers note identifying characteristics of unidentified
females and record their presence and all behaviors involving them as they would with a known
individual. Once a female is established and named, which typically takes less than one month,
we are able to update records of her presence from her initial sighting onwards. For example,
when we note the interval between immigration and first copulation, we have verified this
against copulation records of 'unidentified' females. Thus, we believe that our behavioral records
for each immigrant female are complete from the time of her first being seen in Kanyawara parties. Second, observation rates of the immigrant females during their first six months in the community were higher than those of natal adolescents overall (mean ± S.E.: natal: 345 ± 165 hrs/month, immigrants 447 ± 114 hr/month) and during estrus, specifically (natal: 125 ± 67 hrs/month, immigrants: 232 ± 78 hrs/month). In fact, our ability to observe immigrants is enhanced by their tendency to affiliate with large groups of males as a counterstrategy to the aggression they receive from resident females (Kahlenberg et al., 2008b).

Association Patterns

Association data were recorded as a part of continuous data collection. KCP field staff conduct daily observations, following one chimpanzee party, when possible, from nest to nest, recording the identities of all individuals in the party every 15 minutes. We analyzed the association patterns of target females with a) juvenile males and females (5-8 years of age) excluding the target's dependent siblings, b) adolescent females (9-15 years of age), c) adolescent males (9-14 years of age), d) adult females (>15 years of age, excluding each target's mother), e) adult males (≥15 years) and f) each target's mother.

Association rates were determined by obtaining a simple ratio association index for each adolescent female with each individual in the community (Cairns & Schwager, 1987; Ginsberg & Young, 1992). The simple index is calculated for each dyad as \( \frac{X}{X+Y_{AB}+Y_{A}+Y_{B}} \), where \( X \) is the number of scans during which A and B were observed together, \( Y_{AB} \) is the number of scans during which A and B were both observed in separate groups, \( Y_{A} \) is the number of scans during which only A was observed, and \( Y_{B} \) is the number of scans during which only B was observed. This ratio was calculated for each year (age 9-15 or until emigration or parturition) of the target female. These ratios for each female were then averaged by age class (all juvenile males and
females, adolescent males and females, adult males and females and mothers) for each year and then a final association index for each age class was obtained for each female by averaging across all years she was aged 9-15 (or until emigration or parturition). Individuals (from any age class) present for fewer than 25 observations per year were excluded from analyses.

We used the simple index (Cairns & Schwager, 1987) because, relative to other association indices (e.g. half-weight or twice-weight indices (Cairns & Schwager, 1987), the simple index is statistically unbiased (Ginsberg & Young, 1992) and is more appropriate in situations where associations are determined by membership in the same group (Whitehead & Dufault, 1999).

Nevertheless, we did compare the patterns in our results from the simple index to two other association indices, the half-weight index and another dyadic association index, calculated as the number of scans an individual was present with the female of interest divided by the total number of scans the female was present. All three indices supported the same association patterns.

**Sexual behavior**

The KCP field staff recorded all attempted and completed copulations during daily observations. We analyzed the copulation patterns of adolescent females with adult males (≥ 15 years of age) as a rate per hour of observation while in maximal swelling. Rates were calculated for each four month period beginning with the first observation of maximal sexual swelling in the community and ending with emigration, conception, or last available data (Dec. 2006); periods with fewer than 20 estrous observation hours were excluded. This left us with copulation data for 12 females: 7 immigrants and 5 natal females.
Whenever possible, the initiator of the copulation was noted. The male was considered to have initiated the copulation if he approached the female for intromission or performed a clear solicitation behavior (e.g., penis-flicking, branch-shaking) to the female. Female-initiation was defined by female approach without solicitation by the male, leading to copulation. In 65% of the adolescent female copulations there was one clear initiator, and 10 females had at least 10 such copulations. For each of these females, we calculated the number of copulations she initiated as a proportion of all her copulations with a single clear initiator.

Finally, we looked at mating partner diversity by calculating the percentage of potential adult male partners with which each female mated and the variance in copulation frequency across all males, each plotted against the total number of copulations observed for the female.

