



Female-Female Competition in Bornean Orangutans

Cheryl Knott · Lydia Beaudrot · Tamaini Snaith ·
Sarah White · Hartmut Tschauer ·
George Planansky

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Abstract The mostly solitary ranging of orangutans and the large areas over which they traverse have hampered quantification of Bornean orangutan ranging patterns and feeding competition. Because of their semisolitary existence, female orangutans have few competitive interactions among themselves. However, contest and scramble types of competition occur, and researchers consider both to be important for the species. Using 9 yr of data and >22,300 h of observation of adult female orangutans in Gunung Palung National Park in Indonesian Borneo, we examined both forms of competition. Based on our analyses, we have 4 conclusions: 1) Adult female orangutans have highly overlapping home ranges, and thus there is potential for scramble competition to impose a cost. 2) Adult female orangutans actively avoid each other, suggesting that scramble competition indeed imposes a cost. 3) Adult females have distinct core areas that overlap to a lesser degree than home ranges do. 4) Analyses of contest competition reveal a slight spatial component to female competition for the first time. Preliminary evidence for core area defense and passive range exclusion may be among the mechanisms responsible for maintaining distinct adult female core areas.

Keywords core area · dominance · encounter rates · female competition · GIS · home range · orangutan · passive range exclusion · philopatry · ranging

C. Knott (✉) · L. Beaudrot · S. White
Department of Anthropology, Harvard University, Cambridge, MA 02138, USA
e-mail: knott@fas.harvard.edu

T. Snaith
Department of Anthropology, McGill University, Montreal H3A 2T7, Canada

H. Tschauer
Department of Archaeology and Art History, Seoul National University, Seoul 151-745, Korea

G. Planansky
Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA 02138, USA

Introduction

Differential access to food can lead to significant differences in reproductive success in female primates. We expect females to compete for food when access to high-quality food is limited, (Koenig 2002; Sterck *et al.* 1997; Wrangham 1980). Female apes have low rates of contact aggression, and competition can be subtle (Kahlenberg *et al.* 2008; Pusey *et al.* 1997). However, recent studies of chimpanzees show that rank differences result in dominant females having access to better feeding spots and establishing territories in higher quality areas (Emery Thompson *et al.* 2007; Kahlenberg *et al.* 2008; Murray *et al.* 2006; Williams *et al.* 2002). The differences affect energetic status and hormonal levels and eventually result in higher lifetime reproductive success for dominant females (Emery Thompson 2005). In female orangutans, energetic status influences ovarian function (Knott 1999, 2001), which suggests that differential access to feeding resources directly influences reproduction. However, researchers have not clearly demonstrated or measured female competition for resources in orangutans because low rates of social interaction make direct observation of feeding competition very difficult. We approached the question of female-female resource competition by analyzing patterns of range use. Ranging behavior is poorly documented in orangutans, owing to the difficulty of tracking multiple individuals over large areas. The only rigorous ranging data available are from Suaq Balimbing in Sumatra (Singleton 2000; Singleton and van Schaik 2001, 2002); thus our initial objective was to establish the size and degree of overlap of orangutan home ranges and core areas in a population of Bornean orangutans. We then use the data to examine a set of predictions regarding feeding competition.

The animal literature contains descriptions of 2 basic types of feeding competition (Nicholson 1954). Scramble competition occurs when animals share a common food supply and results in roughly equal reductions in the net caloric intake of individuals. Contest competition refers to overt behaviors of individuals that lead some to obtain a larger share of resources than others (van Schaik 1989). Examples of contest competition include territorial defense, displacement or eviction from feeding spots, and physical confrontations. In group-living animals, either intra- or intergroup contest and scramble competition can occur. Thus, 4 forms of feeding competition emerge: intragroup scramble; intragroup contest; intergroup scramble; and intergroup contest (Sterck *et al.* 1997; van Schaik 1989).

However, one cannot easily apply the intra- and intergroup theoretical framework for feeding competition to orangutans. They live in an individual-based fission-fusion society in which one can recognize social units only by analyzing long-term social association patterns, if at all (van Schaik 1999). Thus, the distinction between intra- and intergroup competition tends to blur. Because the frequency and duration of grouping varies between age-sex classes (van Schaik 1999), we chose to focus on solitary adult female individuals to which we apply intergroup concepts and evaluate the presence of scramble and contest competition.

van Schaik (1989) suggested that intergroup scramble competition can occur when groups that occupy more or less exclusive home ranges mutually avoid one another. Mutual avoidance may limit the costs of scramble competition by decreasing the overlap of search areas and the collective depletion of food resources.

Female orangutans have highly overlapping home ranges (Galdikas 1988; Rijksen 1978; Singleton and van Schaik 2002; van Schaik and van Hooff 1996). If scramble competition occurs, individuals should modify their ranging patterns to reduce its effects. Indeed, Sugardjito *et al.* (1987) suggested that orangutans avoid each other to escape from food competition when nonfig fruits are scarce, and van Schaik (1989) noted that the energetic costs of feeding competition might cause females actively to avoid others.

Intergroup contest competition occurs when dominant groups outcompete subordinate groups for food via aggressive displacement, avoidance of dominants by subordinates, or the ability of dominant groups to defend a larger or higher quality territory (van Schaik 1989). Orangutans feed predominantly on widely dispersed fruit trees with a small crop size that a single female and her dependent offspring can completely consume. Such high-value resources are potentially monopolizable and likely worth defending. Further, overlap among female home ranges should result in frequent opportunities for female encounters and contests over food patches. However, females rarely interact (van Schaik and van Hooff 1996) and even less frequently engage in aggressive interactions over access to food resources (Utami *et al.* 1997). Nonetheless, there may be alternate strategies of contest competition. Wrangham (1980) suggested that avoidance might represent contest competition if avoidance is directional, i.e., subordinates avoid areas or more dominant individuals occupy food patches, and results in skewed resource acquisition.

Though the semisolitary nature of orangutan social structure is likely an outcome of scramble competition for limited resources (van Schaik 1999), no study has directly evidenced intergroup scramble competition. This is not surprising because researchers have performed little empirical work on intergroup scramble competition due to the difficulty of measuring the effect of one group on another, and because they have assumed it has little effect on primate social structure (Janson and van Schaik 1988; van Schaik 1989). To quantify intergroup scramble, the scale of measurement must be larger than what one can easily observe in the field. Developments in spatial analysis and geographic information systems (GIS) have allowed us to evaluate orangutan ranging and interaction patterns on a new scale.

Because extensively overlapping home ranges are a prerequisite to intergroup competition, we first employed GIS to quantify the extent of overlap among the home ranges of female Bornean orangutans. We then looked for avoidance behavior as an indicator of scramble competition and predicted that females occupy relatively exclusive core areas as an outcome of scramble competition. No one has quantified avoidance among adult female orangutans, but researchers have assumed it occurs (Sugardjito *et al.* 1987). Avoidance is likely mutual; however, future work is needed to test whether avoidance is directional and results in differential resource acquisition, which would indicate intergroup contest competition.

