Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park

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Female East African chimpanzees, *Pan troglodytes schweinfurthii*, tend to range apart from each other in dispersed core areas, and they have dominance interactions with each other so rarely that it is difficult for observers to assess a dominance hierarchy. Nevertheless female chimpanzees can have high variance in fitness. Here, we test the hypothesis that female chimpanzee fitness variance is associated with variation in the foraging quality of their ranges. We studied range usage of 21 wild adult female chimpanzees within the Kanyawara community, Kibale National Park, Uganda. Core areas of individuals remained stable over a 9-year period and varied in their density of preferred foods. Females in neighbourhoods containing more preferred foods had elevated ovarian hormone production, shorter birth intervals and higher infant survival. Our results thus suggest that superior access to food may have enabled some community females to reproduce more successfully than others. Although dominance interactions are less frequent among females than among males of this species, we propose that the intensity of selection on intrasexual competition may be similar between the sexes. We discuss potential applications to other fission–fusion species.

Keywords: chimpanzee; endocrinology; habitat ecology; intrasexual competition; *Pan troglodytes schweinfurthii*; ranging; reproductive ecology; reproductive success

Sexual selection theory has traditionally pointed to high variance in male reproductive success as a strong selective pressure for sexual ornamentation and competitive ability, whereas covariates of female reproductive success are less emphasized (Trivers 1972). For female mammals, socioecological models focus on the central role of resource access as a limiter to reproductive success (Gadgil & Bossert 1970; Schneider & Wade 2000) and a major determinant of social relationships (Wrangham 1980; Sterck et al. 1997; Koenig 2002).


Among chimpanzees, *Pan troglodytes*, by contrast, females show high fitness variance without consistent female aggression, philopatry or alliances. Dominant females in one community at Gombe reproduced more quickly and had higher infant survival and faster maturing daughters than did subordinates (Pusey et al. 1997). Yet, female dominance interactions were rare, as they tend to be in this species compared with both conspecific males and females in other primates (de Waal 1982; Goodall 1986; Nishida 1989). Neither aggressive interactions nor ritualized displays occur often enough to have a meaningful impact on the social or feeding behaviour of females, and, even in the 22 years covered by the Gombe study, some female dyads were never observed to have a single dominance interaction. Females typically transfer out of their natal communities at adolescence and rarely form alliances in their new communities. The observed variance in reproductive success, therefore, does not conform to expected patterns of social relationships, and has not been explained.
Although female chimpanzees rarely fight over food, there is evidence that energy availability influences their reproductive rates, as expected. First, across populations, variation in interbirth intervals is correlated with differences in habitat quality (Knott 2001; Emery Thompson 2005a). Second, timing of conception in chimpanzees coincides with the availability of high-quality foods, which show considerable temporal variability (Sherry 2002; Emery Thompson 2005a). Food items also show considerable spatial heterogeneity within chimpanzee home ranges, suggesting an additional dimension to variation in energy availability. Chimpanzees live in a fission–fusion social system in which a group of bonded males aggressively defends a home range, including the food resources and females within it (Nishida 1968; Sugiyama 1968; Wrangham 1975; Williams et al. 2004). While community members maintain long-term affiliative ties, members of the community are typically dispersed across the home range in smaller, temporary associations (parties) that may vary in size in accordance with the presence and number of cycling females with sexual swellings, and the social affinities of community members (Wrangham et al. 1996; Matsumoto-Oda 1999; Pepper et al. 1999; Emery Thompson & Wrangham 2006). At Gombe, mothers share a community range but each female tends to maintain her own small ‘core area’ where she spends the majority of her time (Wrangham 1979). Core areas cluster into localized ‘neighbourhoods’ within the community range (Williams et al. 2002). Therefore, it is possible that individual females increase their fitness by accessing higher-quality areas of the community range, rather than by competing directly at individual food sites (Pusey et al. 1997; Williams et al. 2002).

To test this hypothesis, we collected data on patterns of range use, ovarian hormone levels and reproductive parameters of females in the Kanyawara community of chimpanzees in Kibale National Park, Uganda. We predicted that (1) as in Gombe, Kanyawara females would maintain differentiated core areas, and (2) females in higher-quality core areas would have a reproductive advantage, as indexed by ovarian function, birth rate and offspring survival.

