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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 survivorship. 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).

Resource competition among female primates frequently results in dominants outperforming subordinates (Gouzoules et al. 1982; Harcourt 1987; Bercovitch & Strum 1993; Ellis 1995; Altmann & Alberts 2003b; Creel 2005), sometimes due to reproductive suppression of subordinates (Abbott 1984; Epple & Katz 1984; Ziegler et al. 1987; Abbott 1987; Barrett et al. 1990, 1993; Kuederling et al. 1995; Ziegler & Sousa 2002; Saltzman et al. 2004). Rank and fitness differentials within social groups are commonly associated with female–female aggression and philopatry, and are maintained by alliances among female kin (Wrangham 1980; 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.

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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 km^2 (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) (Romesburg 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

Table 1. Kanyawara chimpanzee subject females and sample sizes

Female	Year of birth*	1996–2000 Nonoestrous scans (ca. h/month)†	1996–2000 Grid cells used‡	2001–2004 Nonoestrous scans (ca. h/month)†	2001–2004 Grid cells used‡	Urine samples§	Offspring born (1988–) survived/died**
AL	1982	8984 (37)	94	9025 (55)	78	114	2/1
AR	1943	6629 (28)	65	4298 (26)	41	73	2/0
BL	1960	3342 (14)	53	6745 (46)	61	36	4/0
EK	1974	2177 (9)	34	2205 (13)	49	21	2/1
FG	1955	6987 (67)	81	n/a	—	14	1/1
GO	1957	2123 (9)	42	41 (5)	4	n/a	1/0
HL	1975	83 (1)	8	n/a	—	n/a	0/0
JK	1992	n/a	—	8276 (50)	75	47	n/a
JO	1960	2006 (8)	58	94 (12)	9	10	1/0
KL	1970	7745 (32)	83	n/a	—	70	0/2
LP	1955	17410 (73)	98	9979 (61)	90	185	2/1
LR	1989	n/a	n/a	7571 (46)	77	224	1/1
MU	1970	463 (2)	15	522 (3)	28	7	1/2
NG	1955	136 (2)	9	n/a	—	n/a	2/0
NL	1982	6438 (37)	80	8162 (500)	74	158	3/0
OU	1979	12648 (53)	83	12925 (79)	74	220	1/0
PE	1970	1198 (5)	40	n/a	—	2	2/1
PU	1955	2535 (11)	48	1883 (20)	44	9	3/0
TG	1980	11183 (47)	71	11233 (68)	71	139	3/0
UM	1981	604 (3)	21	565 (3)	25	16	3/0

*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.

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 ($\overline{X} = 27.5$, 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

Table 2. Habitat characteristics and timber impact in forest sectors comprising central and northern neighbourhood areas (from Skorupa 1988)

			Habitat quality measures							Logging history	
Forest area	Chimpanzee neighbourhood location	Area (ha)	Total stem density (stems/ha)*	Large stem density (stems/ha)†	*Ficus* density (stems/ha)	Canopy ≥15 m (%)	Basal area, frugivore diets‡ (m^2/ha)	Species richness, frugivore trees§	Total primate index**	Timber out-take 1967–1969 (m^3/ha)	Basal area reduction (%)††
K-30	Central	300	255.9	25.2	4.1	72	21.7	11.1	82.5	0	—
K-14	Central	390	267.2	12.0	6.5	50	21.1	9.5	73.2	14.4	24.9
K-15	Northern	360	125.1	8.0	0.6	32	13.6	6.6	45.9	20.9	46.6
K-12/13/17	Northern	1000	127.6	10.5	0.5	21	10.9	6.9	35.1	17.0	50.3

*At least 35 cm in circumference at breast height.
†At least 2.1 m in circumference at breast height or above buttress.
‡Trees in diets of frugivorous monkeys, *Lophocebus albigena* and *Cercopithecus mitis*.
§Species/100 stems, diets of frugivorous monkeys (see above).
**Average proportion of maximum abundance achieved by Kibale primate species in each plot.
††Relative to undistributed Parinari forest (K-30).

oestrone conjugates (E_1C) 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_1C 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: $\chi^2_2 = 1596.69$, $P < 0.0001$ based on