We then examined the locations, outcomes, and attackers of aggressive interactions to test for contest competition. Previous researchers have demonstrated that female orangutans contest for food, and even demonstrate dominance relationships, particularly when forced to feed together in large, productive fig trees, (Sugardjito *et al.* 1987; Utami *et al.* 1997). However, because females aggregate only rarely, investigation of whether contest competition occurs on a larger scale is

important. We looked for indications of contest competition within the entire home range of individual female orangutans. We predict that female orangutans are more likely to contest for resources and win encounters within their own core areas.

The article is divided into two parts. First, we provide estimates of adult female home range sizes in Gunung Palung National Park, Indonesia and measure the degree of home-range overlap among adult female dyads. We define the concept of core area for orangutans and provide the first measurements of adult female resident core areas. In the second part, we consider ranging as it relates to feeding competition. We test for avoidance within overlapping home ranges as a measure of scramble competition, and we test for agonistic interactions over core areas as a measure of contest competition.

We tested 4 predictions:

- 1) Adult female orangutans have extensively overlapping home ranges, a condition under which competition for food resources is predicted to occur.
- 2) Within their overlapping home ranges, adult female orangutans actively avoid each other.
- 3) Adult female orangutans establish relatively distinct core areas within their home ranges.
- 4) Core area residents are more likely to attack other females and win in agonistic interactions within their own core areas.

Methods

Study Site and Population

We collected data at the Cabang Panti Research Site in Gunung Palung National Park, West Kalimantan, Indonesia. The 90,000-ha national park contains a resident population of *ca.* 2500 wild orangutans (Johnson *et al.* 2005). We studied orangutans in the 2100-ha Cabang Panti study site, which spans 7 distinct habitat types: peat swamp, freshwater swamp, alluvial bench, lowland sandstone, lowland granite, upland granite, and montane (Fig. 1). No ex-captive orangutans have been released into the park. We focus on 6 females for which we have extensive data.

Data Collection

The field site and trail system were originally mapped using survey techniques with compass and bearing, clinometer, and measuring tape. Subsequent GPS locations were taken at regular intervals along each trail and were used to construct a digital map of the trail system. We used an image of habitat type delineation within Gunung Palung to create a digital layer showing the distribution of habitat types across the study area.

We collected ranging and behavioral data during focal subject follows between August 1994 and April 2003, a time span of 103 mo. When possible, we followed orangutans for full days from nest to nest unless lost. We drew daily path lengths on gridded paper maps of the trail system via a compass and distance estimates.

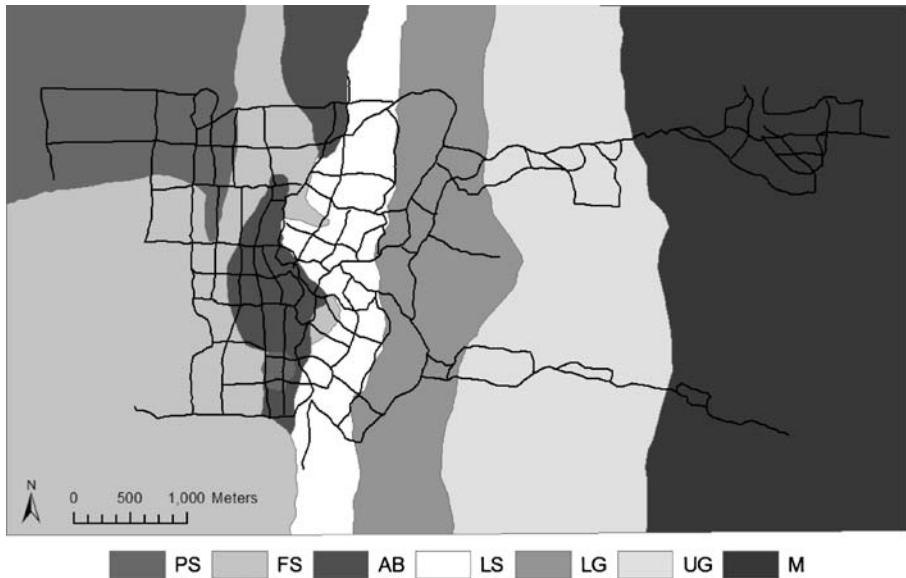


Fig. 1 Cabang Panti study site and trail system. Habitat types include peat swamp (PS), freshwater swamp (FS), alluvial bench (AB), lowland sandstone (LS), lowland granite (LG), upland granite (UG), and montane (M).

Whenever a subject crossed a trail, we confirmed the location via markers located at regular intervals along the trails. Data are spatially biased because there were more orangutans followed near camp, the center of the study site, than elsewhere.

Determination of Home Ranges

The entire ranging data set consists of 3714 daily travel paths of individual orangutans. We focused on the 6 females that we most heavily sampled across the study period: 5 adult females [Beth (BT), Elizabeth (EZ), Kate (KT), Kristen (KR) and Marissa (MR)] and 1 female [Kayla (KL)], which transitioned during the study between adolescence and adulthood. Kristen is the mother of both Kate (the older daughter) and Kayla. The degree of relatedness between the other individuals is unknown.

For both home range size and core area size we used all available daily ranging data regardless of follow length. We vectorized daily travel paths via AutoCAD. We determined home range size via the grid-cell method and the minimum convex polygon (MCP) surrounding all day range vectors per Singleton and van Schaik (2001). One can compare the results with estimates from Sumatran orangutans and from chimpanzees, bonobos, and gorillas (Ganas and Robbins 2005; Hashimoto *et al.* 1998; Lehmann and Boesch 2003; Singleton and van Schaik 2001). We included all follow data in the home range calculations including those that appeared to be excursions from frequently used areas. We used PostGIS to calculate the MCP for individual home ranges, and the degree of overlap among home ranges. We calculated home-range overlap in both directions for each dyad (Singleton and van Schaik 2002).

Determination of Core Areas

We derived our definition of orangutan core area from research on various species in which the investigators determined core area by the density of use per unit of area via the grid-cell method or the kernel method: chimpanzees (Emery Thompson 2005; Lehman and Boesch 2003; Williams *et al.* 2002), wolves (Kusak *et al.* 2005), bobcats (Plowman *et al.* 2006), and woodpeckers (Franzreb 2006).

To determine individual core area sizes we followed the large-grid-cell method that Singleton and van Schaik (2001) used to calculate home range size per Voigt and Tinline (1980), and adapted it for core areas. Emery Thompson *et al.* (2007) calculated chimpanzee core area by dividing the frequency of scans that they observed each chimpanzee in a given 500 m×500 m grid cell by the total number of scans in which they observed the chimpanzee. We modified the methods slightly. Using a 200 m×200 m grid, for each individual we calculated the number of days she used each grid cell divided by the total number of grid cells she entered on all days. We ranked grid cells in descending order by the percentage of daily use. We defined the core area as the grid cells whose accumulated percentage use totaled 50%. We also calculated 80% and 90% core areas (Williams *et al.* 2002) via the same method. We used ArcGIS to determine if the grid cells of the core area of an individual overlapped with those of other individuals. We summed the total number of core area grid cells overlapping per dyad and then calculated the percentage overlap in core area for each dyad based on total core area size.