METHODS

Study Site and Population

The Kanyawara home range spans approximately 32 km² (Wilson 2001), consisting of approximately 60% moist deciduous forest, with small areas of swamp, grassland and colonizing forest (Chapman & Wrangham 1993). The community consisted of 47 chimpanzees at the beginning of the current study in 1996, and numbered 38 individuals (including 10 adult males and 19 subadult and adult females) at the end of the study in May 2004.

Data Collection

Chimpanzees were searched for daily or were followed as they left their sleeping sites. Behaviour was typically recorded simultaneously by three to four observers (i.e. 2–3 Kibale Chimpanzee Project field staff and 1–2 graduate students). Field staff collected group scan samples every 15 min, recording: (1) location of chimpanzees on a trail map, (2) party composition, (3) oestrous status of females and (4) food species and part(s) being consumed. This study incorporates results from 82 956 scan samples (20 649 h) collected between January 1996 and May 2004.

Ranging Data Analysis

In this analysis, we were concerned with the concentration of ranging in particular locations within the larger territory. To assess this we recorded the locations of chimpanzees on a 500 × 500-m grid superimposed over the trail system, and calculated the frequency that each chimpanzee was observed in each of 380 grid cells as a percentage of the total scans in which that chimpanzee was observed. Because sexual receptivity probably influences female ranging patterns (e.g. Hasegawa 1990), we only considered nonoestrous observations. To test for site fidelity, we divided the study into two time periods (1996–2000, 2001–2004) in which we included adult individuals and subadults who ranged independently of their mothers and for whom reproductive information was available (Table 1). Several females died in late 2000 or early 2001, so this division represents an important demographic change in the community.

To compare range usage across females, we conducted hierarchical cluster analyses of the grid cell usage data for each individual. This procedure yields a dissimilarity matrix by calculating the difference (squared Euclidean distance) between grid cell usage frequencies for each chimpanzee dyad, and then produces a dendrogram describing their relative relationships (median clustering method) (Romnesburg 2004). Based on this dendrogram, the cluster of the females with the most similar ranging patterns were considered members of a single ‘neighbourhood’, and the range of each other female was categorized in relation to this group by the evaluation of range histograms. Grid locations of males were also included in the cluster analysis for comparison.

To determine the location of each female neighbourhood within the home range, we calculated the mean percentage usage of each grid square by all females within a particular classification based on the cluster analysis (central, northern, or southern). Our observations of chimpanzees were neither randomly nor evenly distributed, so grid cell usage was expressed as a percentage more or less than expected from the distribution of all chimpanzee observations.

Neighbourhood Habitat Quality

The Kanyawara region can be divided into forest sectors based on logging history and general forest type. Skorupa (1988) reported primate habitat quality statistics for Kanyawara according to these forest sectors, including the impact of logging outtake and densities of stems fruit
trees and primates. Where we could conclusively match a forest sector to a chimpanzee neighbourhood, we report these measures of general habitat quality (Table 2).

Kanyawara chimpanzees preferentially consume non-fig fruits when available (Wrangham et al. 1996; Emery Thompson 2005a), and three particularly preferred species (Mimusops bagshawei, Pseudospondias microcarpa, and Uvariopsis congensis) show strong relationships to reproductive timing (Sherry 2002; Emery Thompson 2005a), although they are sporadically available (Wrangham et al. 1996; Emery Thompson 2005a). In any given month, these drupe fruits may constitute 0–83% of the diet (X̄ = 27.5, Emery Thompson, unpublished data). To evaluate the quality of each female neighbourhood, we determined the locations of all episodes of feeding on non-fig fruits by chimpanzees and compared these grid cells to the cells constituting each neighbourhood. We then calculated four measures of non-fig fruit availability and feeding intensity by neighbourhood. First, we calculated the number of observations of non-fig fruit feeding that occurred within each neighbourhood and used a chi-square analysis to evaluate whether this distribution differed from an even distribution across neighbourhoods. This measure may be biased by more intensive observations in certain regions. However, we are confident that chimpanzees would have been observed feeding at least once in each location of their three most preferred fruit species because these fruits tend to occur in localized patches that are exploited for days or weeks at a time. So, we also calculated the proportion of unique feeding locations that were found within each neighbourhood. Third, as a measure of female access to resources in each neighbourhood, we calculated the percentage of preferred fruits, all fruits and fallback foods (piths and leaves) constituting the diets of female parties in each grid cell. Finally, we determined the degree to which the distribution of events of non-fig fruit feeding by chimpanzees predicted the ranging patterns of females in each neighbourhood. We calculated the regression of the percentage of non-fig fruit use occurring within each cell against the mean percentage of observations that females of a particular neighbourhood spent in those cells. Although we generally expected female ranging habits to correlate with feeding opportunities, we also expected that females with the best quality core areas and the best access to resources would have ranges that accorded most closely to the use of preferred foods.

