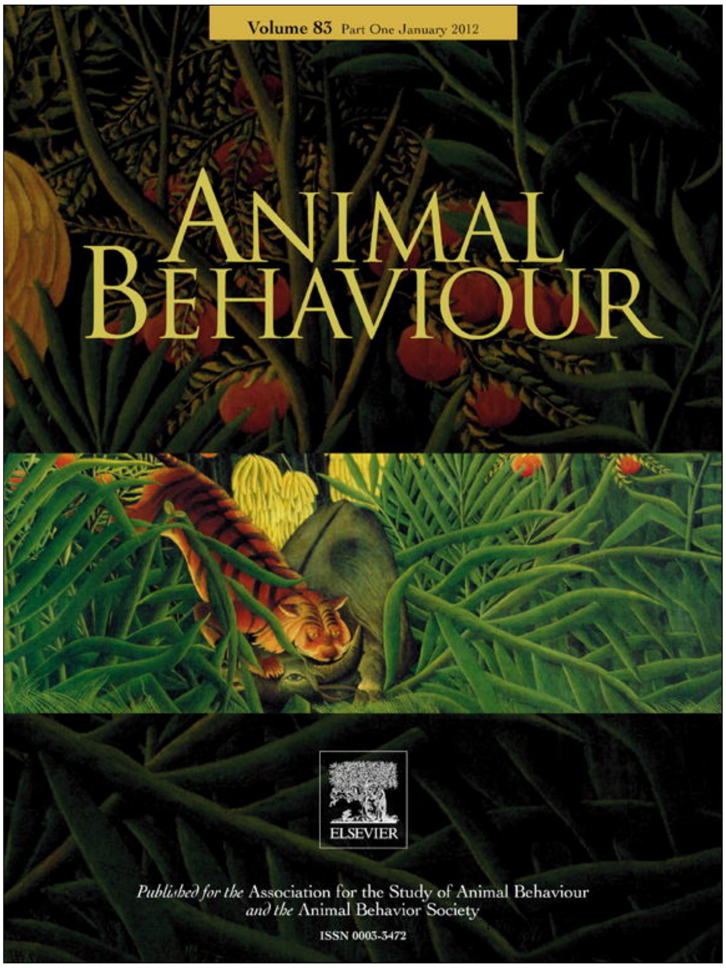
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Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees

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Male chimpanzees, *Pan troglodytes*, defend group territories, and sometimes injure or kill members of other groups. To test which factors best predict the occurrence and outcomes of intergroup encounters, we analysed 15 years of data on intergroup encounters, party composition, ranging and feeding behaviour in the Kanyawara community of chimpanzees, Kibale National Park, Uganda. During this time, researchers observed 120 intergroup encounters, most of which (85%) involved only acoustic contact. The majority of encounters (63%) occurred in the southeast quadrant of the range. Multiple logistic regression found that intergroup encounters occurred more often when chimpanzees were far from the centre of their range, especially in the south, and when eating foods that were most abundant in the south. Multiple linear regression found that chimpanzees travelled further from the centre of their range, and further south, when eating a few key foods, especially fruits of *Uvariopsis congensis*, and when in parties with more males. Upon hearing calls from foreign chimpanzees, Kanyawara chimpanzees were more likely to vocalize in response, and to travel towards the foreign chimpanzees, when they had more males in their party. Measures of two resource values, food and mates, were negatively correlated with the probability of vocalizing and approaching intruders, respectively. These findings indicate that, in this population, resources affect the timing of intergroup encounters, but the decision to escalate a contest depends mainly on numerical strength, rather than the value of resources being contested.

Intergroup competition plays a prominent role in efforts to explain the evolution of social groups (e.g. Wrangham 1980; Macdonald 1983; Packer et al. 1990; Fashing 2001; Bowles 2006; Majolo et al. 2008; Mosser & Packer 2009). Factors affecting the outcomes of intergroup contests may include relative group size, number of males and proximity to territory centre (e.g. Cant et al. 2002; Kitchen 2004; Kitchen et al. 2004; Crofoot et al. 2008; Harris 2010). Important potential benefits include increased access to food (Mosser & Packer 2009; Crofoot & Wrangham 2010), water (Wrangham 1981), sleeping sites (Anderson 1984) and mates (Emlen & Oring 1977). The value of such benefits can vary among group members. As a result, individual participation in intergroup contests is expected to vary according to factors such as sex, age, rank, reproductive status and the particular resource at stake (Boydston et al. 2001; Cooney 2002; Kitchen & Beehner 2007; Bonanni et al. 2010; Mares et al. 2011). Our aim in this paper is to understand the factors promoting intergroup competition by males, particularly the relative importance of competition for mates and land.

Males are expected to be motivated most importantly by competition over mates (Trivers 1972; van Schaik et al. 1992; Robbins & Sawyer 2007). In addition, however, males may also benefit by defending resources of value to their mates (Emlen & Oring 1977). Individual males defend breeding territories in many species, including a variety of African antelope (Jarman 1974) and passerines (Emlen & Oring 1977). Several recent studies of group-living primates have likewise found support for male resource defence (e.g. black and white colobus monkeys, *Colobus guereza*: Fashing 2001; Harris 2010; white-faced capuchins, *Cebus capucinus*: Crofoot 2007). Competition for food resources and for

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females need not be mutually exclusive: in species living in cohesive groups, females may benefit from improved access to food resources as a by-product of male efforts to repel rival males (Wrangham & Rubenstein 1986). This means that the extent to which intergroup competition by males serves functions of mating or resource competition is not easy to assess.

Knowledge of the proximate causes of intergroup aggression can help by showing whether groups encounter one another as a result of random movements (Hutchinson & Waser 2007), or when they are mutually attracted to key resources, such as oestrous females and food. In banded mongooses, *Mungos mungo*, focal groups fight with other groups more frequently when the focal group's females are in oestrus (Cant et al. 2002). In green monkeys, *Chlorocebus sabaeus*, intense intergroup competition occurs when *Pseudospondias microcarpa* fruits are ripening (Harrison 1983). Such contrasts are useful, but in banded mongooses and green monkeys both sexes participate.

Chimpanzees, *Pan troglodytes*, offer excellent opportunities for studying this problem because intergroup aggression is an almost exclusively male behaviour. Chimpanzees live in fission–fusion groups (communities) in which individuals travel, forage and rest in fluid subgroups (parties), which may vary in size throughout the day but which rarely include even a majority of the community's members (Goodall 1986; Mitani 2009). Males generally spend their entire life in their natal group, whereas females typically disperse at sexual maturity (Pusey 1979). Community males occupy a large shared home range that they defend during coordinated patrols of boundaries and in intergroup encounters, which are generally hostile and sometimes result in fatal attacks (Wilson & Wrangham 2003; Boesch et al. 2008; Mitani et al. 2010). Intergroup encounters thus involve variable combinations of males.