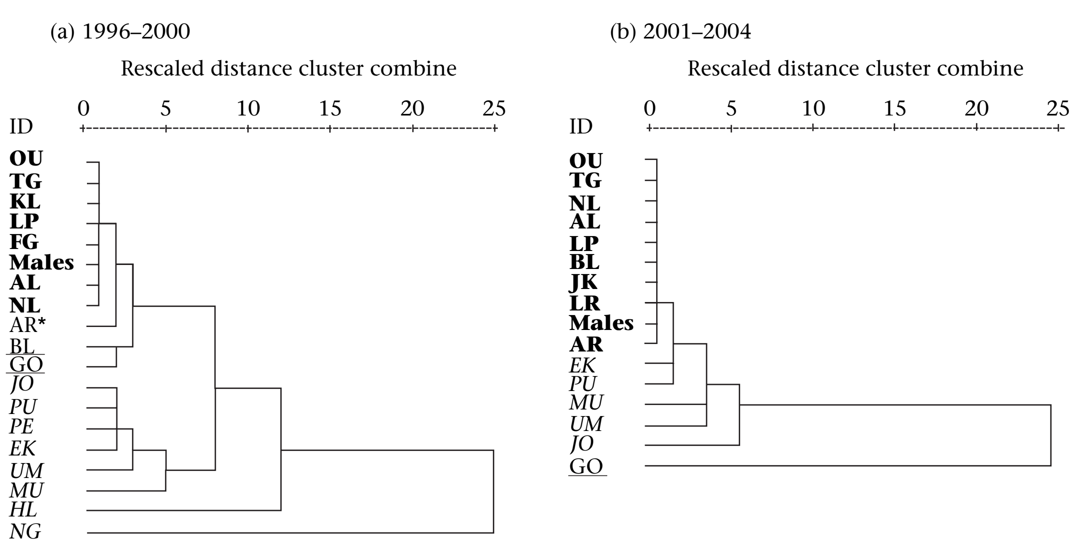

Figure 1. Dendrogram resulting from hierarchical cluster analysis of female chimpanzee range usage at Kanyawara, median method. **Bold** = central; *italics* = strongly northern; underline = strongly southern; * = central, tending south of main cluster. (a) 1996–2000, (b) 2001–2004.