**Glucocorticoid data**

Routine collection of chimpanzee urine was initiated at Kanyawara in November 1997, and has continued through the present day. Detailed information on collection and storage methods is presented by Muller & Wrangham (2004a, b) and Emery Thompson (2005). Samples were analyzed for cortisol using enzyme-immunoassay reagents provided by C.J. Munro at the University of California at Davis and protocols previously described for use with chimpanzees (Muller et al., 2007; Kahlenberg et al., 2008b). Interassay coefficients of variation for this assay were 11.5 and 14.4% (N = 94) for high and low pools, respectively. Intra-assay coefficients of variation for 12 replicates were 5.4 and 9.5% for high and low pools, respectively. To correct for variation in urine concentration, cortisol values were indexed to creatinine, which was quantified colorimetrically. Samples with creatinine measurements below 0.05 mg/ml were excluded from all analyses.
Cortisol shows a distinct circadian pattern in chimpanzee urine, with levels peaking in the early morning, and subsequently declining throughout the day (Muller & Lipson, 2003). To correct for this, we first calculated a regression equation of hour of the day versus cortisol (in ng/mg-Cr) for 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 circadian pattern was consistent across age groups. Following previous analyses (Kahlenberg et al., 2008a), we calculated cortisol values as the time-adjusted residual of this average regression line. These values provide an intuitive gauge of relative cortisol elevation: the “expected” cortisol residual of any female sample is zero (mean of 3064 female samples = 4.2), with positive or negative values representing titers greater or less than expected. To place cortisol fluctuations of adolescents in perspective with other females, we present plots with a y-axis that represents ± standard deviation (168, N = 3064) of all Kanyawara female cortisol titers assayed to date. To further correct for uneven sampling, we calculated a single daily average when multiple samples had been taken and then derived a monthly average for each individual for use in the final analyses.

We calculated age patterns of cortisol for natal females only, as our research group has previously documented significant elevations in the cortisol levels of new immigrants (Kahlenberg et al., 2008b). We analyzed samples from females beginning at the age of 5 and ending with death, dispersal, or conception. One female (JK) received a severe wire snare injury at age 13 which was accompanied by elevated cortisol levels. For this female, we examined only samples collected prior to the injury. We calculated the female mean at each age (by year) and, excluding age classes represented by a single subject, computed a linear regression to test for trends. We considered both chronological age (time since birth) and gynecological age (time
since first maximal sexual swelling). For emigrants, we conducted a similar analysis using 6-month intervals during the three years prior to emigration.

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282**Diet**

283We quantified changes in energy availability in Kanyawara by examining variation in the monthly consumption of fruit (see Emery Thompson & Wrangham, 2008). During daily observations, feeding behavior of the chimpanzee party was recorded every 15 minutes. We calculated the percentage of observations in which chimpanzees ate fruit as a proportion of all observations in which chimpanzees fed. At Kanyawara, this measure of dietary quality is significantly correlated with fruit availability estimates obtained from phenological transects (Wrangham et al., 1991, 1996; Sherry, 2002) and with biomarkers of chimpanzee energetic condition (C-peptide of insulin, Emery Thompson et al., 2009).

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292**RESULTS**

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294**Timing of Dispersal**

295Females of known age who emigrated from Kanyawara did so at an average age of 12.6 years (SE = 1.0, Nu = 4, Nc = 5, range: 10.4 – 15.1). Adding natal females of estimated age gives us a slightly higher figure of 12.9 years (SE = 0.7, Nu = 8, Nc = 5, range: 10.4 – 15.7). This is consistent with the average age estimates of 13 years that we assigned to 8 new immigrants. The interval between sexual maturity, as defined by the first maximal swelling, and emigration was highly variable. Two of eight emigrating females were not observed with a maximal swelling prior to their disappearance. The interval to emigration for the six females who experienced prior maximal swellings was an average of 15.5 months (SE = 3.4, range = 1.2 - 22.7). One natal female remained in Kanyawara to breed. Because first swellings typically preceded emigration,
Mating Behavior and Inbreeding Risk

Five of seven natal females copulated with an adult male during their first maximal swelling cycle. Natal females were first seen to copulate with adult males an average of 0.7 months after their first sexual swelling ($SE = 0.5$, $Nu = 7$, $Nc = 0$, range: $0 – 3.7$), whereas immigrants first copulated with an adult Kanyawara male an average of 2 months after their first swelling in the community ($SE = 0.9$, $Nu = 7$, $Nc = 0$, range: $0 – 4.8$). The only natal female to give birth (LR) did so 37.0 months after her first sexual swelling. Immigrants experienced an average delay of 26.9 months before birth ($SE = 3.3$, $Nu = 5$, $Nc = 3$, range: $10.6 – 36.8$; n.b., gestation length in chimpanzees is approximately 230 days, Wallis 1997; Shimizu et al. 2003).