Three main functions have been proposed for chimpanzee intergroup aggression: acquiring dominance (Wrangham 1999), recruiting fertile females (Boesch 2009) and obtaining access to a larger territory (and therefore increased food resources: Williams et al. 2004). Current data support all three. Attaining dominance over rival communities enables males to acquire more territory (Gombe: Wilson et al. 2004; Ngogo: Mitani et al. 2010), which in turn can provide access to more females as well as to more food (Gombe: Williams et al. 2004; Mahale: Nishida 1979; Nishida et al. 1985). That chimpanzees gain benefits from acquiring more territory has been supported by results from three studies (Nishida 1979; Williams et al. 2004; Mitani et al. 2010). At Mahale National Park, Tanzania, individuals from the large M-Group regularly made incursions into the range of the smaller K-group, supplanting the resident chimpanzees to feed on seasonally available foods (Nishida 1979). In Gombe National Park, Tanzania, several lines of evidence suggest that when territory size was larger, chimpanzees of the Kasekela community had improved access to food: chimpanzees travelled in larger parties (Williams et al. 2004), females had shorter interbirth intervals (Williams et al. 2004), and, controlling for sex, age and reproductive status, individuals weighed more (Pusey et al. 2005). The importance of territory size, and thus presumably food resources, in intergroup aggression is further supported by observations of the Ngogo community in Kibale National Park, Uganda, where chimpanzees expanded their range into an area where they had recently killed multiple members of a rival community (Mitani et al. 2010). Thus, the ultimate benefits of successful intergroup aggression include access to both mates and food, and possibly reduced vulnerability to harm.

By contrast, no studies have yet reported on the proximate contexts in which intergroup encounters tend to occur. Three reasons have been proposed for visiting boundaries, conforming to the proposed ultimate functions. First, males have been observed making deep incursions apparently in search of opportunities to attack neighbours (Wrangham 1999; Boesch & Boesch-Achermann 2000; Wilson et al. 2004; Watts et al. 2006). Second, visits to territorial boundaries in search of females have apparently prompted intergroup aggression (Boesch 2009). Third, intergroup encounters occurred frequently when food became abundant in an area normally occupied by a small community, leading to intrusions by a larger, dominant community competing for the food supply (Nishida 1979).

In this study, we examined the influence of both oestrous females and food resources on the timing of intergroup encounters. Once groups come together, either by chance or as a result of mutual attraction to a key resource, a contest may ensue, in which one or both sides escalate the interaction by displaying at, approaching, chasing and fighting members of the other side. Opponents may choose to escalate if the resource at state is particularly valuable to them. For example, male black howler monkeys, *Alouatta pigra*, respond more aggressively to the calls of foreign males when young infants are present in their own group, presumably to protect their infants from the risk of infanticide (Kitchen 2004). Alternatively, members of a group may escalate when assessment indicates they have superior fighting ability and are thus likely to win the contest (Maynard Smith & Parker 1976). We previously found that fighting ability, as measured by the number of adult males in a party, predicted willingness to vocalize to and approach a simulated intruder (Wilson et al. 2001). In this study, we examined a larger sample of naturally occurring intergroup interactions, and, in addition to examining the effects of the number of defenders, we also tested whether response depends on the resources at stake. Specifically, we tested whether chimpanzees are more likely to respond aggressively when defending abundant food sources, oestrous females or young infants, which are vulnerable to infanticidal attack by foreign males (Watts et al. 2002; Wilson & Wrangham 2003).

METHODS

Study Site and Population

We analysed 15 years of data (1992–2006) from the Kanyawara community of chimpanzees in Kibale National Park, Uganda, located in western Uganda (0°13′–0°41′N and 30°19′–30°32′E). The Kanyawara chimpanzees inhabit an area located along the northwestern edge of the park. The Kanyawara home range is dominated by mid-altitude semideciduous tropical forest, interspersed with other vegetation classes including papyrus swamp, grassland and regenerating forest (Wrangham et al. 1994; Struhsaker 1997).

Following observations of the Kanyawara community by Ghiglieri (1984) in 1979–1980 and by Isabirye-Basuta (1988) in 1983–1985, Wrangham established the Kibale Chimpanzee Project (KCP) in 1987, and has maintained continuous observation of the chimpanzees since 1988. By January 1990, the adult males could be observed systematically. As has been the case for other chimpanzee studies (Goodall 1986; Boesch & Boesch-Achermann 2000), intergroup encounters were not observed in the early years of the study. Years of observation are generally required before the community membership and home range are sufficiently well known to distinguish intergroup encounters from other encounters, and before habituation reaches the level needed to permit the regular, long observation periods needed to follow chimpanzees to the periphery of their range, where intergroup encounters are most likely to occur (Wilson & Wrangham 2003). Observers first reported an unambiguous encounter between Kanyawara chimpanzees and members of another community in 1992. We therefore limited analysis to data collected starting in 1992. Unhabituated chimpanzee communities neighbour Kanyawara on all sides, except the northwest, where the park borders a tea plantation.

During the study period, the Kanyawara community contained a median 47 chimpanzees (range 43–51), including a median of 11 adult males (range 10–13) and 15 adult females (range 12–19). For the purposes of this study, we defined adult as 12 years or older. Male chimpanzees are not fully grown until they are 14–15 years old (Pusey 1990), but by age 12, they usually travel independently and can hunt successfully (Gilby et al. 2006), and thus may contribute significantly to group fighting ability.

Research Questions and Model Selection

We selected models using an information-theoretic approach (Anderson 2008). For each question, we developed a set of a priori candidate models, representing hypothesized relationships among variables of interest (Table 1). For each candidate model, we calculated the values for AIC, ΔAIC (which is equal to $\text{AIC}_\text{i} - \text{min}$ AIC, where min AIC is the minimum AIC value of all models), and the Akaike weight, w_i (the weight of evidence that model i is the best model given the data and the set of candidate models under consideration; Anderson 2008). For data sets with smaller sample sizes, we used AICc, which includes a correction for small sample size (Anderson 2008).

To determine which factors best predicted the occurrence and outcome of intergroup encounters, we examined a priori models designed to answer the following four research questions.

(1) Which social and ecological factors best predict the probability of an intergroup encounter occurring on a given day?

(2) Which social and ecological factors best predict movement towards areas where intergroup encounters are most likely to occur?

(3) For any food categories found to have strong temporal associations with intergroup encounters, are there also strong spatial associations?

(4) Which social and ecological factors best predict escalation of intergroup encounters, as measured by vocal and approach responses?

We examined models for questions (1) and (2) at the level of the 'follow': the observations recorded by a single team of observers on a single day. Days on which multiple teams of observers followed separate parties thus had multiple follows. Models for question (3) were examined at the level of the 500 × 500 m grid cell. Models for question (4) were examined at the level of the intergroup encounter. The sets of models used to answer our four main research questions thus included 3–20 explanatory variables in each model. To ensure that these models did not suffer from multicollinearity, we calculated variance inflation factors (VIF) for each explanatory variable in each set of models. The resulting VIF values were all less than 2 (median = 1.2, range 1.0–1.8, $N = 36$ explanatory variables in four sets of models). A VIF value greater than 10 is generally considered high (Kleinbaum et al. 1988).