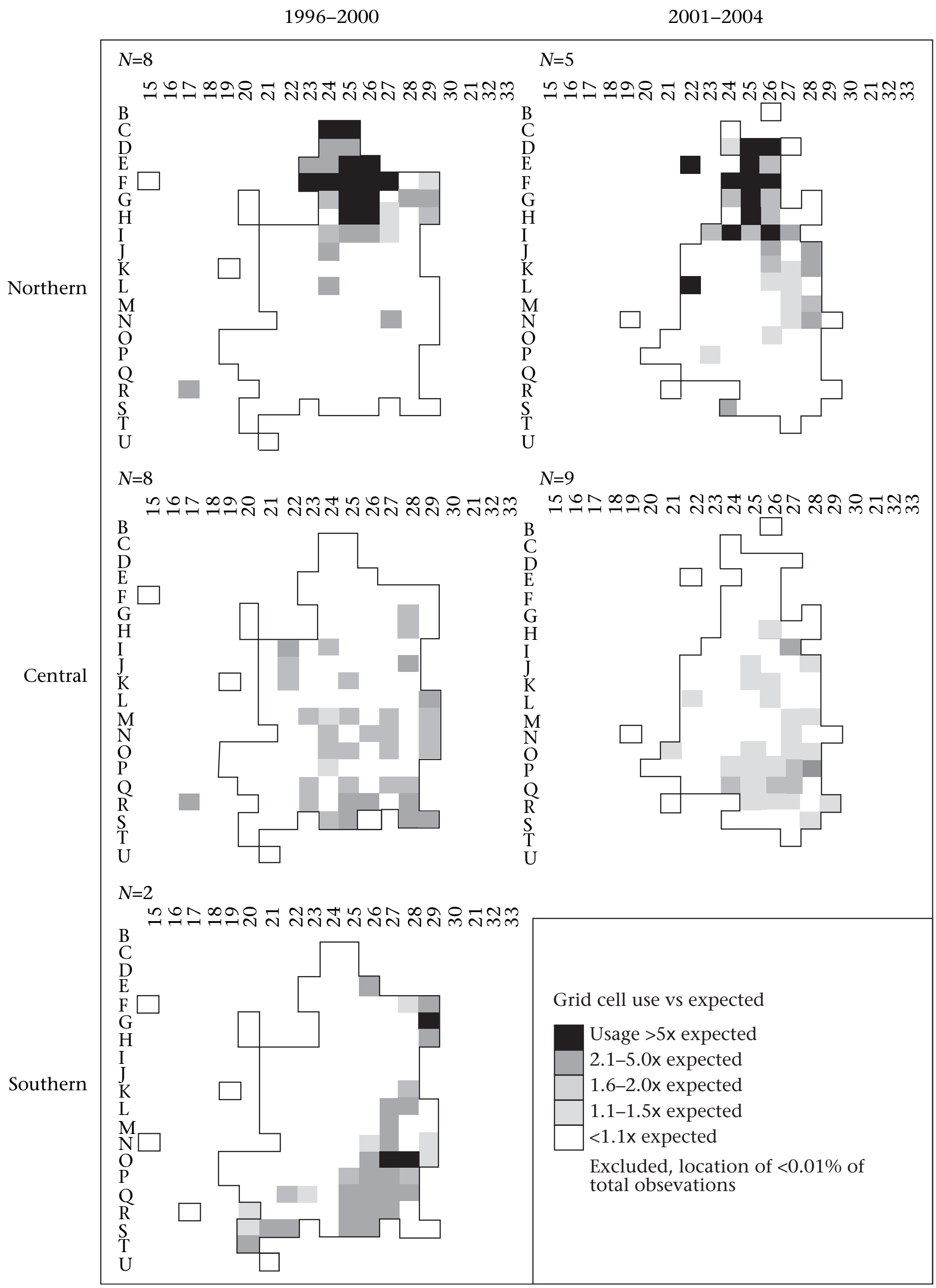

Figure 2. Range concentrations of female Kanyawara chimpanzees within each spatial cluster: (a) 1996–2000, (b) 2001–2004. Shaded areas illustrate the observed/expected percentage of utilization of each grid square (500 × 500 m) by that group of females, with expected distributions based on the frequency of all chimpanzee observations per grid cell. Blank cells outside of border were excluded from analysis; they were not used by chimpanzees or were used in less than 0.01% of total observations.

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 ($\chi^2_1 = 308.49$, $P < 0.0001$).

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 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 (1996–2000: $\chi^2_2 = 21.65$, $P < 0.0001$; 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 ($t_{302} = 3.544$, $P = 0.0005$). 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 ($t_{302} = 4.942$, $P < 0.0001$) or central ($t_{302} = 2.756$, $P = 0.006$) 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 ($R^2 = 0.119$, $N = 111$, $P = 0.0002$; $t_{218} = 3.959$, $P = 0.0001$).

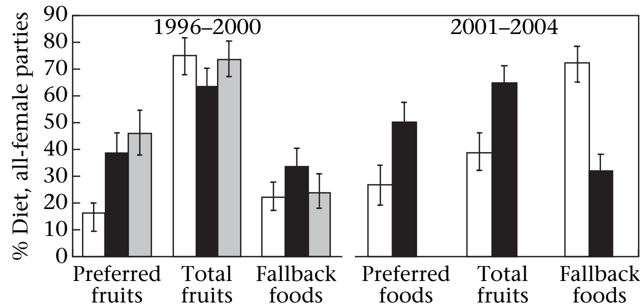

Figure 3. Dietary composition of all-female parties ranging in grid cells constituting each neighbourhood. Bars represent the mean ± standard error across cells. □: northern neighbourhood; ■: central neighbourhood; ▩: southern neighbourhood.