Worton (1989) reviewed the limitations of the grid cell method in advocating the use of kernel methods in ranging studies. Though there has been some use of kernel methods for determining core area size in chimpanzees (Williams *et al.* 2002), we chose the grid-cell method for its consistency with previous orangutan and chimpanzee research (Emery Thompson *et al.* 2007; Lehmann and Boesch 2003; Singleton and van Schaik 2001). Nevertheless, future analyses of orangutan core areas may apply the kernel method or other applications.

Overlap in Grid Cell Usage

We measured day-use overlap by calculating the number of times each dyad used the same 200 m×200 m area on the same day, regardless of whether they were present in the grid square at the same time or interacted. We restricted the analysis to days when we followed both individuals of a dyad from night nest location to night nest location and calculated the percentage of grid-cell overlap.

Female Encounters

We calculated encounter rates as the percentage of full-follow days on which any encounter between focal females occurred. We defined an encounter as cofeeding, cotravel, or simply presence within 50 m of one another. A full-day follow from one member of a dyad was sufficient to determine whether an encounter took place. In contrast with association rates, which measure the duration of dyadic interactions, encounter rates measure the frequency of interactions.

Matrix Analyses

We performed row-wise matrix correlations and partial row-wise matrix correlations via Matman 1.1 (Hemelrijk 1990) on 4 ranging variables. Though we expect the variables to correlate highly, we wished to test this assumption and to examine the relationships among the variables. We thus ran 4 separate matrix correlations: home-range overlap and core-area overlap, home-range overlap and encounter rates, core-area overlap and encounter rates, and grid-cell overlap and encounter rates. For the matrix correlation in which we compared grid-cell overlap and encounter rates, we reduced the data set used for calculating encounter rates to include only days on which we followed both members of a dyad.

Expected Encounter Rates

To test whether adult female orangutans avoided one another, we calculated expected encounter rates and compared them with observed encounter rates via a coefficient of dispersion based on a Poisson distribution. We followed the ideal gas model Waser (1976) originally applied to primates to calculate expected encounter rates, and we incorporated modifications by Mitani *et al.* (1991) to account for differences in velocity among individuals. We also added a correction factor for area of home-range overlap devised by Kinnaird and O'Brien (2000). Our equation is as follows:

$$Z_{\text{exp}} = 2d(p_{ij})(o_{ij})(v_i^2 + v_j^2)^{1/2}$$

wherein d = a distance criterion chosen by the investigator to define associations (Mitani *et al.* 1991). Mitani *et al.* (1991) used a d value of 30 m based on the finding that during associations, orangutans typically stayed within a 30-m radius of each other. However, later orangutan field researchers have designated 50 m as the standardized association distance (Morrogh-Bernard *et al.* 2002); thus we defined the d value as 50 m. For the other variables in the equation, p = the density (females/m²) for each dyad, o_{ij} = the probability that individuals i and j are present in the area of overlapping home ranges at the same time (Kinnaird and O'Brien 2000), v_i = the mean travel velocity of individual i (Mitani *et al.* 1991), and v_j = the mean travel velocity of individual j .

Hutchinson and Waser (2007) noted that although Kinnaird and O'Brien (2000) corrected for home-range overlap in their equation, they did not account for density increases in areas of home-range overlap. We accounted for this by measuring density (p) for each female dyad p_{ij} :

$$p_{ij} = 1/(h_i - l_{ij}) + 2/l_{ij} + 1/(h_j - l_{ij})$$

wherein h = home range size and l = area of home-range overlap.

We tested for differences between observed and expected encounter rates by calculating a coefficient of dispersion (CD) to determine whether the observed values were Poisson distributed as recommended by Hutchinson and Waser (2007):

$$\text{CD} = s^2/Y$$

wherein s^2 = the variance and Y = the sample mean of observed dyadic encounter rates. We calculated variance across individuals to look at overall female avoidance. If distributions of numbers of rare events occur independently, they follow the Poisson distribution. If the occurrence of one event increases the likelihood of a second event, the distribution is clumped. If the occurrence of one event reduces the likelihood of a second event, the distribution is repulsed either spatially or temporally. Values are near 1 in the case of Poisson distributions, >1 in clumped samples, and <1 in the event of repulsion (Sokal and Rohlf 1981). The approach assumes that the number of encounters is Poisson distributed, which occurs only if trajectories are straight. Because this is clearly not always the case with orangutan ranging, the method will tend to reject the null hypothesis too often (Hutchinson and Waser 2007).

Female Rank and Spatial Distribution of Agonistic Encounters

We examined all agonistic encounters between females to determine female rank. Such encounters included contact and noncontact aggression of 1 female toward another, or both females toward each other. The primary type of aggression was one female chasing another one. We recorded the identity of the winner and the loser of the agonistic encounter. Losers were individuals who retreated or reduced their feeding as a result of the encounter. We displayed the location of fights relative to home ranges and core areas via ArcMap.

We explored the spatial distribution of contest competition by examining the attackers, locations, and outcomes of agonistic encounters between adult females. First we determined the attacker in each fight to evaluate whether core area residents were more likely to attack other females ranging within their own core areas. Then we tested for whether females were more likely to engage in fights within their own core areas by comparing the proportion of fights within core areas with the probability that at any given point one or both females would be within their core areas. We calculated the probability that either female would be in her 50% core area as:

$$P(A) + P(B) - P(A \times B)$$

wherein P = probability, A = individual 1, B = individual 2. Thus, $0.5 + 0.5 - (0.5 \times 0.5) = 0.75$. Lastly, we examined whether females were more likely to win fights within their own core areas.

Results

Ranging Data

The ranging data we used to calculate home range and core area size are from 1921 daily traces, representing 22,308 h of observation, of the 6 focal females. To calculate grid-cell overlap between dyads we used 800 full-day follows. The mean active period (time awake) from the 800 follows is 682 min and the mean distance traveled is 818 m/d.

Table I Home range and core area estimates for 6 adult females

Individual	No. of days followed	Small grid home range (ha)	Large grid home range (ha)	Polygon home range (ha)	50% Core area (ha) ^a	80% Core area (ha) ^a	90% Core area (ha) ^a	50% Core area as % of home range ^{a,b}
Beth	170	281	380	496	48	132	192	12.6%
Elizabeth	158	322	416	412	76	164	228	18.2%
Kate	214	410	576	731	76	208	308	13.2%
Kayla	179	293	508	605	80	208	296	15.7%
Kristen	229	356	468	524	72	180	248	15.3%
Marissa	986	578	700	806	40	124	224	5.7%

^a Core area size based on large grid cell analysis.