There was a significant positive relationship between gynecological age (defined here as the time since first observed maximal sexual swelling in the Kanyawara community), and copulation rate with adult males ($R^2 = 0.51$, $df = 7$, $p = 0.047$, Figure 1). There was no significant difference between natal females and immigrants in their rates of copulation, matched for gynecological age group (Wilcoxon matched-pairs test, $z = -1.69$, $N_1 = N_2 = 7$ age groups, $p = 0.09$). One natal female (LR) maintained consistently higher copulation rates than all other adolescent females. This individual was the sole natal female who did not emigrate from the community. Comparing immigrant females with only the natal females who later emigrated, we did find a significant difference, with immigrant females copulating at moderately higher rates in each age group ($z =$
However, even these differences were small when considered against the high copulation rates generally achieved by chimpanzees (Watts, 2007; Wrangham, 2002): during the first 2 years of sexual cycling in the community, immigrants had an average rate of 0.15 copulations/hour, while natal emigrants had copulation rates of 0.11 copulations/hour.

We expected that natal females would be unlikely to solicit matings with adult males if they were motivated to avoid inbreeding. However, for those copulations with one clear initiator, just over half were initiated by the female (54.9% ± 0.1 S.E., 10 females). Females varied greatly in the percentage of copulations they initiated (7-77%, N = 10), but there was no significant difference between natal females and immigrant females in this measure (Mann-Whitney U test, z = -0.801, N₁ = 5, N₂ = 5, p = 0.49).

Similarly, we expected that if natal females were avoiding inbreeding, they would differ from immigrants in the distribution of their matings among male partners, avoiding known kin or males of the same age cohort. We calculated regressions of number of matings (log-transformed) versus the percentage of available partners mated. The slopes of these regressions did not differ for natal and immigrant females (t = 0.711, df = 10, p = 0.49, Figure 2a).

Similarly, when we compared the number of matings with the variance in copulation frequency across partners, we found no significant difference between slopes for natal and immigrant females (t = -1.718, df = 10, p = 0.12, Figure 2b). Thus, there was no evidence that natal females consistently avoided mating with certain partners.

There was only one female who had known adult male kin, two elder brothers, in the group. This was LR, the female who remained to breed in her natal community. She mated with her brothers...
at rates of 0.06 and 0.05 copulations/hour of maximal swelling, which is similar to the median rate of 0.05 copulations/hour (range 0.03-0.13) for other adult partners.

**Association Patterns**

As expected, adolescence was associated with decreased association of a female with her mother and increased association with adolescent and adult males. For the 5 natal females with living mothers and association data through the time of emigration, there tended to be a marked decrease in maternal association in the 1-2 years prior to dispersal (Figure 3).

There were substantial differences in association indices of adolescent females with various age-sex classes (Figure 4). Adolescent females associated most often with adolescent and adult males and least often with juvenile males and adult females (Friedman, N=20; $X^2=60.3$, df=5, $p<0.001$). Association patterns of natal females and immigrants were similarly distributed across age-sex classes (Friedman, $N_I=12$; $X^2=37.0$, df=5, $p<0.001$; $N_f=8$; $X^2=27.9$, df=5, $p<0.001$), except that immigrant females associated significantly more frequently with adolescent and adult males than did natal females (Mann-Whitney U, $N_N=12$, $N_I=8$ $Z=-2.006$, $p=0.047$; $N_N=12$, $N_I=8$, $Z=-2.237$, $p=0.025$).