### Urinary Steroid Analysis

Field personnel have collected urine samples opportunistically from all chimpanzees since November 1997. Samples were collected on plastic sheets or pipetted directly from vegetation (Knott 1997) and frozen until analysis at the Primate Reproductive Ecology Laboratory at Harvard University. All samples were analysed for

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**Table 1. Kanyawara chimpanzee subject females and sample sizes**

<table>
<thead>
<tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Nonoestrous scans (ca. h/month)</td>
<td>Grid cells used</td>
<td>Nonoestrous scans (ca. h/month)</td>
</tr>
<tr>
<td>AL</td>
<td>1982</td>
<td>8984 (37)</td>
<td>94</td>
<td>9025 (55)</td>
</tr>
<tr>
<td>AR</td>
<td>1943</td>
<td>6239 (28)</td>
<td>65</td>
<td>4298 (26)</td>
</tr>
<tr>
<td>BL</td>
<td>1960</td>
<td>3342 (14)</td>
<td>53</td>
<td>6745 (46)</td>
</tr>
<tr>
<td>EK</td>
<td>1974</td>
<td>2177 (9)</td>
<td>34</td>
<td>2205 (13)</td>
</tr>
<tr>
<td>FG</td>
<td>1955</td>
<td>6987 (67)</td>
<td>81</td>
<td>n/a</td>
</tr>
<tr>
<td>GO</td>
<td>1957</td>
<td>2123 (9)</td>
<td>42</td>
<td>41 (5)</td>
</tr>
<tr>
<td>HL</td>
<td>1975</td>
<td>83 (1)</td>
<td>8</td>
<td>n/a</td>
</tr>
<tr>
<td>JK</td>
<td>1992</td>
<td>n/a</td>
<td>—</td>
<td>8276 (50)</td>
</tr>
<tr>
<td>JO</td>
<td>1960</td>
<td>2006 (8)</td>
<td>58</td>
<td>94 (12)</td>
</tr>
<tr>
<td>KL</td>
<td>1970</td>
<td>7745 (32)</td>
<td>83</td>
<td>n/a</td>
</tr>
<tr>
<td>LP</td>
<td>1955</td>
<td>17410 (73)</td>
<td>98</td>
<td>9979 (61)</td>
</tr>
<tr>
<td>LR</td>
<td>1989</td>
<td>n/a</td>
<td>n/a</td>
<td>7571 (46)</td>
</tr>
<tr>
<td>MU</td>
<td>1970</td>
<td>463 (2)</td>
<td>15</td>
<td>522 (3)</td>
</tr>
<tr>
<td>NG</td>
<td>1955</td>
<td>136 (2)</td>
<td>9</td>
<td>n/a</td>
</tr>
<tr>
<td>NL</td>
<td>1982</td>
<td>6438 (37)</td>
<td>80</td>
<td>8162 (500)</td>
</tr>
<tr>
<td>OU</td>
<td>1979</td>
<td>12648 (53)</td>
<td>83</td>
<td>12925 (79)</td>
</tr>
<tr>
<td>PE</td>
<td>1970</td>
<td>1198 (5)</td>
<td>40</td>
<td>n/a</td>
</tr>
<tr>
<td>PU</td>
<td>1955</td>
<td>2535 (11)</td>
<td>48</td>
<td>1883 (20)</td>
</tr>
<tr>
<td>TG</td>
<td>1980</td>
<td>11183 (47)</td>
<td>71</td>
<td>11233 (68)</td>
</tr>
<tr>
<td>UM</td>
<td>1981</td>
<td>604 (3)</td>
<td>21</td>
<td>565 (3)</td>
</tr>
</tbody>
</table>