Table 1
Variables selected for use in a priori model analyses of intergroup encounters in chimpanzees

Abbreviation	Description
No. of males	Number of adult males (≥12 years old)
No. of oestrous females	Number of females with fully tumescent sexual swellings
No. of infants	Number of infants in party (≤3 years old)
Obs. time	Observation time (number of 15 min scans per follow)
Dist. from centre	Distance (m) from centre of range
Far	Furthest distance (m) from centre of range visited during a follow
South	Minimum UTM *Y* coordinate (m) visited during a follow
Food value	Percentage of a given month's total feeding time observed within a given 500 × 500 m grid cell
BAN, PSD, UVA, etc.	Percentage of feeding time spent eating food of a given category (ripe fruits of the genus indicated, unless another part is designated); see Table 2 for food codes

For party follows, mean values of party composition and spatial variables were used; for encounters, values from the scan closest to the start of the encounter were used.

Basic Observation Methods

Basic behavioural and ecological data have been collected by K.C.P. since 1987, using essentially the same methods throughout (e.g. Conklin-Brittain et al. 1998; Wilson et al. 2007; Gilby et al. 2010). On most days, a team of two Ugandan field assistants, often accompanied by the field manager, one or more graduate students, and/or visiting scientist(s), followed a party of chimpanzees. Each evening, chimpanzees make sleeping nests in trees, usually in a new location each night. When chimpanzees were followed to their night nests the previous night, follows began before dawn at that nest site. Otherwise, the observers searched for chimpanzees, checking at recent feeding sites and listening for calls. Observers generally attempted to follow parties from dawn to dusk. When parties split, observers generally stay with the larger subgroup. Staying with the larger subgroup could potentially bias our results; for example, previous studies have found that subgroups with more males are more likely to visit the periphery (Watts & Mitani 2001; Wilson et al. 2007). However, our data set includes follows of many small parties as well as large parties, so we believe that the potential bias induced by our observation methods is slight, for the purposes of this study.

During each party follow, observers conducted scan samples at 15 min intervals, recording the location of the party by hand on printed maps of the study area and recording the identity of all individuals present. Observers recorded the status of each female's sexual swelling as none, partially tumescent or fully tumescent. Female chimpanzees generally mate only when they have a fully tumescent sexual swelling, and are most fertile in the last week of tumescence (Emery Thompson 2005). If members of the party were feeding, observers recorded the species and the part being eaten. While such scan samples were not suitable for measuring individual-level rates of behaviour, they provided statistically reliable measures of diet composition similar to data from focal observations conducted simultaneously (Gilby et al. 2010). Observers also kept a narrative ad libitum record of chimpanzee behaviour throughout the day, recording the time and other details of mating, aggression, tool use, hunting, intergroup encounters and other events. All data are digitized and stored in a relational database in Microsoft Access at the Department of Human Evolutionary Biology, Harvard University.

Location Data and Ranging Behaviour

We used maps of daily ranging patterns to determine the location of feeding events, the location of intergroup encounters, and the size and shape of the home range. We plotted the location of each 15 min scan within the corresponding 500 × 500 m cell of a grid overlain on maps of the study area (Wilson et al. 2001). In addition to this coarse-grained measure of locations, we plotted the more precise 15 min map locations of the Kanyawara chimpanzees at the start of each intergroup encounter, and for at least 1 h after, onto a digitized map of the study area using ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, U.S.A.).

Estimates of the Kanyawara community's home range were obtained using Biotas 2.0 (Ecological Software Solutions LLC, Hegymagas, Hungary) to determine the minimum convex polygon

(MCP) that enclosed the centres of every unique grid cell entered during each day for a given time period (Wilson et al. 2001). Annual ranges were recorded using 98% of all locations to exclude overly influential outliers. To provide a context for the annual ranges, we determined the 'total range', defined as the MCP enclosing 100% of unique daily grid cell locations for the entire study period, and the 'nesting range', defined as the MCP enclosing 99% of each day's first location recorded before 0700 hours. All parts of the range outside the nesting range were considered the 'periphery' (Wilson et al. 2007). We calculated the 'range centre' based on the mean *X* and *Y* coordinates for all unique daily grid cell locations.

Measures of Feeding Behaviour

At 15 min intervals during party follows, one observer recorded the species and the part (i.e. ripe fruit, unripe fruit, young leaves, etc.) that was being eaten, if any. While these data were collected at the party level, they correlate well with feeding data from focal follows (Gilby et al. 2010). For purposes of analysis, we considered each part of a given food species to constitute a food category, except for one category, herbs, which consisted of the pith and leaves of a wide range of terrestrial herbaceous species. For each day, we calculated the percentage of time spent feeding on each food category as the percentage of all 15 min scans for which feeding occurred, and for which chimpanzees were recorded feeding on that category. We then identified the top food categories (those constituting at least 0.5% of feeding time). The resulting 17 food categories (Table 2) together accounted for approximately 88% of all feeding observations.

Data from feeding scans are an indirect measure of what foods are available in the environment that could potentially differ from what chimpanzees are actually eating if observational measures suffered from biases, such as difficulty of observation in different habitats. To test the correspondence between behavioural measures and actual environmental abundance, we compared the percentage of feeding scans on which chimpanzees were recorded eating ripe fruit with measures of abundance estimated from recording the phenological state of approximately 227 trees on a 12 km transect every 2 weeks (Wrangham et al. 1991) during the period January 1992–February 2006. Of the 17 top food categories identified in the present study, 12 were tree fruits. The phenology trail included 10 of these species, omitting only *Linociera johnsonii* and *Ficus capensis.* To test the extent to which feeding scans corresponded to what chimpanzees were actually eating, we compared the percentage of feeding scans recorded for each of three species (*Mimusops bagshawei*, *Pseudospondias microcarpa* and *Uvariopsis congensis*) with the mean number of seeds from that species found in dung samples (Wrangham et al. 1994) collected during each month's observations of chimpanzees (January 1990–May 1994). To test whether spatial patterns in feeding behaviour represented the actual distribution of trees in the forest, we examined data from vegetation transects conducted in the three forest compartments (K15, K14, K30) that together cover the central part of the Kanyawara range. As described by Chapman et al. (1995), 26 sampling transects were established throughout the trail system (1990–1992). Each transect was 200 m by 10 m, providing a total sampling area of 5.2 ha. Each tree measuring at least 10 cm DBH (diameter at breast height) within 5 m of each side of the trail was individually marked with a numbered aluminium tag, and DBH was measured. For each compartment, we calculated the density of stems of each of the top 12 fruit trees. To compare the spatial distribution of each species as estimated from feeding locations and from vegetation transects, for each category, we plotted the mean distance north of the range centre for feeding locations versus the proportion of stems found on transects in the southern compartment, K30 (the number of stems per ha in K30 divided by the sum of stems per ha in all three compartments).