^b Home range size based on large grid cell method.

Home Range and Core Area Size

Adult female home range size via the small-grid-cell (100 m×100 m), large-grid-cell (200 m×200 m), and polygon methods are in Table I and Fig. 2. Mean home range values are 373 ha for the small-grid estimate, 508 ha for the large-grid estimate, and 595 ha for the polygon estimate. The mean core area is 65 ha and the mean core area as a percentage of home range is 13.4% (Table I). Thus, individuals spend the majority of their time in a small subarea of their home ranges (Fig. 3).

Female-female Encounters

Table II contains the percentage of days in which there was an encounter between a dyad based on days in which there was a full-day follow of ≥1 member of the dyad.

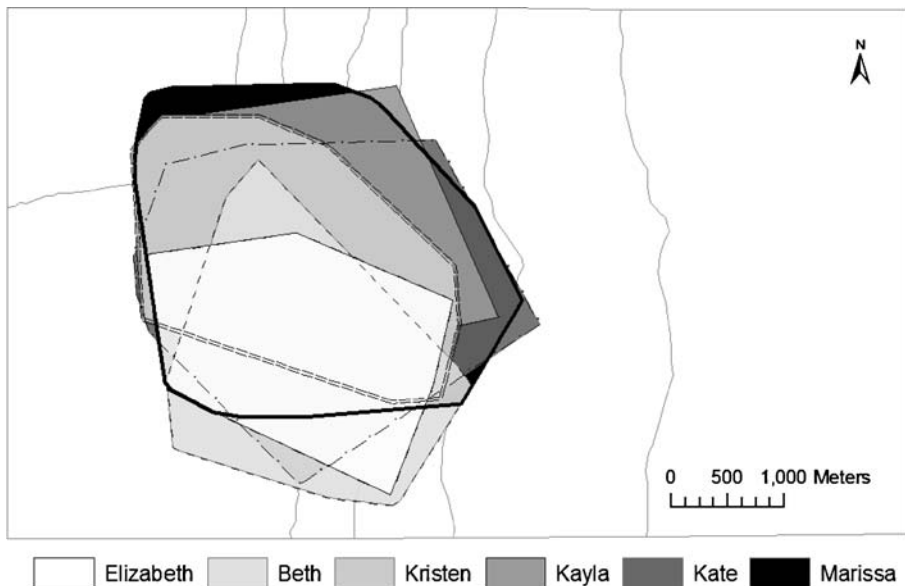


Fig. 2 Home-range overlap of adult females.

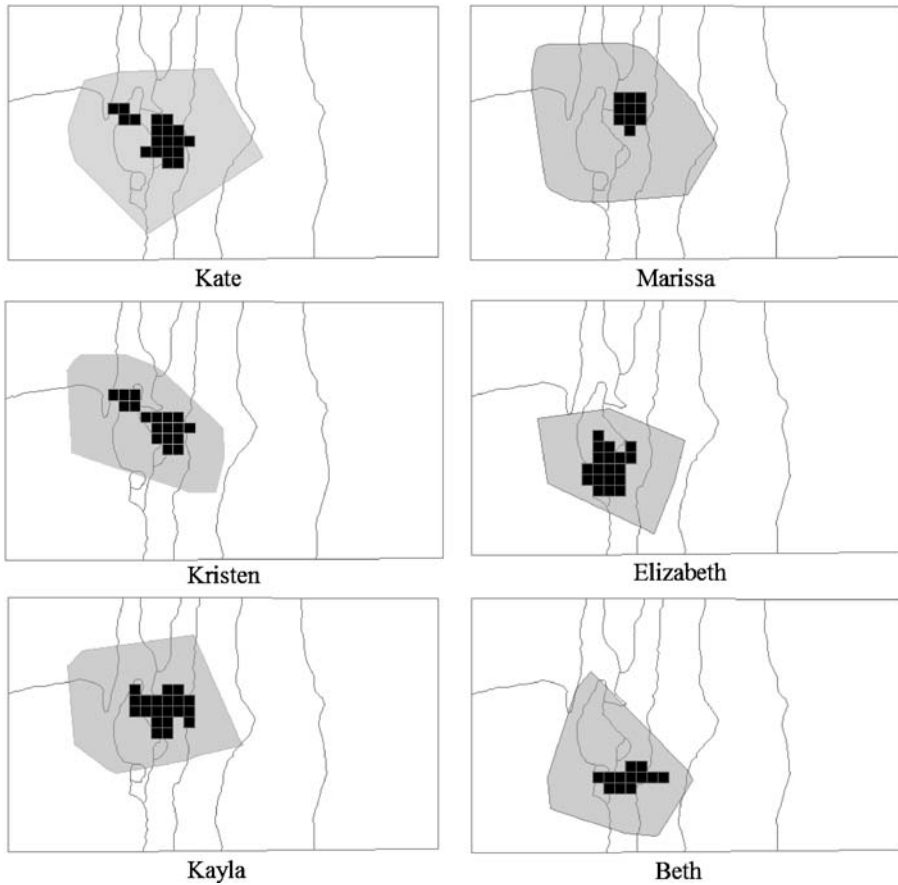


Fig. 3 Individual home range and core areas of 6 adult females. Grid cell squares are 200×200 m.

Overall encounter rates were 5.7%, 33.3% for mother-daughter dyads, 5.22% for sisters, and 1.4% for nonrelatives. The highest rates between dyads were between Kristen and each of her 2 daughters, Kristen/Kayla (48.9%) and Kristen/Kate (17.8%). The 2 sisters, Kate/Kayla, interacted on 5.2% of follow days, which was similar to the rates for presumed nonrelatives Beth/Elizabeth (4.3%) and Kristen/Marissa (4.0%), whose genetic relationship is not known. Kate/Beth, Kate/Marissa,

Table II Percentage encounter rates among adult females

	Beth	Elizabeth	Kate	Kayla	Kristen	Marissa
Beth	*	4.27	1.43	0	0	0
Elizabeth	—	*	0.54	0	0	0.41
Kate	—	—	*	5.22	17.79	1.63
Kayla	—	—	—	*	48.94	1.90
Kristen	—	—	—	—	*	4.04
Marissa	—	—	—	—	—	*

These encounter rates are based on full day follows of either member of a dyad.

Table III Results of matrix correlations run in Matman 1.1

Matrix 1	Matrix 2	<i>p</i> value	τ value
Home range overlap	Core area overlap	0.0020	0.7050
Home range overlap	Encounter rates	0.0020	0.7249
Core area overlap	Encounter rates	0.0175	0.6708
Grid cell overlap	Encounter rates	0.0010	0.6644

The correlation between home-range overlap and core-area overlap was a row-wise correlation. The remaining 3 were partial row-wise correlations holding constant the number of days we followed each dyad.

Kate/Elizabeth, Elizabeth/Marissa, and Kayla/Marissa encountered each other on <2% of their focal days. Several females never encountered one another during focal follows, despite thousands of hours of observation. There were 5 such dyads of the 15 total: Beth/Marissa, Beth/Kristen, Elizabeth/Kristen, Kayla/Beth, and Elizabeth/Kayla.