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: E_1C: $t_{18} = 2.195$, $P = 0.04$; 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: E_1C: $P < 0.001$; 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

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

Neighbourhood	Number of grid cells in neighbourhood	Percentage of feeding locations within neighbourhood range		
		Mimusops bagshawei	*Uvariopsis congensis*	*Pseudospondias microcarpa*
1996–2000				
Northern	33	18	10	8
Central	31	39	42	42
Southern	34	46	58	100
2001–2004				
Northern	34	37	16	0
Central	28	48	42	73

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

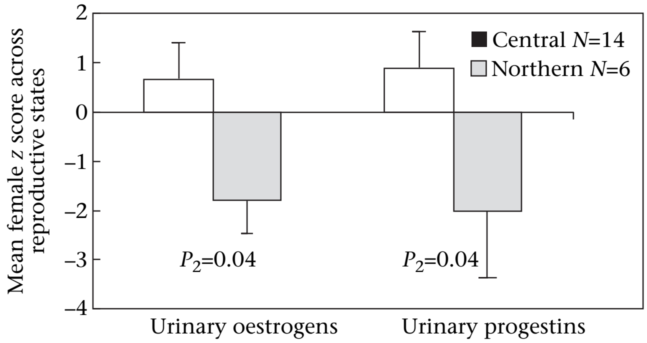

Figure 4. Urinary oestrone conjugates (E_1C) and pregnanediol-3-glucuronide (PdG) in central and northern female Kanyawara chimpanzees, standardized for reproductive state. N = number of females; P values from t test. Southern females were omitted because of inadequate sampling.

($N = 3$ 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).

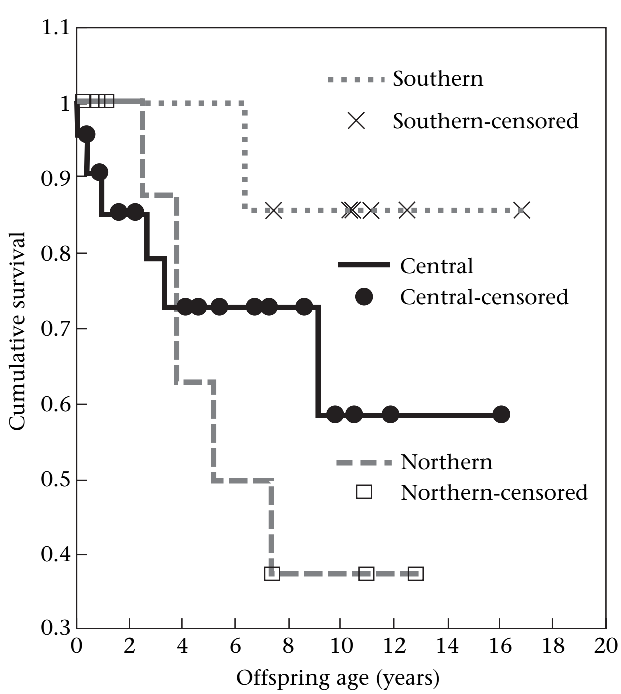

Figure 5. Proportion of infants expected to survive at ages 0–17 based on infant and juvenile mortality data for northern, central and southern females using Kaplan–Meier survival analysis.

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; Altmann & 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 Taï 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 Taï 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

Abbott, D. H. 1984. Behavioral and physiological suppression of fertility in subordinate marmoset monkeys. *American Journal of Primatology*, **6**, 169–186.

Abbott, D. H. 1987. Behaviourally mediated suppression of reproduction in female primates. *Journal of Zoology*, **213**, 455–470.

Akman, M., Erden, H., Bener, F., Liu, J. & Bahceci, M. 2002. Can luteal phase estradiol levels predict the pregnancy outcome in *in vitro* fertilization cycles of good responders whose excess embyros yield blastocysts? *Fertility and Sterility*, **77**, 638–639.

Altmann, J. & Alberts, S. C. 2003a. Intraspecific variability in fertility and offspring survival in a non-human primate: behavioral control of ecological and social sources. In: *Offspring: Human Fertility Behavior in a Biodemographic Perspective* (Ed. by K. Wachter), pp. 140–169. Washington, D.C.: National Academy Press.

Altmann, J. & Alberts, S. C. 2003b. Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, **15**, 401–409.

Barrett, J., Abbott, D. H. & George, L. M. 1990. Extension of reproductive suppression by pheromonal cues in subordinate female marmoset monkeys, *Callithrix jacchus*. *Journal of Reproduction and Fertility*, **90**, 411–418.

Barrett, J., Abbott, D. H. & George, L. M. 1993. Sensory cues and the suppression of reproduction in subordinate female marmoset monkeys, *Callithrix jacchus*. *Journal of Reproduction and Fertility*, **97**, 301–310.