*Chimpanzees are a male philopatric species, so most female ages are estimates.
†Scans of the subject females during periods of full anogenital swelling were excluded from analysis.
‡Number of unique grid cells in which each female had been observed.
§Urinary steroid analysis controlled for individual and longitudinal differences in sampling frequency, see Methods. Note that several individuals died or disappeared before urine collections began.
**Surviving = lived to age 4 or had not yet reached age 4 but was alive at the time of the study.
oestrone conjugates (E$_1$C) and pregnanediol-3-glucuronide (PdG), metabolites of ovarian steroid hormones, using enzyme immunoassay reagents provided by the Clinical Endocrinology Laboratory at University of California, Davis (C. J. Munro). Thorough assay procedures and validations are provided elsewhere (Emery Thompson 2005b). To control for uneven sampling across females and expected hormonal fluctuations over time (Emery Thompson 2005a), we calculated an average E$_1$C and PdG value for each unique combination of female, month and reproductive state. We controlled for reproductive state by converting these monthly averages into $z$ scores relative to the mean of all Kanyawara females in each reproductive state (Emery Thompson 2005b), and then considered each female’s grand mean relative to others.

Ovarian hormone levels are a powerful tool for evaluating fecundity at a proximate level (Ellison 1995), because they reflect the size and function of the ovarian follicle and corpus luteum and are associated with increased probabilities of ovulation, fertilization and implantation (Eissa et al. 1986; Yoshimura & Wallach 1987; Lenton et al. 1988; Akman et al. 2002). Thus, higher ovarian hormone levels predict increased conception probability in chimpanzees (Emery Thompson 2005b), as well as in humans (Lipson & Ellison 1996), gorillas (Nadler & Collins 1991) and baboons (Wasser 1996).

Reproductive Data

Interbirth intervals were calculated using Kaplan–Meier survival analyses on all complete and incomplete intervals. Twenty-four of 37 infants were first encountered as newborns (<2 weeks old), and the birthdates of the remainder were estimated based on the size of the infant and the time since the mother was last observed, with all error estimates less than 6 months (±1 month, 7 infants; ±2 months, 4 infants; ±6 months, 2 infants). If a female switched neighbourhoods during the study, we categorized her in the neighbourhood in which she spent the majority of the birth interval. Because two southern females would have contributed only three birth intervals to these data, they were excluded from this analysis. Although it is feasible that infants born to rarely encountered females could have been missed if infants died soon after, the oestrous cycle monitoring, ovarian steroid analysis and frequent pregnancy testing (Aimstick, Craig Medical, Vista, California, U.S.A.) make it unlikely that a pregnancy would have gone undetected.

Offspring survivorship was assessed with a Kaplan–Meier survival analysis for 41 offspring born after 1988 whose mothers’ neighbourhoods could be assigned. These are understood to be underestimates of life expectancy at birth, since individuals born during observation could only have reached an age of 17. We considered infants that were orphaned during infancy or juvenile females that were believed to have emigrated as incomplete intervals (i.e. alive) terminating on the death of the mother or the date of transfer, respectively. Infant survival data were available up to 15 May 2005.
RESULTS

Female Spatial Distribution

Hierarchical cluster analyses of ranging distributions for both periods revealed a distinct cluster of females whose ranges were most similar (Fig. 1). The range of these females was located centrally to other females whose activities were concentrated near the northern and southern borders (Fig. 2). In both periods, the range use of all-male parties was indistinguishable from the central female cluster.

In the first period, 1996–2000, the central neighbourhood contained eight of 18 females. The eldest female in the community (AR) fell just outside of the main cluster, showing foci of range use in both central and southern areas. Two females (GO, BL) ranged considerably south of the central group and formed a second spatial cluster. The remaining eight females ranged to the north, with the majority forming a third cluster with similar ranging habits.

