



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.

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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, socio-ecological 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 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) (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

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