Bentley, G. R., Harrigan, A. M. & Ellison, P. T. 1998. Dietary composition and ovarian function among Lese horticulturalist women of the Ituri Forest, Democratic Republic of Congo. *European Journal of Clinical Nutrition*, **52**, 261–270.

Bercovitch, F. B. 1987. Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). *American Journal of Primatology*, **12**, 189–195.

Bercovitch, F. B. & Strum, S. C. 1993. Dominance rank, resource availability, and reproductive maturation in female savanna baboons. *Behavioral Ecology and Sociobiology*, **33**, 313–318.

Boesch, C. 1997. Evidence for dominant wild female chimpanzees investing more in sons. *Animal Behaviour*, **54**, 811–815.

Boydston, E. E., Kapheim, K. M., Szykman, M. & Holekamp, K. E. 2003. Individual variation in space use by female spotted hyenas. *Journal of Mammalogy*, **84**, 1006–1018.

Chapman, C. A. & Wrangham, R. W. 1993. Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. *American Journal of Primatology*, **31**, 263–273.

Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P. & Struhsaker, T. T. 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conservation Biology*, **14**, 207–217.

Creel, S. F. 2005. Dominance, aggression, and glucocorticoid levels in social carnivores. *Journal of Mammalogy*, **86**, 255–264.

Eissa, M. K., Obhrai, M. S., Docker, M. F., Lynch, S. S., Sawers, R. S. & Newton, R. R. 1986. Follicular growth and endocrine profiles in spontaneous and induced conception cycles. *Fertility and Sterility*, **53**, 81–87.

Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethology and Sociobiology*, **16**, 257–333.

Ellison, P. T. 1995. Understanding natural variation in ovarian function. In: *Human Reproductive Decisions: Biological and Social Perspectives* (Ed. by R. I. M. Dunbar), pp. 22–51. London: St. Martin's Press/Galton Institute.

Ellison, P. T. 2003. Energetics and reproductive effort. *American Journal of Human Biology*, **15**, 342–351.

Ellison, P. T., Peacock, N. R. & Lager, C. 1989. Ecology and ovarian function among Lese women of the Ituri Forest, Zaire. *American Journal of Physical Anthropology*, **78**, 519–526.

Ellison, P. T., Panter-Brick, C., Lipson, S. F. & O'Rourke, M. T. 1993. The ecological context of human ovarian function. *Human Reproduction*, **8**, 2248–2258.

Emery Thompson, M. 2005a. Endocrinology and ecology of wild female chimpanzee reproduction. Ph. D. thesis, Harvard University.

Emery Thompson, M. 2005b. Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): methodological considerations and the role of hormones in sex and conception. *American Journal of Primatology*, **67**, 137–158.

Emery Thompson, M. & Wrangham, R. W. 2006. Comparison of sex differences in gregariousness in fission–fusion species: reducing bias by standardizing for party size. In: *Primates of Western Uganda* (Ed. by N. E. Newton-Fisher, H. Notman, V. Reynolds & J. Paterson), pp. 209–226. New York: Springer.

Emery Thompson, M., Wrangham, R. W. & Reynolds, V. 2006. Urinary estrone conjugates and reproductive parameters in Kibale (Kanyawara) and Budongo (Sonso) chimpanzees. In: *Primates of Western Uganda* (Ed. by N. E. Newton-Fisher, H. Notman, V. Reynolds & J. Paterson), pp. 227–246. New York: Springer.

Epple, G. & Katz, Y. 1984. Social influences on estrogen excretion and ovarian cyclicity in saddle back tamarins (*Saguinus fuscicollis*). *American Journal of Primatology*, **6**, 215–227.

Frank, L. G. 1996. Female masculinization in the spotted hyena: endocrinology, behavioral ecology, and evolution. In: *Carnivore Behavior,* *Ecology, and Evolution* (Ed. by J. L. Gittleman), pp. 78–131. Ithaca, New York: Cornell University Press.

Gadgil, M. & Bossert, W. H. 1970. Life historical consequences of natural selection. *American Naturalist*, **104**, 1–24.

Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Belknap Press.

Gouzoules, H., Gouzoules, S. & Fedigan, L. M. 1982. Behavioural dominance and reproductive success in female Japanese monkeys (*Macaca fuscata*). *Animal Behaviour*, **30**, 1138–1150.