Table 2

Percentage of monthly feeding time and spatial distribution of feeding by chimpanzees on the top 17 food categories

Species	Code	% Monthly feeding time			% Grid cells in which this food was eaten (1992–2006)
		Median	Min	Max	
Celtis africana (leaves)	CAF_YL	2.2	0.0	36	54
Celtis durandii	CDU	0.0	0.0	59	24
Cordia abyssinica	COA	0.0	0.0	34	35
Ficus exasperata (leaves)	FEX_YL	0.0	0.0	31	27
Ficus exasperata (ripe fruit)	FEX	1.2	0.0	84	30
Ficus natalensis	FNA	2.7	0.0	67	34
Ficus sansibarica (*brachylepis*)	FBR	3.9	0.0	77	39
Ficus saussureanna (*dawei*)	FDA	0.0	0.0	45	21
Ficus sur (*capensis*)	FCA	0.0	0.0	27	24
Herbs	THV	18	0.0	55	81
Linociera johnsonii	LNC	0.0	0.0	69	16
Mimusops bagshawei	MMS	0.0	0.0	81	26
Musa spp. (stems)	BAN	0.0	0.0	33	14
Procolobus tephrosceles (meat)	RDC	0.0	0.0	14	28
Pseudospondias microcarpa	PSD	0.0	0.0	89	12
Teclea nobilis	TEC	0.0	0.0	51	16
Uvariopsis congensis	UVA	0.0	0.0	76	28
Drupe fruits		14	0.0	94	57
Figs		35	0.0	85	61
Leaves and stems		25	1.2	81	83
Top 17 foods		91	38	100	87

We used three methods to examine the spatial patterns of feeding behaviour: (1) feeding per grid cell, (2) feeding activity centres and (3) distance to edge of nesting range (to determine the extent to which each food category tended to be located near the periphery). For (1), we totalled the number of feeding scans for each food category within each grid cell during the entire study period. For (2), we calculated the mean *X* and *Y* coordinates for all observed feeding locations for each category. For (3), for each occurrence of feeding, we determined the grid cell in which that event took place. We used ArcView to measure the distance from the centre of each grid cell to the nearest edge of the nesting range. Grid cells located in the periphery (i.e. outside the nesting range) were defined as having a negative distance from the edge of the nesting range. Then, for all feeding occurrences for that food category, we determined the median distance to the edge of the nesting range. To examine temporal patterns of feeding behaviour, we calculated the percentage of each month's observed feeding time that was spent eating each food category.

Intergroup Encounters

Intergroup encounters occasionally involve direct visual observation of unfamiliar chimpanzees. More frequently, however, intergroup encounters involve only acoustic contact between chimpanzees separated by hundreds of metres, with thick vegetation preventing any visual contact (Goodall 1986; Boesch & Boesch-Achermann 2000; Wilson & Wrangham 2003). Observers inferred distant vocalizations to be from other communities when the vocalizations appeared to come from a distance and direction towards or beyond the edge of the Kanyawara community's range. Chimpanzees typically respond strongly to such vocalizations by looking in the direction of the calls, showing signs of alarm such as piloerection and reassurance behaviours such as touching, embracing or mounting each other, and sometimes responding to the calls by vocalizing and/or moving towards the calls (Wilson & Wrangham 2003).

To obtain a complete list of intergroup encounters that occurred during the study period, we read through each day's narrative notes, and also read through the field diary, where observers regularly keep track of intergroup encounters and other significant events. We included only events that observers inferred to be intergroup encounters, based on evidence described above. We rejected cases that were ambiguous or unlikely to have been actual intergroup encounters. For each encounter, we determined the time and the location of the Kanyawara chimpanzees at the start of the encounter, whether Kanyawara chimpanzees gave a vocal response, the latency of that response (measured from the time at which calls from foreign chimpanzees were first heard), whether the Kanyawara chimpanzees moved towards or away from the foreign chimpanzees and the latency of that movement response. We scored the 'contact' of each encounter as 'acoustic' (vocalizations heard from foreign chimpanzees, with or without vocal response from Kanyawara chimpanzees), 'visual' (foreign chimpanzees seen by observers and apparently also seen by Kanyawara chimpanzees, but without physical contact), and/or 'physical' (Kanyawara chimpanzees came into direct physical contact with foreign chimpanzees). We further scored the vocal and movement response to each encounter based on the vocal behaviour and the net movement of Kanyawara chimpanzees within 1 h from the time at which foreign chimpanzees were first heard or seen. We chose 1 h as the cutoff point for two reasons: (1) once detected, the presence of foreign chimpanzees could potentially affect vocal and travel behaviour long after the first detection event, and (2) with the time resolution of the map data (15 min intervals), an hour's worth of map points were often needed to determine whether net movement towards or away from the calls occurred. Vocal response was scored as 'yes' if Kanyawara chimpanzees gave loud calls (e.g. waa-barks, pant-hoots) after hearing calls from foreign chimpanzees, and if observers described these calls as responses to the foreign chimpanzees. Screams and other vocalizations resulting from within-party social encounters were not considered vocal responses to foreign chimpanzees. The direction of the movement response was scored as an 'approach' if chimpanzees moved at least 50 m towards the foreign chimpanzees, 'avoid' if chimpanzees moved at least 50 m away from the foreign chimpanzees, and 'no movement' if they moved less than 50 m in any direction. Encounters that were separated by more than 1 h were scored as separate encounters.

For each follow, we scored whether any intergroup encounters were observed. To examine temporal patterns in rates of encounters, we calculated for each month the rate of intergroup encounters observed per 100 h of observation time.

Statistical Analysis

We conducted statistical tests in R (v2.0.1, 2004-11-15, The R Foundation for Statistical Computing, Vienna, Austria).

Probability of encounter

To determine which factors best predicted the occurrence of an intergroup encounter, we conducted multiple logistic regression tests with the occurrence of at least one intergroup encounter as the dependent variable (no $= 0$, yes $= 1$). For explanatory variables, we developed a set of candidate models representing plausible hypotheses based on spatial, social and feeding behaviour. We considered two spatial variables, based on the hypothesis that chimpanzees would be more likely to encounter neighbours towards the periphery of their range, especially (based on preliminary analysis for this population) towards the south of their range. As a measure of travel to the periphery, we used 'furthest point', the maximum distance from the range centre visited during each follow. As a measure of southward travel, we used 'southernmost point', as measured by the minimum value of the UTM Y coordinate. We considered two social variables: the number of adult males and the number of oestrous females (defined as females with fully tumescent sexual swellings). We hypothesized that parties containing more males would be more motivated to seek out encounters with neighbours, to win contests against them (the probability of winning being higher when more males are present). Likewise, we hypothesized that males in parties containing few fecund females would be more motivated to search for females from other groups. Regarding feeding variables, we hypothesized that intergroup encounters would occur most frequently when food was abundant in border regions. Three food categories had centres of activity that were located more than one standard deviation south of the mean centre of activity for the top 17 species: *Musa*, *Pseudospondias* and *Uvariopsis*, which respectively had centres of activity located 914, 1584 and 1748 m south of the range centre. We therefore focused on these three species. Finally, we expected that longer observation time (as measured by the number of 15 min scans per follow) would generally increase the probability of observing an intergroup encounter; for this reason, we included observation time in all models.

With $K = 9$ parameters (including the intercept), a total of $((2^K) - 1) = 511$ models are possible. Anderson (2008) advises that rather than exploring all possible models (and thereby running the risk of finding spurious effects), investigators should develop a smaller set of candidate models, each of which represents a plausible hypothesis. We therefore constructed a smaller set of 11 candidate models. One model included only observation time, and two models included only observation time and one of the two spatial variables. We included observation time and both spatial variables in the remaining nine models, which explored permutations of the social and feeding variables. To avoid inflating the number of models, we considered the three food categories together, rather than testing all possible combinations of these food categories.