Matrix Analyses

Table III contains the results of matrix analyses between home-range overlap, core-area overlap, grid-cell overlap, and encounter rates. There are significant positive relationships in all 4 of the analyses: home-range overlap and core-area overlap ($\tau=0.7050$, $n=30$, $p=0.002$), home-range overlap and encounter rates ($\tau=0.7249$, $n=30$, $p=0.002$), core-area overlap and encounter rates ($\tau=0.6708$, $n=30$, $p=0.0175$), and grid-cell overlap and encounter rates ($\tau=0.6644$, $n=30$, $p=0.001$).

Prediction 1: Home-range Overlap

Table IV contains the percentage of home-range overlap between female dyads from the perspective of each individual. Mean percentages of home-range overlap between dyads are 67.8% overall, 65.1% for nonrelatives, 75.6% for sisters, and

Table IV Percentage of home-range overlap among female dyads from the perspective of each individual

	Beth	Elizabeth	Kate	Kayla	Kristen	Marissa
Beth	*	86.9	52.2	36.8	49.3	43.2
Elizabeth	72.3	*	51.0	37.6	49.6	43.1
Kate	77.0	90.6	*	82.7	89.9	81.8
Kayla	44.9	55.2	68.5	*	89.1	72.3
Kristen	52.2	63.0	64.4	77.2	*	64.1
Marissa	70.2	84.3	90.1	96.3	98.5	*

One can read the table from the perspective of the individual in either the column or the row. Each column shows the percentage of the home range of the individual in the column that is located in the home range of the individual in the row. Likewise, each row shows the percentage of the home range of the individual in the row that is located within the home range of the individual in the column. For example, 86.9% of Elizabeth's home range falls within Beth's home range, but only 72.3% of Beth's home range falls within Elizabeth's.

Table V Percentage grid-cell overlap per dyad

	Beth	Elizabeth	Kate	Kayla	Kristen	Marissa
Beth	*	2.38	1.65	–	–	0
Elizabeth	2.53	*	0	–	0	0.11
Kate	1.38	0	*	6.47	14.86	0.38
Kayla	–	–	2.48	*	–	0.11
Kristen	–	0	11.29	–	*	0.77
Marissa	0	0.43	1.93	1.44	5.07	*

The table is based on the number of grid cells a dyad overlapped in on the same day summed and then divided by the sum number of cells entered by the individual. We did not follow some dyads on the same day and thus could not measure grid-cell overlap.

80.2% for mother-daughter pairs. The extensive home-range overlap supports our first prediction that female orangutans have extensive home-range overlap.

Prediction 2: Active Avoidance

The mean daily grid-cell overlaps among dyads are 2.42% overall, 1.01% for non-relatives, 4.48% for sisters, and 13.1% for mother-daughter pairs (Table V). Thus, despite an overall home-range overlap of 67.8%, females very rarely used the same 200 m × 200 m area on a given day.

Of the 15 dyads, 12 encountered each other less often than expected by chance. The mean encounter rate is 0.0574 with a variance of 0.016. Based on the values, the coefficient of dispersion is 0.0278, which is a very strong repulsion of the Poisson distribution and indicates active avoidance. The 3 exceptions to the pattern are informative. Two dyads encountered each other more often than expected: the 2 mother-daughter pairs KR/KT (exp=14.2%, obs=17.7%) and KR/KL (exp=9.4%, obs=48.9%). Members of 1 dyad (KR/MR) encountered each other at approximately the same rates expected by chance (exp=3.94%, obs=4.04%). KR/MR was the most antagonistic dyad in the study, responsible for 44.8% of the agonistic encounters observed.

Table VI Percentage of 50% core-area overlap among female dyads from the perspective of each individual

	Beth	Elizabeth	Kate	Kayla	Kristen	Marissa
Beth	*	41.7	0	0	0	0
Elizabeth	26.3	*	15.8	0	5.3	0
Kate	0	15.8	*	36.8	57.9	26.3
Kayla	0	0	21.9	*	25.0	28.1
Kristen	0	5.6	61.1	44.4	*	33.3
Marissa	0	0	50.0	90.0	60.0	*

One can read the table from the perspective of the individual in either the column or the row. Each column shows the percentage of the core area of the individual in the column that is located in the core area of the individual in the row. Likewise, each row shows the percentage of the core area of the individual in the row that is located within the core area of the individual in the column. For example, 41.7% of Elizabeth's core area falls within Beth's core area, but only 26.3% of Beth's core area falls within Elizabeth's.

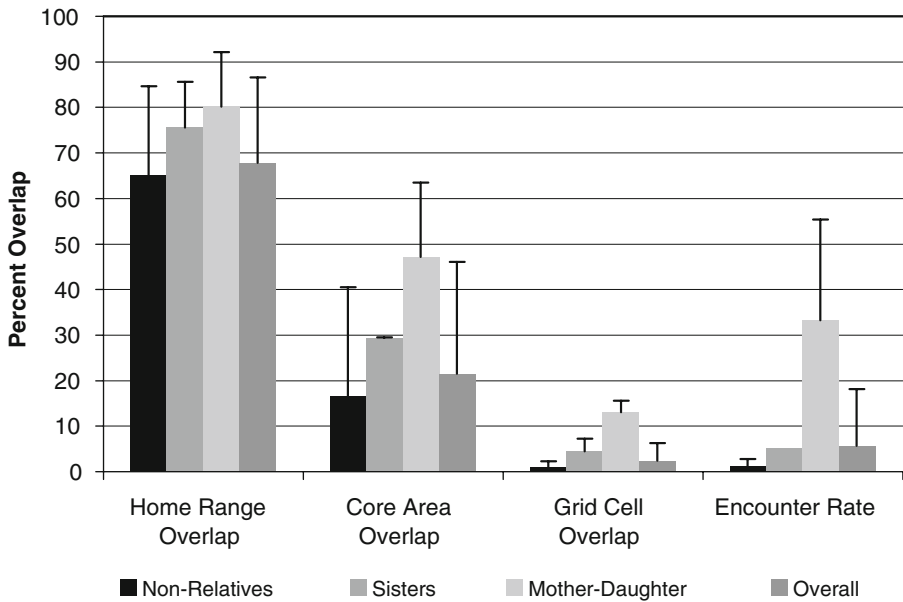


Fig. 4 Comparison of mean percentage home-range overlap, core-area overlap, grid-cell overlap, and mean encounter rates for 15 adult female dyads by degree of relatedness. Standard deviations, where applicable, are shown.