Harcourt, A. H. 1987. Dominance and fertility among female primates. *Journal of Zoology*, **213**, 471–487.

Hasegawa, T. 1990. Sex differences in ranging patterns. In: *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies* (Ed. by T. Nishida), pp. 99–114. Tokyo: University of Tokyo Press.

Hill, K., Boesch, C., Goodall, J., Pusey, A. E., Williams, J. & Wrangham, R. W. 2001. Mortality rates among wild chimpanzees. *Journal of Human Evolution*, **40**, 437–450.

Hofer, H. & East, M. 1995. Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. In: *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (Ed. by A. R. E. Sinclair & P. Arcese), pp. 332–365. Chicago: University of Chicago Press.

Kahlenberg, S. M. 2006. Female–female competition and male sexual coercion in Kanyawara chimpanzees. Ph. D. thesis, Harvard University.

Knott, C. D. 1997. Field collection and preservation of urine in orangutans and chimpanzees. *Tropical Biodiversity*, **4**, 95–102.

Knott, C. D. 2001. Ape models of female reproductive ecology. In: *Reproductive Ecology and Human Evolution* (Ed. by P. T. Ellison), pp. 429–463. Chicago: Aldine.

Knott, C. D. 2005. Energetic responses to food availability in the great apes: implications for hominid evolution. In: *Seasonality in Primates: Studies of Living and Extinct Human and Non-human Primates* (Ed. by D. K. Brockman & C. P. van Schaik), pp. 351–378. Cambridge: Cambridge University Press.

Koenig, A. 2002. Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, **23**, 759–783.

Kuederling, I., Evans, C. S., Abbott, D. H., Pryce, C. R. & Epple, G. 1995. Differential excretion of urinary oestrogen by breeding females and daughters in the red-bellied tamarin (*Saguinus labiatus*). *Folia Primatologica*, **64**, 140–145.

Lehmann, J. & Boesch, C. 2003. Social influences on ranging patterns among chimpanzees (*Pan trolodytes verus*) in the Tai National Park, Cote d'Ivoire. *Behavioral Ecology*, **14**, 642–649.

Lehmann, J. & Boesch, C. 2005. Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). *Behavioral Ecology and Sociobiology*, **57**, 525–535.

Lenton, E. A., Gelsthorp, C. H. & Harper, R. 1988. Measurement of progesterone in saliva: assessment of the normal fertile range using spontaneous conception cycles. *Clinical Endocrinology*, **38**, 637–646.

Lipson, S. F. & Ellison, P. T. 1996. Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Human Reproduction*, **11**, 2090–2096.

Matsumoto-Oda, A. 1999. Mahale chimpanzees: grouping patterns and cycling females. *American Journal of Primatology*, **47**, 197–207.

Muller, M. N. & Wrangham, R. W. 2002. Sexual mimicry in hyenas. *Quarterly Review of Biology*, **77**, 3–16.

Nadler, R. D. & Collins, D. C. 1991. Copulatory frequency, urinary pregnanediol, and fertility in great apes. *American Journal of Primatology*, **24**, 167–179.

Newton-Fisher, N. E. 2002. Ranging patterns of male chimpanzees in the Budongo Forest, Uganda: range structure and individual differences. In: *New Perspectives on Primate Evolution and Behaviour* (Ed. by C. S. Harcourt & B. Sherwood), pp. 287–308. Westbury Academic & Scientific.

Nishida, T. 1968. The social group of wild chimpanzees in the Mahale mountains. *Primates*, **19**, 167–224.

Nishida, T. 1989. Social interactions between resident and immigrant female chimpanzees. In: *Understanding Chimpanzees* (Ed. by P. G. Heltne & L. A. Marquardt), pp. 68–89. Cambridge, Massachusetts: Harvard University Press.

Pepper, J. W., Mitani, J. C. & Watts, D. P. 1999. General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, **20**, 613–632.

Pusey, A. E. 1980. Inbreeding avoidance in chimpanzees. *Animal Behaviour*, **28**, 543–552.

Pusey, A. E. 1990. Behavioural changes at adolescence in chimpanzees. *Behaviour*, **115**, 203–245.