Travel to the periphery

Given the probability that neighbouring groups are more likely to be encountered in the periphery of the community's range, we sought to identify which factors affect travel to the periphery, whether or not an intergroup encounter occurs on a given day. Because individuals may vary in their motivation to travel to the periphery, we examined this question at both the party level and the individual level.

At the party level, we used multiple linear regression analyses to select the best model for predicting travel towards the periphery, as measured by the variables furthest point and southernmost point. The set of hypotheses for travel to the periphery is similar to that for probability of intergroup encounters, in that we hypothesized that observation time, feeding behaviour, and the number of males and oestrous females might all affect travel to the periphery. In particular, we expected parties with more males to be more likely to visit the periphery of their range, as had been found for a 3-year subset of these data (Wilson et al. 2007). We further hypothesized that parties with fewer fecund females would be more likely to visit the periphery, searching for peripheral females of their own community and/or fecund females from neighbouring communities. Additionally, we hypothesized that chimpanzees base their travel decisions on foraging efficiency, travelling further towards the periphery when foods are more abundant there. Because all major foods may affect travel decisions, we included models with percentage of feeding time spent eating each of the top 17 foods. We examined a set of eight models each for furthest point and southernmost point.

At the individual level, we tested whether male dominance rank affected travel towards the periphery. Following Watts & Mitani (2001), we predicted that males with higher dominance rank, and thus higher probability of siring offspring (Wroblewski et al. 2009), would have a stronger motivation for defending the territory from foreign males. To test this, we calculated the difference between the maximum distance that the entire party travelled from the range centre during the day with the maximum distance from the range centre travelled by each individual male that same day. Thus, if a male failed to go as far towards the periphery as the rest of the party being followed, he would have a positive value. We examined this difference both on days when the party travelled extremely far from the centre (at least 2 SD more than the mean distance from centre = 3118 m), and on days without such extreme travel. We excluded from this analysis two males (Julian and Lamy, who died in 1994 and 1996, respectively) that were sampled on only 1 and 6 days, respectively, for which parties travelled extremely far from the range centre, compared to the median = 91 days (range 10–122) for the other males.

Spatial correlations with feeding behaviour

To further examine potential spatial correlations between feeding behaviour and intergroup encounters, we conducted multiple linear regressions using the total number of intergroup encounters per grid cell as the dependent variable, and the number of feeding locations per grid cell for each food category as the independent variables. We constructed seven models, based on combinations of the three food categories found to have a temporal association with intergroup encounters.

Responses to encounters

To determine which factors best predicted the escalation of intergroup encounters, we conducted multiple logistic regression, with two different dependent variables related to outcome (whether or not Kanyawara chimpanzees gave a vocal response; and whether they approached the foreign chimpanzees; no = 0, yes = 1, in each case). We constructed six a priori models representing hypotheses relating to both fighting ability and resource value. Because of strong theoretical (e.g. Wrangham 1999) and experimental (Wilson et al. 2001; Herbinger et al. 2009) evidence that, for chimpanzees, fighting ability and willingness to escalate intergroup contests depend on the number of adult males, we included ‘males’ in all six models. Escalation may also depend on the value of resources being contested. We considered four different measures of resource value. As a measure of mate value, we used the number of oestrous females in the party. Given that chimpanzees sometimes kill infants during intergroup encounters (Goodall 1986; Wilson & Wrangham 2003; Watts et al. 2006), we hypothesized that males would respond more intensively to intergroup threat to protect young infants. As a measure of infant protection, we used the number of infants younger than 3 years of age in the party. Infants killed during intergroup encounters have had an estimated age of 3 years or younger (Arcadi & Wrangham 1999). For food value, we followed the definition used by Harris (2010): the percentage of that month’s feeding time observed in the quadrat in which the interaction took place (in this case, the 500 × 500 m grid cell). As a proxy of overall resource value to owners, we used the distance from the centre of the range (e.g. Crofoot et al. 2008).

RESULTS

Ranging and Party Composition

During 180 months of observation, observers followed chimpanzees for a median 5.3 h (range 0.25–14 h) per follow for 5527 follows, totalling 35 083 h. The number of observation hours per month increased over time, with marked increases in the late 1990s and mid 2000s (Fig. 1a). The total area used by Kanyawara chimpanzees during the study period covered 41.1 km^2. Night nest locations occurred within a smaller area of 25.4 km^2. In a given year, the chimpanzees used a subset of this total area, with a median annual home range of 16.4 km^2 (range 10.8–29.5). The estimated annual home range size generally increased from 1992 to 1998, and declined thereafter (Fig. 1b). While estimates of range size during the early years of the study may have been low due to incomplete habituation of the study subjects, the number of observation hours per year did not significantly predict the annual range size (simple linear regression: $F_{1,13} = 1.5$, $P = 0.24$), indicating that the changes in estimated range size were not simply artefacts of changes in observation time.

Parties contained a mean 9.2 ± 7.0 individuals per follow, of which 3.0 ± 3.0 were adult males, 2.3 ± 1.8 were adult females, and 0.3 ± 0.7 were females with fully tumescent sexual swellings. Average party size and composition varied greatly on the temporal scales of days and months, but when considered across the entire study period, no statistically significant relationship existed between year and the mean number of either males or oestrous females observed each month (simple linear regression: males: $F_{1,178} = 0.17$, $P = 0.68$; oestrous females: $F_{1,178} = 1.2$, $P = 0.28$).

Observations of Intergroup Encounters

Observers reported a total of 120 intergroup encounters. Most of these encounters ($N = 102$) involved only acoustic contact. Fifteen

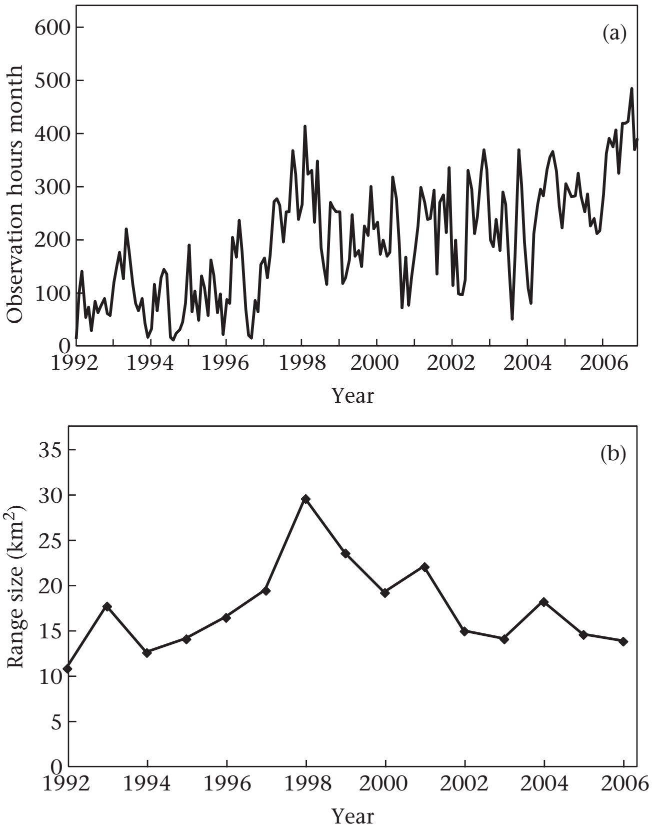

Figure 1. (a) Number of observation hours of chimpanzees per month during 1992–2006. (b) Size of annual home range, 1992–2006. Home ranges size was calculated from the minimum convex polygon enclosing 98% of locations based on unique daily grid cells.