In the second period, 2001–2004, nine of 15 females composed the central cluster. This group included all living members of the original central neighbourhood, suggesting strong site fidelity. Indeed, females in the northern and southern neighbourhoods during this period had also occupied the same neighbourhoods in 2001–2004. However, a number of changes in community demography occurred in early 2001, affecting range distributions. One of the southern females (GO) died of respiratory illness, and the only remaining southern female (BL) began to be observed more frequently in central areas. A female from the northern neighbourhood (JO) also died following an illness, after which her adolescent daughter (JK) moved into the central neighbourhood. Thus, in about 2001, the southern neighbourhood completely disappeared. Specific areas of the home range used by central and northern females were similar to those used in 1996–2000, although the northern

neighbourhood extended further south into previously underexploited areas on the eastern edge of the home range (Fig. 2).

During both periods, cluster analysis revealed that central females showed tight similarity in ranging patterns, whereas northern females, who were all clearly north of the central cluster, had more differentiated ranging patterns within their neighbourhood. That is, while northern females tended to use the same grid cells in the northern area of the home range, individuals used these cells differently.

Core Area Quality

To compare habitat quality between northern and central neighbourhoods, we reviewed forest surveys conducted by Skorupa (1988). Two forest sectors surveyed by Skorupa, comprising 13.6 sq km, fell unambiguously within the range of the northern females, while two additional sectors, comprising 6.9 sq km, were contained within the central female range. These surveys showed large differences in forest quality. The northern neighbourhood had suffered considerably greater logging impact (1967–1969). Thus, the central neighbourhood had roughly double the density of total trees, including both large trees and fig trees (Ficus spp.), as well as a higher density and diversity of primates.

The data on density of trees, figs and frugivorous primates suggest that chimpanzees in the central neighbourhood had more abundant or higher-quality food than those in the northern neighbourhood. Feeding data support this. During the period 1996–2000, 53% of observations of non-fig fruit feeding occurred within grid cells assigned to the central neighbourhood, 55% occurred within the southern neighbourhood cells, and only 19% occurred in northern neighbourhood cells (chi-square test: $\chi^2 = 1596.69$, $P < 0.0001$ based on

![Figure 1](image-url). Dendrogram resulting from hierarchical cluster analysis of female chimpanzee range usage at Kanyawara, median method. **Bold** = central; **italics** = strongly northern; **underline** = strongly southern; * = central, tending south of main cluster. (a) 1996–2000, (b) 2001–2004.
observed versus expected frequencies). Similarly, during 2001–2004, 45% of observations of non-fig fruit feeding occurred in the central neighbourhood, while only 28% occurred in the northern neighbourhood ($\chi^2 = 308.49$, $P < 0.0001$).

Males were also observed more often in the central neighbourhood than in the northern neighbourhood (Fig. 1), as expected if the central neighbourhood had more fruit available. This raises the possibility of biased sampling if groups of males were more likely to be

![Figure 2](image-url)
observed or followed by researchers. We therefore calculated the number of unique feeding locations within each neighbourhood, without respect to intensity of use. Again, feeding locations for the three preferred fruit species were strongly concentrated within the southern and central neighbourhoods ($\chi^2_{1} = 21.65, P < 0.0001$; 2001–2004: $\chi^2_{1} = 7.37, P < 0.01$; Table 3). Northern areas contained very few preferred fruit trees.

In addition to the evidence that preferred foods may have been more available and more frequently used in the southern and central versus northern neighbourhoods, we found evidence that the dietary composition of females, specifically, varied in the same manner according to range. Each neighbourhood contained at least some cells in which preferred (non-fig) fruits were the only item consumed, and each neighbourhood contained at least some cells in which preferred fruits were never consumed, making significance testing impractical. However, in both study periods, the average consumption of preferred fruits by female parties ranging in the southern or central grid cells was approximately twice as frequent as in the northern areas (Fig. 3). From 1996 to 2000, total fruit consumption (including figs) in northern grid cells was comparable to that in the other neighbourhoods; however, from 2001 to 2004, the majority of the diet in northern grid cells (72%) consisted of leaves and piths.