Pusey, A. E., Williams, J. & Goodall, J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, **277**, 828–831.

Pusey, A. E., Oehlert, G. W., Williams, J. & Goodall, J. 2005. Influence of ecological and social factors on body mass of wild chimpanzees. *International Journal of Primatology*, **26**, 3–31.

Romesburg, H. C. 2004. *Cluster Analysis for Researchers*. Moorisville, North Carolina: Lulu Press.

Saltzman, W., Prudom, S. L., Schultz-Darken, N. J., Wittwer, D. J. & Abbott, D. H. 2004. Social suppression of cortisol in female marmoset monkeys: role of circulating ACTH levels and glucocorticoid negative feedback. *Psychoneuroendocrinology*, **29**, 141–161.

van Schaik, C. P. & van Noordwijk, M. A. 1985. Interannual variability in fruit abundance and the reproductive seasonality in Sumatran long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology*, **206**, 533–549.

Schneider, J. E. & Wade, G. N. 2000. Inhibition of reproduction in service of energy balance. In: *Reproduction in Context: Social and Environmental Influences on Reproduction* (Ed. by K. Wallen & J. E. Schneider), pp. 35–82. Cambridge, Massachusetts: MIT Press.

Sherry, D. S. 2002. Reproductive seasonality in chimpanzees and humans: ultimate and proximate factors. Ph.D. thesis, Harvard University.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231–1234.

Skorupa, J. P. 1988. The effects of selective timber harvesting on rain-forest primates in Kibale Forest, Uganda. Ph.D. thesis, University of California, Davis.

Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, **41**, 291–309.

Strier, K. B., Mendes, S. L. & Santos, R. R. 2001. Timing of births in sympatric brown howler monkeys (*Alouatta fusca clamitans*) and northern muriquis (*Brachyteles arachnoides hypoxanthus*). *American Journal of Primatology*, **55**, 87–100.

Struhsaker, T. T. 1997. *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. Gainesville: University Press of Florida.

Sugiyama, Y. 1968. Social organization of chimpanzees in the Budongo Forest, Uganda. *Primates*, **9**, 225–258.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

de Waal, F. B. M. 1982. *Chimpanzee Politics: Power and Sex Among Apes*. Baltimore, Maryland: Johns Hopkins University Press.

Wasser, S. K. 1996. Reproductive control in wild baboons measured by fecal steroids. *Biology of Reproduction*, **55**, 393–399.

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P. & Goodall, J. 2002. Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, **63**, 347–360.

Williams, J., Oehlert, G. W., Carlis, J. V. & Pusey, A. E. 2004. Why do male chimpanzees defend a group range? *Animal Behaviour*, **68**, 523–532.

Wilson, M. L. 2001. Imbalances of power: how chimpanzees respond to the threat of intergroup aggression. Ph.D. thesis, Harvard University, Cambridge, Massachusetts.

Wilson, M. L. & Wrangham, R. W. 2003. Intergroup relations in chimpanzees. *Annual Review of Anthropology*, **32**, 363–392.

Wittig, R. M. & Boesch, C. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology*, **24**, 847–867.

Wrangham, R. W. 1975. The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D. thesis, University of Cambridge.

Wrangham, R. W. 1979. Sex differences in chimpanzee dispersion. In: *The Great Apes* (Ed. by D. A. Hamburg & E. R. McCown), pp. 481–489. San Franciso: Benjamin/Cummings.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262–299.

Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P. & Isabirye-Basuta, G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: *Great Ape Societies* (Ed. by T. Nishida), pp. 45–57. Cambridge: Cambridge University Press.

Yoshimura, Y. & Wallach, E. E. 1987. Studies of the mechanism(s) of mammalian ovulation. *Fertility and Sterility*, **47**, 22–34.

Ziegler, T. E. & Sousa, M. B. C. 2002. Parent–daughter relationships and social controls on fertility in female common marmosets, *Callithrix jacchus*. *Hormones and Behavior*, **42**, 356–367.

Ziegler, T. E., Savage, A., Scheffler, G. & Snowdon, C. T. 1987. The endocrinology of puberty and reproductive functioning in female cotton-top tamarins (*Saguinus oedipus*) under varying social conditions. *Biology of Reproduction*, **37**, 618–627.