cases involved visual but not physical contact, and three cases involved direct physical contact. In 11 of the 18 observed cases of visual and/or physical contact, the unhabituated foreign chimpanzees fled soon after seeing researchers. In addition to these observed encounters, two intergroup killings were inferred to have taken place, based on the circumstantial evidence associated with bodies of the victims (Wrangham 1999; Muller 2002). Encounters were observed during 103 of 5527 follows (1.9%) for which party composition and map location data were available. On nine follows, two intergroup encounters were observed. Party follow data were not available for the remaining eight encounters. The rate of intergroup encounters per 100 h of observation time per month increased over the years (simple linear regression: $F_{1,178} = 7.9$, $P < 0.01$, $\beta = 0.035 \pm 0.012$), although this annual trend explained little of the variance among months ($R^2 = 0.042$), which had median of 0.0 encounters per 100 observation hours (range 0.0–5.3). The majority of encounters occurred during just 2 months: June ($N = 56$; 46.7%) and May ($N = 12$; 10%). Most encounters occurred towards the periphery of the range, although some encounters occurred close to the range centre (Fig. 2). Including the locations of two fatal attacks, intergroup encounters occurred a median of 1867 m from the range centre (range 288–4406 m, $N = 120$; map location could not be determined for two of the observed encounters). On follows with intergroup encounters, chimpanzees ranged further from the centre of their range (mean ± SE maximum distance from centre: follows with intergroup encounters: 2074 ± 630 m, $N = 5424$; follows without intergroup encounters: 1477 ± 814 m, $N = 103$; Welch's two-sample t test: $t_{108.6} = -9.46$, $P < 0.0001$). Most of the encounters occurred either southeast ($N = 76$; 63%) or southwest ($N = 35$; 29%) of the range centre, with only a few ($N = 9$; 8%) in the northeast and none in the northwest. Encounters occurred throughout the day, but they occurred most often in the morning (median = 1010 hours, range 0600–1853 hours, $N = 119$; time was not known for one encounter).

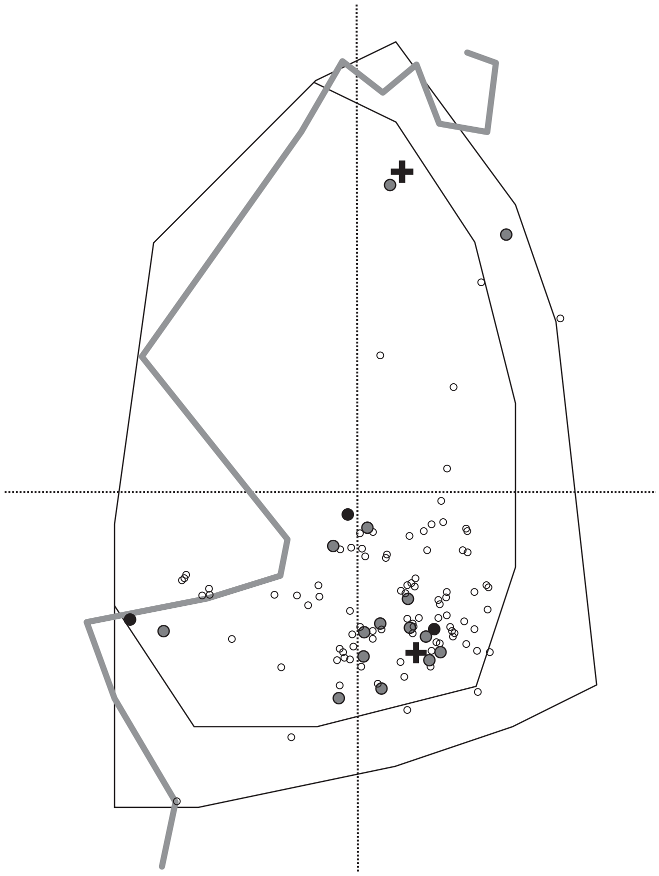

Figure 2. Locations of chimpanzees at the start of intergroup encounters ($N = 120$). The thick irregular line denotes the park boundary. The inner polygon encloses the nesting range, and the outer polygon encloses the total range used during the study period. Type of contact during each encounter: acoustic (small open circles), visual (larger grey circles), physical (larger black circles) and killings (crosses). The dotted vertical and horizontal lines cross at the range centre and indicate the four quadrants of the range (northwest, northeast, southeast, southwest).

During the 120 observed encounters, chimpanzees gave a vocal response in 69 cases, did not respond in 47 cases, and in four cases the vocal response was unclear from the available data. When chimpanzees did give a vocal response, the median latency was 0 min (range 0–55 min) after the start of the encounter ($N = 67$; in two cases chimpanzees gave a vocal response but the latency could not be determined). Kanyawara chimpanzees approached the foreign chimpanzees in 37 cases, moved away from them in 36 cases, did not move in 37 cases, and movement could not be determined for 10 cases. When Kanyawara chimpanzees did approach, the median latency was 1 min (range 0–60 min, $N = 72$).

Feeding Behaviour: Temporal Patterns

The top 17 food categories included ripe fruit from 12 tree species (five figs and seven drupe fruits), young leaves from two tree species, stems of bananas (*Musa* spp.), herbs and meat from red colobus monkeys, *Procolobus tephrosceles* (Table 2).

Temporal patterns varied greatly among the food categories (Table 2). For example, chimpanzees ate at least some herbs during 178 of 180 months (median = 18%, range 0–55%; Fig. 3a). Other foods were eaten only during synchronized fruiting events. For example, chimpanzees ate *Uvariopsis* during only 40 of 180 months (median = 0%). However, during irregularly spaced peaks of abundance, *Uvariopsis* accounted for up to 76% of the diet per month (Fig. 3b). Peaks occurred anywhere from 5 months to 3 years apart. *Uvariopsis* most commonly peaked in June, in the early dry season, although it occasionally peaked in December.

Simple linear regression found that the observed feeding time on 10 species correlated with the abundance of that species in the environment, as measured by the percentage of trees on the phenology transect of that species with ripe fruit that month (see Supplementary Material, Table S1). Observed feeding time correlated even more strongly with the mean number of seeds obtained from dung samples that month (see Supplementary Material, Table S2).

Feeding Behaviour: Spatial Patterning

Analysis revealed pronounced spatial heterogeneity in the location of food resources, as illustrated by the centre of feeding activity for all 17 top food categories (Fig. 4). Some foods, such as herbs, were eaten throughout the community's range, with the feeding activity centre located near the range centre. Other foods occurred within more restricted parts of the range, with *Cordia* and *Linociera* most common in the north, figs, *Teclea* and *Mimusops* in the centre, and *Pseudospondias* and *Uvariopsis* in the southeast (Fig. 4). The median distance to the edge of the nesting range varied greatly among the top food categories (median = 1493 m, range 611–1993 m). *Pseudospondias* and *Uvariopsis* were located particularly close to the edge, with the median distance to the edge of the nesting range equal to 611 m and 791 m, respectively.