Prediction 3: Establishment of Distinct Core Areas

On average, core areas consisted of only 13.4% of an individual's home range (Fig. 3), with a mean size of 65 ha. Mean percentages of core-area overlap are 21.5% overall, 16.4% for nonrelatives, 29.3% for sisters, and 47.1% for relatives (Table VI). Kristen's percentage overlap is higher with her elder daughter, Kate, than her younger daughter, Kayla (though KT/KR interact less). Seven of the 15 dyads showed no overlap in core area usage. Thus, compared to home-range overlap, core areas have significantly less overlap (paired *t*-test, $p < 0.0001$; Fig. 4).

Prediction 4: Contest Competition Over Core Areas

Most female agonistic encounters were between juvenile and adolescent daughters and their mothers as the mothers encouraged them to travel independently. Excluding them from the analysis, we identified 29 agonistic encounters, 28 of which had a clear winner.

All adults participated in ≥ 1 agonistic encounter with another adult female. Five of the 15 possible dyads participated in agonistic encounters ($n=19$). The other agonistic encounters occurred between a resident female and an unidentified female ($n=10$). Some dyads showed clear dominance relationships. The MR/KR dyad engaged in 13 agonistic encounters, more than any other dyad in the study. They were also the only presumed nonrelatives to encounter each other at predicted frequencies. KR was the clear winner in 100% of the encounters. Thus, KR clearly was dominant to MR. MR was dominant to EZ in 2 of 2 encounters, a rate too low to

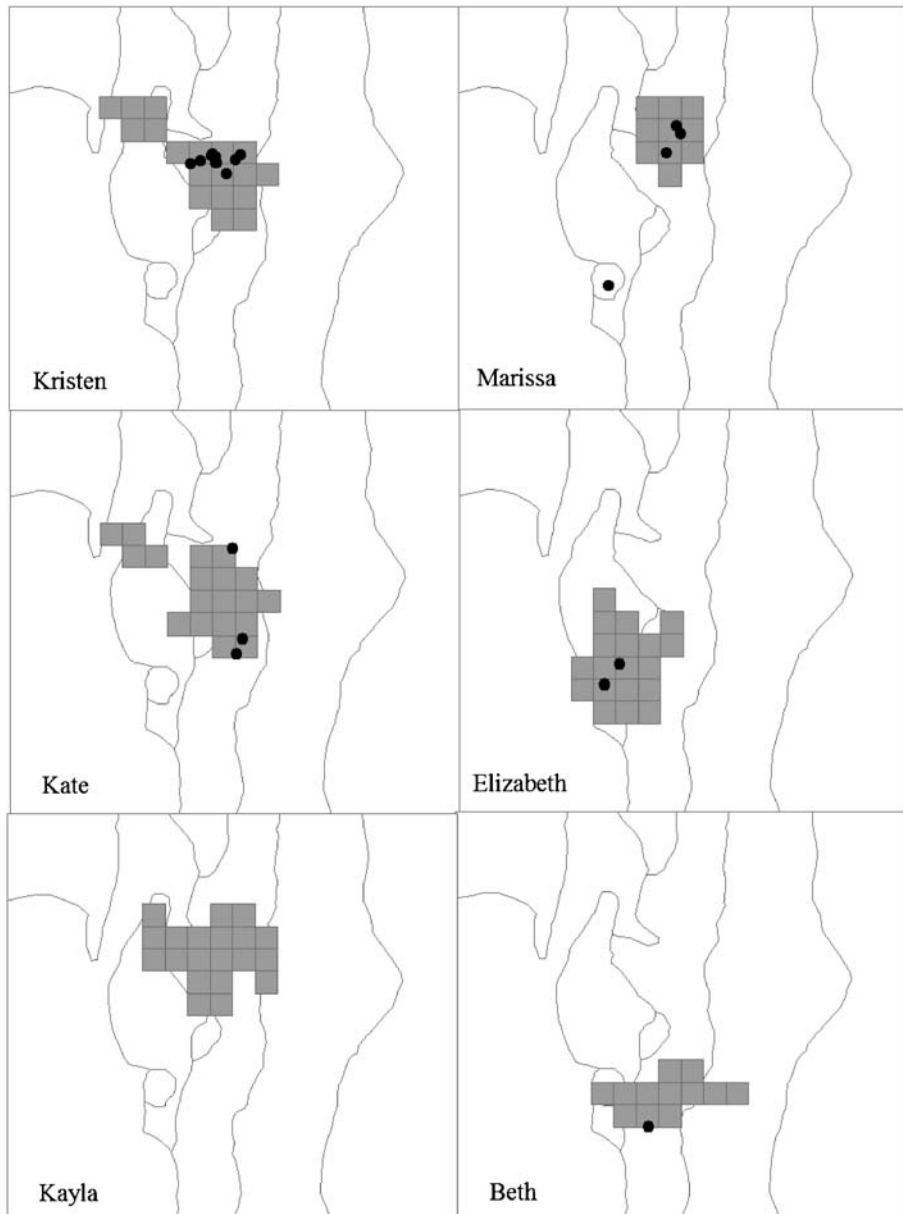


Fig. 5 Agonistic interactions within the core area of one or both participants. Each fight is displayed in relation to the core area of the winner of the fight. Grid cell squares are 200×200 m.

confirm a dominance relationship. EZ/BT interacted the most of any nonrelative pair and showed no antagonism.

All fights with a clear winner were won by the attacker regardless of the spatial relationship of the fight to the participants' core areas. Thus, we found no evidence that females are more likely to attack if they are within their own core area. The probability that either female would be in her 50% core area is 0.75. The percentage

of fights occurring within the core area of one or both participants is 65.5% (19/29) (Fig. 5). Because the percentage of fights within core areas is lower than the calculated probability that either female would be in her core area, it appears that adult females did not fight over core areas more often than is expected by chance. Of the 9 fights that took place outside of the focal subject's core area, 5 occurred with unidentified females.

Females were more likely to win fights within their own core areas. The core area resident won most fights (88.9%; 8 out of 9) that were exclusively in the core area of one fighter. The remaining core area fights occurred within overlapping core areas. Of the 10 fights, 8 were between KR and MR. The other 2 fights in core-area overlaps were between KT and MR and MR and an unidentified female. There is evidence for a spatial component to contest competition because females were more likely to win fights within their core areas, but we found no evidence that they were more likely to attack other females within their own core area. Thus, prediction 4 is only partially supported.

Discussion

In looking for indicators of female-female competition in orangutans our main predictions concerned 1) female home range and core area size, 2) the extent of home-range overlap between females, 3) the relationship between observed and expected encounter rates, and 4) the outcome and location of agonistic encounters with respect to individual core areas. The results support 3 of our 4 hypotheses, and our data indicate that adult female orangutans do indeed engage in both scramble and contest competition.