As expected, the distribution of episodes of non-fig fruit feeding was a significant predictor of grid cell usage by all neighbourhoods, although the strength of this relationship varied. In 1996–2000, frequency of non-fig fruit consumption in each cell strongly predicted the range usage of southern females ($R^2 = 0.590, N = 153$ grid cells, $P < 0.0001$). The majority of the variance in central range use was also predicted by non-fig fruit consumption ($R^2 = 0.539, N = 153, P < 0.001$), although the slope of the relationship was significantly weaker than that for southern females ($t_{152} = 3.544, P = 0.0005$). Northern females’ ranges showed only a very loose relationship with this index of habitat quality ($R^2 = 0.065, N = 153, P = 0.001$), significantly weaker than that for ranges of southern ($t_{152} = 4.942, P < 0.0001$) or central ($t_{152} = 2.756, P = 0.006$) females. In 2001–2004, non-fig fruit consumption was a significantly better predictor of central female range ($R^2 = 0.660, N = 111, P < 0.0001$) than it was of northern female range ($R^2 = 0.119, N = 111, P = 0.0002; t_{218} = 3.959, P = 0.0001$).

Table 3. Female neighbourhood quality assessed by feeding locations of three preferred fruit species

<table>
<thead>
<tr>
<th>Neighbourhood</th>
<th>Number of grid cells in neighbourhood</th>
<th>Percentage of feeding locations within neighbourhood range</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mimusops bagshawai</td>
</tr>
<tr>
<td>1996–2000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern</td>
<td>33</td>
<td>18</td>
</tr>
<tr>
<td>Central</td>
<td>31</td>
<td>39</td>
</tr>
<tr>
<td>Southern</td>
<td>34</td>
<td>46</td>
</tr>
<tr>
<td>2001–2004</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern</td>
<td>34</td>
<td>37</td>
</tr>
<tr>
<td>Central</td>
<td>28</td>
<td>48</td>
</tr>
</tbody>
</table>

Neighbourhoods had a small degree of overlap and did not encompass the entirety of the chimpanzee range.

Figure 3. Dietary composition of all-female parties ranging in grid cells constituting each neighbourhood. Bars represent the mean ± standard error across cells. □: northern neighbourhood; ■: central neighbourhood; ■■: southern neighbourhood.

In summary, data on tree density, frugivore density, and locations and patterns of chimpanzee fruit-eating consistently indicated higher food quality in the central neighbourhood than in the northern neighbourhood.

Reproductive Consequences of Core Area Usage

Females in the central area had significantly higher levels of urinary oestrogen and progesterone conjugates than did northern females after adjustment for reproductive state (Student’s t test: E1C: $t_{18} = 2.195, P = 0.04$; PdG: $t_{18} = 2.161, P = 0.04$; Fig. 4). Although some females were represented by relatively few urine samples, we found that the variance in hormonal titers between females significantly exceeded the variance in multiple samples from the same individual over the study period (ANOVA: E1C: $P < 0.001$; PdG: $P < 0.03$ for all reproductive states). Enhanced ovarian function was accompanied by a large difference in interbirth intervals. The mean ± SE interbirth interval for the community at large was 39.8 ± 7.3 months ($N = 6$) following the death of an infant, and 81.8 ± 16.2 months ($N = 15$ complete, 16 incomplete) if the previous infant survived to 4 years. The mean interbirth interval for central females was 31.8 ± 8.2 months ($N = 4$) following infant death and 70.3 ± 6.5 months ($N = 10$ complete, 10 incomplete) after infant survival, while the mean for the northern females was 55.9 ± 0.0 ($N = 2$) after infant death and 114.1 ± 25.7 months.
(N = 3 complete, 5 incomplete) after infant survival. The sample of birth intervals for northern females was small, particularly because so few of their infants survived. Nevertheless, the difference between northern and central females in mean birth interval approached significance (following infant death: log rank = 3.86, P = 0.05; following infant survival: log rank = 3.26, P = 0.07).