Comparison of data from feeding records and vegetation transects found that species with more southerly feeding locations tended to be more abundant in the southern part of the range

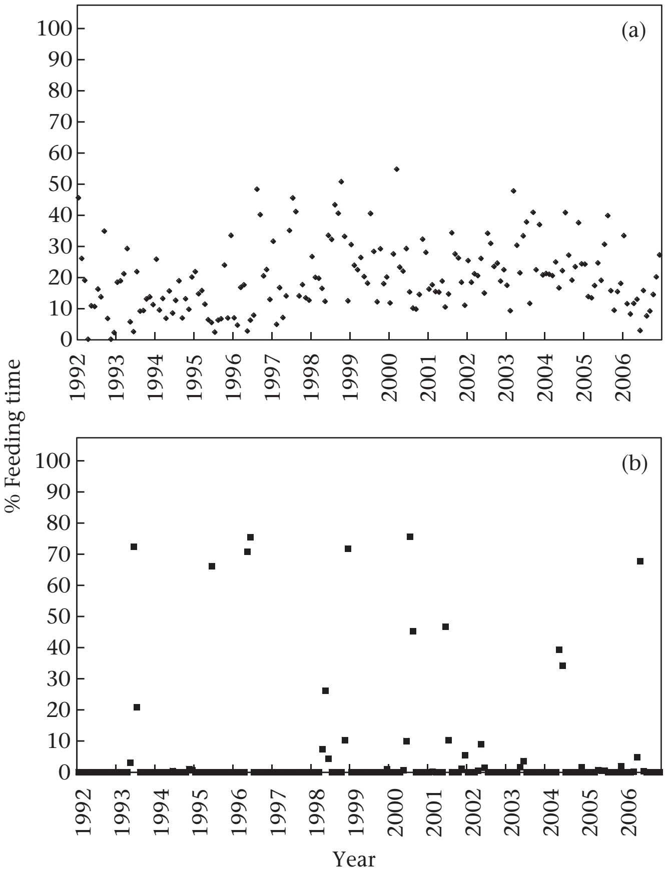

Figure 3. Temporal patterning of the percentage of monthly feeding time that chimpanzees spent eating (a) herbs and (b) ripe fruits of *Uvariopsis congensis* ($N = 180$ months).

(Kendall rank correlation: $\tau = -0.39$, $N = 12$, $P = 0.08$; Fig. 5). *Uvariopsis* was particularly abundant in the south, with 60.4 stems/ha, the highest abundance of any of the top food species. *Pseudospondias* was found only in the south.

Intergroup Encounters: Probability of Occurrence

We examined a set of 11 a priori models constructed to predict the occurrence of intergroup encounters during daily follows (Table 3). The best model is considered to be the one with the lowest AIC and the highest Akaike weight (w_i) values. As a rule of thumb, models with ΔAIC < 2 are considered to have strong support, and are included in a confidence set of models, while models with ΔAIC > 7 are considered to be poorly supported (Anderson & Burnham 2002). Logistic regression analysis found that intergroup encounters were more likely to be observed on longer follows, when chimpanzees travelled further from their range centre and further south, and on days when they spent more time eating foods located far to the south (Table 3). Models 2 and 3 had ΔAIC $= 2$, suggesting that the number of adult males and oestrous females might also influence the probability of intergroup encounters. However, Model 4, which included both variables, had an even higher ΔAIC ($= 4.0$), indicating that the model including all of these variables was unlikely to be the best model. Additionally, models that included either or both of the party composition variables, but not the feeding variables, had greater ΔAIC and negligible w_i values. Model 1 was therefore the best model in this set.

Table 4 shows the model parameter estimates for Model 1. The coefficients for the spatial variables appear small compared to the other coefficients, because they are based on a scale of metres (rather than, say, kilometres). Note that the coefficient for southernmost point is negative, because the Y coordinate decreases southwards. Although time spent eating *Pseudospondias* influenced the probability of intergroup encounters occurring, the 95% confidence interval included zero, indicating that this effect was not statistically significant. In contrast, observation time, travel further from the centre and further south, and time spent eating *Musa* and *Uvariopsis* were all associated with increased probability of intergroup encounters.

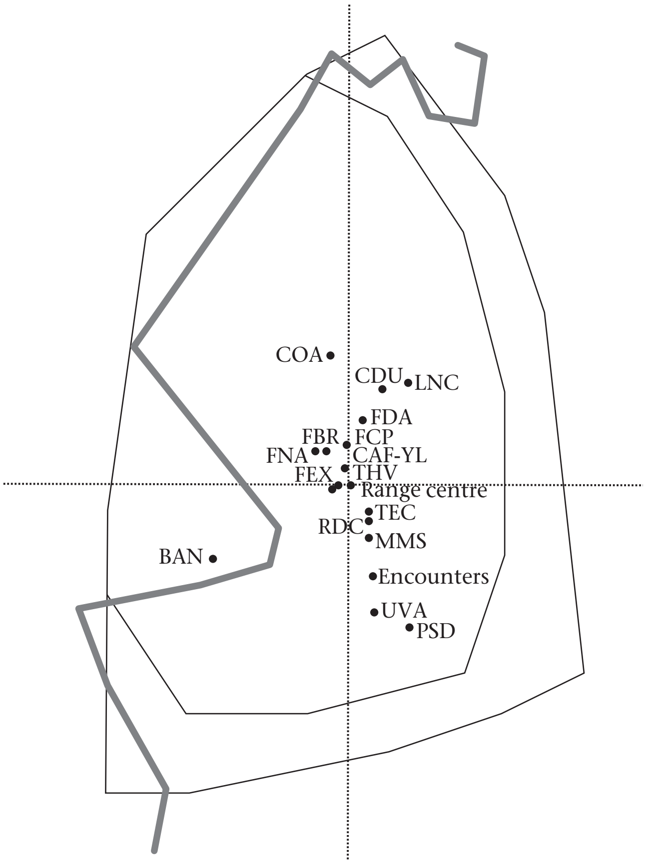

Figure 4. Mean centre of activity for each of the top 17 food categories, in relation to the centre of the range and the mean centre of activity for the location of chimpanzees at the start of intergroup encounters. Species are labelled with codes listed in Table 2.

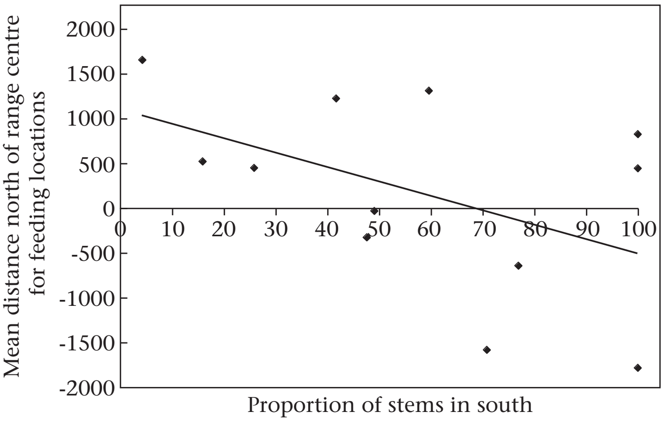

Figure 5. Spatial distribution of 12 top fruit tree species based on chimpanzee feeding locations (mean distance north of range centre for all observed feeding locations on each species) versus the proportion of stems of each species found on vegetation transects in the southern compartment (K30) of the chimpanzees' range.