Home Range Size and Overlap

Singleton and van Schaik (2001) found that mean adult female home range size via the polygon method was 699 ha for 3 females (range, 608–853 ha). Our estimate is fairly similar, 595 ha for 6 females (range, 412–806 ha). However, it is 15% smaller on average, which may be attributable to the differences in habitat quality and population density between the 2 sites. Singleton and van Schaik (2001) suggested that the low species richness of the Suaq swamp results in a clumped distribution of fruiting tree species at any given time, leading the orangutans there to use a larger area to maintain an adequate diet. We propose that high population density and patchy resources may increase the amount of scramble competition. Orangutans may respond to increased scramble competition by increasing home range size. Because intergroup scramble competition is often a reflection of population density (Sterck *et al.* 1997; van Schaik 1989), adult females at Suaq may be subject to greater scramble competition for resources than at Gunung Palung due to higher orangutan density within their overlapping home ranges. However, given the differences between sites, it is striking how similar home range size is.

Singleton and van Schaik (2001) found that mean home range size is 272 ha (range, 197–323 ha) via the small-grid-cell method and 481 ha (range 436–520) via the large-grid-cell method. By comparison, we found that mean home range size is

373 ha (range, 281–578) via the small-grid-cell method and 508 ha (range, 380–700) via the large-cell method. Given that Singleton and van Schaik (2001) had fewer data per female, it is not surprising that their estimates of home range size via the small-grid-cell method are smaller than ours because the method is most accurate for intensively studied individuals. Adult female orangutans have highly overlapping home ranges. Singleton and van Schaik (2001) developed the methods to calculate home-range overlap, but they did not report the dyadic values or the overall mean overlap value among individuals. Though previous researchers showed home-range overlap via maps of estimated home range locations, we are the first to present quantitative data on the percentage of home-range overlap between individual dyads. Matrix analyses also confirmed our expectation for significant positive relationships between home-range overlap and core-area overlap, between encounter rates and home-range overlap, and between core-area overlap and grid-cell overlap.

The high degree of home-range overlap between Kristen and her 2 adult daughters is further evidence for female philopatry in orangutans (Fig. 4). Though the data are limited to a small number of individuals, they support a female philopatric tendency (Singleton and van Schaik 2002; van Schaik and van Hooff 1996).

Home-range overlap results in shared access to resources. It is critical that individuals adjust their ranging behavior to optimize energy intake from shared resources, especially given the extreme fluctuations in food availability in Borneo and the effects on ovarian function (Knott 1999, 2001). One may adjust the extent of home-range overlap according to the density of individuals and resources because the presence of other individuals within overlapping home ranges both reduces the amount of food available and makes food availability less predictable (Isbell 1991). Within overlapping areas, mutual avoidance indicates scramble competition. We therefore argue that the high degree of home-range overlap coupled with evidence for largely exclusive core areas and active, presumably mutual, avoidance among adult female orangutans, quantified here, indicates the presence of scramble competition.

Establishment of Distinct Core Areas

Researchers have referred to orangutan core areas (Galdikas 1978; Hurr 1975; Rijksen 1978), to the extent that te Boekhorst *et al.* (1990) included core area as part of the dominant view on orangutan ranging: “the females are believed to occupy overlapping home-ranges with discernible core-areas” (p. 1098). However, they have not quantified the term in the orangutan literature as they have for other species. Singleton (2000) described the “central zone, or core area, in which they normally reside, of around 500 ha in extent, that has relatively fixed boundaries, is stable over time, and may overlap with as many as 15 other adult females” (pp. 82–83). Although what Singleton described clearly exists, our definition of core area employs a stricter definition that has been applied to other species. Moreover, we chose to focus our analyses on the smallest of our 3 measures of core area (50%) to study the areas of highest use. Though orangutans have large overlapping home ranges, females have small areas in which they spend half of their time. The existence of more distinct individual core areas may be a means by which individuals secure access to some resources. We suggest that it is a foraging strategy that optimizes food intake and counteracts the effects of scramble competition.

Active Avoidance

Canopy observations by humans (Laman, *pers. comm.*) indicate that one can see orangutan movements and approaches at much greater distances than ground-level observation would indicate. Thus, it is likely that an arboreal orangutan is able to detect the presence of another orangutan from a much greater distance than a human observer on the ground can. Though adult female orangutans do not use vocalizations for spacing in the way that males use the long call (Mitani 1985), spacing mechanisms may nevertheless operate. Based on simultaneous follows of female dyads, we showed that most unrelated female dyads avoid each other when ranging in the same area. We suggest that visual detection may be one method by which they do so, even though human observers may be unaware of the near encounters.

Mitani *et al.* (1991) found that the rate at which adult female orangutans encounter and associate with other orangutans was greater than predicted by chance at Kutai and Gunung Palung. However, they considered encounters between adult females and other age-sex classes. Mitani *et al.* (1991) noted that associations were commonly in a mating context. In contrast, our data show that encounters between adult female nonrelatives are less than expected by chance. Instead of the Wilcoxon matched-pairs signed-ranks test that Mitani *et al.* (1991) used, we followed Hutchinson and Waser (2007) in using the Poisson distribution to test for avoidance to account for non-independence of encounter rates due to the use of consecutive periods of observation and the simultaneous observation of 2 orangutans.

Female orangutans at Suaq Balimbing associate with other orangutans more than expected by chance (Singleton and van Schaik 2002; van Schaik 1999). However, it is important to note that the equation for calculating expected association rates differs from the equation for expected encounter rates. Therefore the association rate results from Suaq are not directly comparable to our study of encounter rates. Singleton (2000) calculated expected encounter rates for Suaq via a method similar to ours, but did not report encounter rates for adult females separately from overall expected encounter rate values. Thus, though results from Singleton (2000) suggest that overall encounter rates at Suaq are higher than expected, it is unclear whether this is significant for encounters between adult females. Further studies examining association and encounter rates are needed to make intersite comparisons.

We argue that active avoidance among adult female Bornean orangutans is a foraging strategy used mutually to reduce the likelihood of encountering food patches that are being or have been depleted by another feeding orangutan. Via a study on the effect that foraging with a social partner for limited food has on foraging strategies, MacDonald and Agnes (1999) found that captive *Pongo pygmaeus abelii* avoided visiting sites where they had seen their social partner consume the available food. By avoiding food competitors, female orangutans may be able to increase their caloric intake. Active avoidance of other adult female orangutans may also serve to reduce the occurrence of contest competition over resources. Thus, active avoidance may serve the dual function of reducing the effects of scramble competition and the frequency of contest competition. In the KR/MR dyad, avoidance did not occur and the frequent antagonism present in the encounters may indicate that they were contesting for access to a particularly high-quality area.

Contest Competition and Core Areas

Agonistic encounters among adult female orangutans are remarkable on 3 counts: 1) The events are rare. Adult females seemed to limit contest competition through active avoidance. 2) When females fought, they were not necessarily more likely to attack within their own core area; however, core area residents were much more likely to win fights that occurred in nonoverlapping core range areas. Thus, based on available data there is limited evidence of a spatial relationship between contest competition events and core area locations. 3) Core areas of adult female orangutans were small enough potentially to be defensible. We propose that the primary mechanism of defense is likely passive range exclusion through mutual avoidance, with only occasional antagonistic competition.