Infant survival statistics over the study period also showed profound differences (Fig. 5). With a limiting age of 17 (due to study length), mean ± SE infant survival was 11.7 ± 1.2 years (N = 41 infants, 29 censored (i.e. living)). Offspring of southern females had the highest survival (15.4 ± 1.4 years, N = 7, 6 censored). Central offspring survived for 11.1 ± 1.6 years (N = 23, 17 censored), while northern infants only survived for a mean of 7.6 ± 1.5 years (N = 11, 6 censored).

**DISCUSSION**

Our results indicate that female chimpanzees in the Kanyawara community used the community range in a differentiated manner, forming distinct northern, central and southern clusters. Females with core areas in the north had reduced access to preferred fruit trees, low ovarian hormone levels and decreased reproductive success as indexed by interbirth intervals and infant survivorship.

Lower habitat quality in the northern neighbourhood was reflected in general forest structure and locations of preferred chimpanzee foods. These habitat differences may have been partly due to a greater intensity of logging in the northern neighbourhood, but effects of soil type, drainage and altitude may also be important. Differences in tree density between the northern and central neighbourhoods are also likely to account for differences in frugivore density (Struhsaker 1997; Chapman et al. 2000).

The strong stability of female spatial relationships over the 9-year span of this study conforms to Williams et al.’s (2002) suggestion that female chimpanzees gain important advantages from site fidelity, such as increased knowledge of feeding locations. Northern females may also ameliorate the effects of lower food quality by adopting social strategies that reduce feeding competition. Ranging patterns of individual northern females were more differentiated from one another than those of either central or southern females, suggesting less overlap in individual core areas or less association between individuals. Indeed, the northern females at Kanyawara are less gregarious than the central females (Emery Thompson & Wrangham 2006).

Our limited data on the southern females suggest that these females may have had the highest quality range and the best reproductive outcomes. High-quality resources in the south might also have made this region desirable to the neighbouring chimpanzee community in the south, however, raising the possibility that intercommunity fighting contributed to the dissolution of the southern neighbourhood after 2001. The southern neighbourhood at Kanyawara provides an important indication that habitat quality may not be the only consideration in determining female core area use. Female chimpanzees seem to face a compromise among considerations of habitat quality, scramble competition and threat from neighbouring communities. The presence of only two females in the southern neighbourhood suggests that other females may have avoided this border area despite its food richness.

The southern females also provide an important contrast to northern females in terms of the consequences of range location. Although each neighbourhood is situated close to a border area, northern females suffered the highest infant and juvenile mortality and the lowest fecundity, whereas southern females appeared to fare the best. Unfortunately, we cannot identify the cause of
mortality in most cases. However, low mortality rates in the southern neighbourhood suggest that, even though these females were living in a high-quality border zone and did not typically enjoy the protection of community males, intercommunity aggression was not a major threat to infant and juvenile survivorship. Females in both southern and northern communities were less gregarious than central females and spent less time in the presence of observers (Emery Thompson & Wrangham 2006). Thus, direct feeding competition and anthropogenic illnesses are unlikely sources of mortality. We also have no evidence of predation on chimpanzees at Kanyawara. Our available evidence therefore suggests that the best explanation for differences in survivorship is differing maternal and juvenile nutrition and resultant somatic condition.

Assuming no difference in female life span or age at maturity among neighbourhoods and a mean reproductive span of 16 years (Hill et al. 2001), our data for central mothers predict a mean of 3.7 offspring born; 2.2 of these offspring can be expected to survive to maturity. Northern mothers, by contrast, should have produced a mean of 2.7 offspring, of whom only 1.0 can be expected to survive to maturity. This evidence for an approximate doubling of reproductive success in one cluster compared to another suggests that, in chimpanzees, there can be intense selection pressures for females to occupy high-quality core areas.

The differences between neighbourhoods that we found in fruit availability, fecundity and infant survival support the role of energy availability in the reproductive success of females. Such differences are consistent with the role of nutrition in mediating reproductive function in humans (Ellison et al. 1989, 1993; Ellison 1995, 2003; Bentley et al. 1998) and nonhuman primates (van Schaik & van Noordwijk 1985; Bercovitch 1987; Bercovitch & Strum 1993; Strier et al. 2001; Altman & Alberts 2003b, 2003a; Knott 2005). Conception timing and ovarian hormone levels in Kanyawara chimpanzees have both been correlated to the utilization of preferred non-fig fruits (Sherry 2002; Emery Thompson 2005a), supporting a causal link between lower habitat quality and poorer reproductive variables in northern females.