There was a non-significant trend for females who dispersed at a younger-than-average age (N=4) to have lower association indices across age-sex classes, particularly with adolescent and adult males, than late dispersing females (N=4) (Figure 5a). In line with this tendency, LR (who stayed to breed in her natal group) had association indices similar to females who emigrated late. Early emigrating females also demonstrated a trend toward lower association indices with their mothers than females who emigrated late or not at all (data standardized by age; Mann Whitney U test $z=-1.879$ $p=0.06$; Figure 5b).
**Physiological Stress**

Urinary cortisol levels were remarkably stable during adolescence. There was a marginally significant trend toward decreasing cortisol with age between 5 and 12 years ($R^2 = 0.51$, df = 7 age groups, N= 3-9 females/year, p = 0.05). However, this actually represented a very low range of variation (time-adjusted residuals: -25.7 to -58.6), equivalent to 0.2 standard deviations of the mean for all Kanyawara females. Because females matured on different reproductive schedules, an analysis based on chronological age might mask underlying variation with regard to gynecological age. However, cortisol profiles aligned relative to gynecological age also showed little variation ($R^2 = 0.30$, df = 5, N = 4-5 females per year, p = 0.26. Figure 6a). In general, the time-adjusted cortisol residuals for natal adolescent females were negative, indicating that stress hormone levels were lower than average for immigrant and adult Kanyawara females (c.f., Kahlenberg et al., 2008b).

To examine whether social stress could act as a trigger for dispersal, we examined cortisol titers of females aligned relative to the time of emigration. We found no indication that either an abrupt or gradual increase in cortisol preceded emigration ($R^2 = 0.55$, df = 5, N = 2-5 females per year, p = 0.09; Figure 6b). Within the constraints of our small sample size, we also asked whether females with relatively high cortisol during adolescence were more likely to disperse early. There was no evidence for this. In fact, females who emigrated before the average age had slightly lower cortisol titers on average (-95.0 ± 18.2 SE, N = 3) than females who emigrated late or not at all (-51.2 ± 23.1, N = 4). Similarly, females who emigrated soon after sexual cycling had slightly lower cortisol levels (-85.8 ± 27.2, N = 2) than females who had not emigrated within a year of cycling (-63.6 ± 21.8, N = 5).

**Ecological Variation**
We predicted that changes in energy availability might affect the timing of dispersal if females choose times of positive energy balance to undertake the potential costs of emigration or, alternatively, if resource pressure leads them to look elsewhere for new foraging grounds. Among transfer events with available dietary data, there was a tendency for both emigrations (6/8) and immigrations (5/7) to occur in months of above average fruit consumption by Kanyawara chimpanzees (% fruit composition in diet, reference data from Emery Thompson & Wrangham, 2008). However, fruit consumption in these months was not significantly different from the set of months in which no transfer event occurred (69.3% ± 4.0 SE vs. 64.8% ± 1.4, Mann-Whitney U, z = -0.937, NT = 15, N0 = 154, p = 0.35). Nevertheless, two additional findings support the hypothesis that energetic condition impacts emigration timing. First, there was a strong negative correlation between latency to emigrate (in months) and average fruit consumption in the three month period leading up to and including the month of first maximal sexual swelling (Figure 7a, rs = -0.75, N = 8, p = 0.031). Three females that matured during periods of above average fruit consumption emigrated within 2 months. Second, among the remaining five females with delayed dispersal, emigration coincided with periods when fruit consumption in Kanyawara increased significantly (Figure 7b, rs = 0.829, N = 6 months, p = 0.042). Because our dietary measures do not incorporate individual differences in feeding behavior, a larger sample and more sensitive measures of individual energetic condition are needed to confirm this finding.

DISCUSSION

At Kanyawara, we observed considerable variation in female dispersal behavior. This is consistent with observations at other chimpanzee study sites (Pusey, 1979; Nishida et al., 2003). We 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.