Orangutans are classically a nonterritorial species (Mitani and Rodman 1979; van Schaik and van Hooft 1996). Mitani and Rodman (1979) developed an index of range defensibility in which $D = d/\sqrt{(4A/\pi)}$, wherein d = day journey length and A = area of range. They showed that D should be ≥ 1 for territories to be defensible. van Schaik and van Hooft (1996) noted that large range size makes territoriality virtually impossible for orangutans. This is certainly the case for overall home range size wherein $D=0.297$. However, if we measure the defensibility of core areas, $D=0.899$. Thus, adult female orangutan core areas are much closer to the requirement for defensibility ($D=1.0$) than overall home range areas. However, in spite of the potential for core area defense, the low level of agonistic encounters suggests that core area defense is rare.

Mechanisms other than direct aggressive contests may lead to relative nonoverlap of core areas, most notably passive range exclusion (PRE). Mutual avoidance of aggressive contests creates range exclusion without active defense (Kaufmann 1983), and its effect is most significant for species that forage individually (Stewart *et al.* 1997). Given that adult female orangutans actively avoid each other, that fights are rare, and that they forage as independent entities of a fission-fusion society, orangutan core areas may be an excellent example of the effect of passive range exclusion. Moreover, relatively exclusive core areas as the outcome of mutual avoidance occur in other species. Coati bands, which forage on forest litter invertebrates, benefit by mutually restricting their food searches to predominantly exclusive core areas, which allows them to avoid recently depleted areas (Kaufmann 1962). Kaufmann (1983) argued that coati band core areas qualify as territories even without active defense. Thus, orangutan core areas may function as territories in which adult females focus their foraging efforts on relatively exclusive resources.

In summary, our analysis of adult female agonistic encounters highlights 3 facets of orangutan behavior: 1) the rarity of contest competition, 2) a limited amount of evidence for core area defense, and 3) the proposal that passive range exclusion explains the relative nonoverlap of adult female core areas.

Comparison with Chimpanzees

Our results for female orangutans show several similarities with those of female chimpanzees, particularly those from East Africa. Female chimpanzees in some East African communities also have core areas within home ranges and fission into

smaller groups when food becomes scarce to reduce the impact of scramble competition (Williams *et al.* 2002; Wrangham and Smuts 1980). Thus, rates of aggression among females are generally low (Goodall 1986; Kahlenberg 2006). Because core areas differ in habitat quality, which is associated with differences in reproductive success (Emery Thompson *et al.* 2007; Williams *et al.* 2002), female aggression can be intense when new immigrants enter a community and attempt to establish a home range within a resident's core area (Kahlenberg *et al.* 2008; Townsend *et al.* 2007). Similarly, we found low rates of aggression in orangutans. However, there are important differences. In chimpanzees, females typically emigrate into a new community (Pusey 1980), whereas in orangutans females appear to establish home ranges and core areas near their mothers. In addition, rates of contest competition are still very low in the Cabang Panti population of orangutans, lower than the ones in East African chimpanzees, and very much lower than in West Africa, where female contest competition over food is much more common and a clear dominance hierarchy exists (Wittig and Boesch 2003). In addition, female chimpanzees must account for threats from neighboring communities in their foraging decisions (Emery Thompson *et al.* 2007), a factor not known to be present for orangutans, though, as in chimpanzees, female-female competition may factor into home range establishment.

Effects of Spatial Bias

It is important to take into account the potential effects of spatial bias on our data set. Like most other great ape studies, we did not find individuals randomly, but start location was biased based on the search strategy of human observers. We recorded more data per individual closer to camp. Previous researchers have acknowledged this bias but have been limited to correct for its effects (Emery Thompson *et al.* 2007; Singleton and van Schaik 2001, 2002). This may be particularly important for core area results, which measure the most heavily used areas. However, it is notable that even with the spatial bias driving the bulk of data collection to the center of the study site, females nonetheless maintain fairly distinct individual core areas. It is probable that after declustering, we would find that core areas overlap <13.4% on average. Thus, we are confident in our interpretation that adult female core areas are relatively nonoverlapping in comparison with home-range overlap despite the potential influence of spatial bias.

Home-range estimates are probably only minimally biased due to the considerable number of follows per individual as well as multiday follows that allow the MCP to include apparent outliers. Moreover, the MCP method typically overestimates home range size. Given that we followed the females extensively, it is more likely that home range size is overestimated rather than underestimated despite observation bias in certain locations. However, we abandoned orangutans when they ventured >500 m off the trail system; thus range boundaries could be altered in certain locations.

Future Directions for Research

Competition clearly exists among female orangutans. Utami *et al.* (1997) showed that dominance hierarchies also exist and are measurable via contest competition in

fig trees. We showed that adult female orangutans actively avoid each other because of scramble competition and engage in contest competition over core areas. However, we did not determine a clear hierarchy for behavior outside of rare feeding aggregations at food sources. We suggest 2 additional methods for future measurements of rank in orangutans: assessing core area habitat quality and dyadic avoidance patterns. To measure rank via core area, one must quantify the quality of each habitat type and then map the distribution of food resources across the study site. It will then be possible to determine which core areas contain higher-quality resources and to use core area quality to assess rank differences by measuring resource access. To measure rank via avoidance data, the first requirement will be to determine the distance at which an orangutan is able to detect another orangutan. One can use daily ranging data to evaluate whether both members of a dyad mutually avoid each other on reaching the detection distance or only one individual turns away. In the latter case, one can then use avoidance to determine rank among individuals assuming that lower-ranking individuals avoid higher-ranking ones.

Feeding competition should be important for female orangutans because they evidence ovarian responsiveness to energetic status when there is differential food availability (Knott 1999, 2001). Within a population, there is a wide variation in interbirth intervals, e.g., 7.4–11.1 yr at Ketambe (Wich *et al.* 2004). However, there is no report on whether certain individuals in a population reproduce more quickly, on average, than do others. We hypothesize that some individuals are able to reproduce faster because they have access to better resources when their core areas are located in higher-quality habitats, as Emery Thompson *et al.* (2007) showed for chimpanzees.

Future studies may be able to test further whether contest competition is more likely to occur in core areas. For example, with more information on dominance relationships between females, we could test whether dominants are more likely to win in agonistic encounters within overlapping core areas. Further, methodological advances, such as the use of GPS monitoring to track range movements and to pinpoint fights, will increase the accuracy of our measurements and may present an enhanced picture of the relationships. In addition, future analyses can reveal the relationship between female fights and other variables such as the temporal and spatial availability of resources and female reproductive state.

Researchers know little about how female orangutans settle on a home range and core area except that the areas overlap with those of their mother and close female relatives. Other females in adjacent areas may suffer a cost for this establishment if the younger females push into part of their range. It is intriguing that nearly half of the fights were attacks on Marissa by Kristen, who had 2 adult daughters. The possible role that mothers play in helping daughters establish home ranges warrants further investigation. In addition, the continuation of long-term field studies will elucidate shifts in home range and core area size and location as new females establish their ranging patterns and old females die.

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