There are possible alternative or intermediary explanations for the observed relationships. One possibility is that females with higher fitness attributes, such as larger body size or better competitive abilities, succeed in settling in higher-quality core areas. However, it is difficult to imagine this effect acting independently of subsequent effects of differing dietary quality, given that adult chimpanzee body weights can show significant seasonal weight fluctuations (Pusey et al. 2005). Indeed, if we assume that core area settlement is nonrandom, we have all the more reason to believe that there are important consequences of core area location. In Kanyawara, increasing age appears to be a strong predictor of dominance rank among females (Kahlenberg 2006). While both of the southern females at Kanyawara were past prime, there were no systematic differences in the ages of central and northern females. Differences in the socioecology of neighbourhoods (e.g. presence of males, party sizes, human contacts) may be proposed to influence female fecundity via variation in social stress. Our results suggest that this is not the case, however. While central females have the most interaction with aggressive males and the most contact with human observers, they have higher fecundity than northern females.

Differential range use could have effects on reproductive success besides access to food resources. Females ranging in peripheral areas may be more susceptible to infanticides by neighbouring communities (Wilson & Wrangham 2003), although this did not appear to be the case for southern Kanyawara females. Increased maternal sociality has been linked to infant survivorship in some primates (Silk et al. 2003), so range dispersion could also affect reproductive success by affecting gregariousness.

The degree of female reproductive variance reported here suggests that there ought to be competition over where female chimpanzees settle within the home range. Results from other field studies suggest that immigrant adolescent females do encounter resistance from resident females (Pusey 1980, 1990; Nishida 1989); we are currently investigating rates of aggression during immigration events at Kanyawara, as well as the rank relationships of northern and central females when they join parties together. We hypothesize that female chimpanzees establish their dominance relationships in the context of core area establishment, and that the resultant ranging heterogeneity reduces the need for frequent, potentially costly contest competition. Thus, rather than indicating a lack of differentiated social status, the relative rarity of overt dominance interactions observed among female chimpanzees may result from stable dominance relationships.

These results may not be generalizable to all chimpanzee communities. Notably, female chimpanzees in the Tai community in Cote d’Ivoire (Pan troglodytes verus) show increased gregariousness and wider ranging habits than do Kanyawara chimpanzees (Lehmann & Boesch 2003, 2005); they also show more clearly defined rank relationships in the context of feeding competition (Boesch 1997; Wittig & Boesch 2003), with higher-ranking females ranging further and making more use of peripheral areas (Lehmann & Boesch 2005). It is unclear what is responsible for the differences in social structure between Tai and East African sites (Kibale, Gombe). Similarly, chimpanzees in Budongo Forest, Uganda, live in a relatively small range of high resource density (Newton-Fisher 2002), and likewise appear to have very little differentiation of female ranges (Emery Thompson et al. 2006). Thus, although our results do not necessarily apply to chimpanzees in general, they suggest that reproductive skew among female chimpanzees may be largely determined by local ecological factors that remain to be characterized.

Few species can be expected to show spatially based reproductive skew within groups, because within social communities, females normally travel together. However, analogous fission–fusion patterns occur outside of the primate order and may be expected to be associated with similar ecological constraints, as well as similar reproductive variance. Within-group female range heterogeneity has been observed in one fission–fusion species, the
spotted hyaena, *Crocuta crocuta*. Low-ranking female hyaenas at Masai Mara ranged closer to territorial boundaries, particularly when prey were scarce, and had lower reproductive success than did high-ranking females (Boydston et al. 2003). How much of the fitness variance was due to variation in food intake was unclear, however, since subordinate hyaenas also experience severe aggression and infanticide of their litters (Hofer & East 1995; Frank 1996; Muller & Wrangham 2002). To our knowledge, therefore, our results for Kanyawara chimpanzees are the first example of intragroup variation in female reproductive success correlated with habitat variation and space use. Attention to these variables warrants future attention in a range of species.

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**References**