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

We found two patterns that suggest plausible proximate models for variation in dispersal behavior. First, dispersal was associated with dietary quality, such that females experiencing conditions of high fruit consumption emigrated soon after menarche and others emigrated during periods of increasing fruit consumption. This may explain disparities in emigration timing, if females wait until they have sufficient energy reserves to afford the high costs of dispersal, which could include long travel distances, lack of knowledge about new foraging areas, increased feeding competition, and aggression by resident females in the new community, and time spent in more than one community. However, it is possible that the emigration patterns we observed were directly related not to dietary quality, but to a correlated variable such as the changing size or composition of social parties (Chapman et al., 1994; Hashimoto et al., 2003; 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
nearby communities (Pusey et al., 1997). This hypothesis is difficult to examine without detailed knowledge of neighboring chimpanzee groups and habitats. Furthermore, the reproductive advantage of dispersing vs. remaining may differ across sites, given that studies in different chimpanzee communities suggest that the age at first birth may be comparatively delayed (Boesch & Boesch-Achermann, 2000) or advanced (Nishida et al., 2003) in natal vs. dispersing individuals, and that in some populations a high proportion of natal females fails to disperse (Pusey et al. 1997). Nonetheless, the importance of this decision may explain observations like those at Gombe, where nulliparous females sometimes spend time visiting one or more neighboring communities before returning temporarily or permanently to their natal group (Pusey, 1979). Without access to habituated neighboring communities, we cannot be certain how frequently this happens at Kanyawara, but unusual periods of absence by adolescent females make it likely. Our sample of adolescent females, however, is overwhelmingly comprised of the daughters of females in the high-quality foraging ranges, thus we cannot easily explain disparities in dispersal behaviors by social status alone. It is interesting that LR, who did not emigrate, was the daughter of the alpha female, was high-ranking compared to other nulliparous females, and inherited her mother's high-quality foraging range (Kahlenberg et al., 2008a).

Relative morphological (skeletal) maturation could also be an important variable influencing dispersal timing, if it influences female competitive success and access to high-quality feeding areas in the new community. Alternately, as adolescent subfecundity in chimpanzees is lengthy and highly variable (1.2 – 4.1 years at Mahale, Nishida et al., 2003; 0.7 – 4.9 years at Gombe, Wallis, 1997), differences in the development of ovulatory function among females may better predict timing of dispersal. An appropriate test of this hypothesis would incorporate measures of ovarian hormone production in both emigrants and immigrants.
This and other hypotheses arise from and highlight two significant questions. First, why do females cycle and mate in their natal community prior to emigration? Because ovulatory function takes time to develop in anthropoids (Lunenfield et al., 1978; Resko et al., 1982; Zehr et al., 2004), an extended period of subfecundity permits females to cycle several times prior to emigration with little inbreeding risk, providing opportunity to obtain social, sexual and foraging knowledge in a context when they are among familiar individuals but semi-independent of their mothers (Shepherd, 1983; Strier, 1997). A second question is why females experience such a long delay between dispersal and reproduction. This may simply reflect the long duration of adolescent subfecundity, though our data and those from Mahale (Nishida et al., 2003) suggest that immigrants have delays in reproduction relative to natal females. Similarly, even females who changed foraging areas within the community at Gombe had disrupted reproduction (Williams et al., 2002). Such a delay could occur as a consequence of social and energetic stresses of the dispersal process. Reproductive delay would also diminish infanticide risk through increasing the probably of paternity within the new community's male cohort by establishing a mating history and forging social bonds.

While there has been considerable theoretical inquiry regarding the evolution of sex-biased dispersal, and models have been proposed to explain the advantages of male versus female dispersal in various species, few primate studies have examined the proximate mechanisms influencing dispersal. For chimpanzees, in which dispersal is almost exclusively by females, dispersal is not strictly predicted by the physiological events of puberty nor by stress in the natal community. Our data from Kanyawara suggests that individual variation in sociality, temporal variation in energy availability, and perhaps subtle variation in developmental trajectories, play roles in female decisions to seek new communities.
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<table>
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<th>Female</th>
<th>Date of Birth&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Immigration Status</th>
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<th>Association data</th>
<th>Copulation data</th>
<th>Cortisol data (N days)</th>
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<sup>1</sup> Dates of birth given as July 2 are estimated to the nearest year. Others are known to within one month.

<sup>2</sup> It is unclear whether BW was a natal female or a previous immigrant who subsequently left the community.

<sup>*</sup> Died prior to emigration; ** had not emigrated by time of publication; Y =yes; N=No; n/a=data type was not applicable.
Figure Legends

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

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

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

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

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

Figure 6. Longitudinal patterns of urinary cortisol in adolescent chimpanzees females (mean ± standard error of individuals) aligned (a) relative to gynecological age [first maximal swelling = 0], and (b) relative to time of emigration. Y-axis is set to ± 1 standard deviation of cortisol concentrations in all female samples of this population.

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

[Graph showing copulation rate over months from first swelling or immigration for different groups: Immigrant, Natal Emigrant, Natal Non-Emigrant (LR).]
Figure 2.

(a)
Figure 3.

Figure 4.
Figure 6.
(a)
Figure 7a.