Table 3
Logistic regression of factors predicting the probability of a chimpanzee intergroup encounter occurring during a follow

Model no.	No. of males	No. of oestrous females	BAN	PSD	UVA	South	Far	Obs. time	K	AIC	ΔAIC	w_i
1			•	•	•	•	•	•	7	832.2	0.0	0.53
2	•		•	•	•	•	•	•	8	834.4	2.0	0.20
3		•	•	•	•	•	•	•	8	834.4	2.0	0.20
4	•	•	•	•	•	•	•	•	9	836.4	4.0	0.07
5						•	•	•	4	846.7	14.4	0.00
6	•					•	•	•	5	848.4	16.0	0.00
7		•				•	•	•	5	848.6	16.2	0.00
8	•	•				•	•	•	6	850.4	18.0	0.00
9						•		•	3	857.5	25.1	0.00
10							•	•	3	945.4	113	0.00
11								•	2	978.7	146	0.00

• Indicates parameter included in model; K: number of estimable parameters in model (= number of covariates plus intercept); AIC: Akaike's Information Criteria; ΔAIC: $AIC_i - \min AIC$; min AIC: minimum AIC value of all models: w_i Akaike weight: weight of evidence that model i is the best model in the candidate set (Anderson 2008). Models are ordered from lowest to highest AIC scores. Model 1 was the best model.

Post hoc examination of the data on both daily and monthly scales support the finding that *Uvariopsis* and *Musa* independently affected intergroup encounter rates. However, while the estimated coefficient for *Uvariopsis* was smaller than that for *Musa*, *Uvariopsis* appeared to affect intergroup encounter rate more consistently. On a daily scale, intergroup encounters occurred on 10 out of 151 follows (6.6%) in which chimpanzees ate *Musa* stems, but on 45 out of 414 follows (11%) in which chimpanzees ate *Uvariopsis* fruits. Chimpanzees ate both *Musa* and *Uvariopsis* on only four follows, and no intergroup encounters occurred on those days. On a monthly scale, the 49 months in which chimpanzees ate *Musa* accounted for 46% of encounters ($N = 55$), whereas the 40 months in which chimpanzees ate *Uvariopsis* accounted for 62% of all encounters ($N = 74$). Of these encounters, 36 occurred during the 14 months in which chimpanzees ate both *Musa* and *Uvariopsis*. *Musa* accounted for 25% or more of feeding time during only 3 months, during which one encounter occurred. In contrast, during the 12 months in which *Uvariopsis* accounted for 25% or more of feeding time, 56 encounters occurred (47% of all encounters).

Factors Affecting Travel Towards the Periphery

Travel towards the periphery depended on multiple factors (Tables 5–8). Chimpanzees travelled further from the range centre, and travelled further south, when in parties with more males, and when follows were longer. The number of females with fully tumescent sexual swellings in a party strongly affected southward travel: parties with more oestrous females travelled less far to the south (Table 8). The number of oestrous females was also associated with reduced travel away from the centre, but this effect was not as strong or consistent (Table 6). The best model for travel away from the centre, as indicated by the lowest AIC score, did not contain oestrous females (Table 5). Model 2, which did contain oestrous females, received only slightly less support ($\Delta AIC = 1$), indicating that oestrous females probably did influence travel away from the centre. However, the 95% confidence intervals for the coefficient included zero, indicating that the effect was not statistically significant (Table 6). When chimpanzees spent more time eating four of the five fig species, two of the seven drupe fruits (*Mimusops* and *Teclea*) and red colobus meat, they stayed closer to the range centre, but they travelled further from the centre when eating four other drupe fruits (*Cordia, Celtis durandii, Pseudospondias* and *Uvariopsis*; Table 6). The 95% confidence intervals included zero for herbs, *Linociera*, *C. africana* leaves and *F. sur*, indicating that these food categories did not have a statistically significant effect on travel away from the centre. Chimpanzees travelled further south the longer they spent eating *Psuedospondias* and *Uvariopsis*, whereas they travelled further north the longer they spent eating *Cordia*, *Celtis durandii* and *Linociera* (Table 8). Chimpanzees travelled far from the range centre, and far to the south, to eat stems of bananas (*Musa* spp.), which were located outside the park boundaries (Fig. 4). Time spent eating banana stems was negatively correlated with time spent eating preferred foods, such as the seven drupe fruits included among the top 17 foods (sum of monthly feeding time on the seven drupe fruits versus the percentage of time eating banana stems: Pearson's correlation: $r_{178} = -0.17$, $t_{178} = -2.3$, $P < 0.05$), indicating that chimpanzees travelled outside the park to eat banana stems when preferred foods were scarce.

We found that dominance rank affected the extent to which individual males travelled as far from the centre as the rest of the party. Lower-ranking males travelled less far from the range centre than the rest of the party, for days in which the party travelled extremely far from the range centre (simple linear regression: $F_{1,11} = 7.8$, $\beta = 19.4$, $P = 0.02$), but not on other days ($F_{1,11} = 2.8$, $\beta = 2.2$, $P = 0.12$; Fig. 6). Thus, the further parties travelled from the

Table 4
Model averaged* parameter estimates for the probability of a chimpanzee intergroup encounter occurring during a follow

Parameter	Estimate	SE	95% CI	
			Lower	Upper
Males	−0.00047	0.011	−0.021	0.02
Oestrous females	−0.0048	0.039	−0.087	0.069
BAN	0.025	0.0069	0.096	0.037
UVA	0.018	0.0045	0.0088	0.027
PSD	0.0058	0.0071	−0.0096	0.037
South	0.00066	0.00012	−0.00093	−0.00044
Far	0.00048	0.00017	0.00014	0.00080
Obs. time	0.037	0.0071	0.023	0.051

See Tables 1 and 2 for parameter descriptions.
* Models 1–3 were used to calculate model averaged parameters.

Table 5
Multiple linear regression of factors predicting the furthest point from the range centre visited by chimpanzee groups during a follow

Model no.	No. of males	No. of oestrous females	Top 17 foods	Obs. time	K	AIC	ΔAIC	w_i
1	•		•	•	20	88198	0	0.62
2	•	•	•	•	21	88199	1	0.38
3		•	•	•	20	88527	329	0.00
4			•	•	19	88585	387	0.00
5	•	•		•	4	89057	859	0.00
6	•			•	3	89064	866	0.00
7		•		•	3	89564	1366	0.00
8				•	2	89633	1435	0.00

See Table 1 for parameter descriptions.
• Indicates parameter included in model.

Table 6
Model averaged* parameter estimates predicting the furthest point visited by chimpanzee groups during a follow

Parameter	Estimate	SE	95% CI	
			Lower	Upper
No. of males	74.1	3.82	66.6	81.6
No. of oestrous females	−7.29	6.50	−20.1	5.44
Obs. time	3.31	0.63	2.08	4.55
Pseudospondias	8.27	0.871	6.56	9.97
Musa (stems)	7.00	1.27	4.52	9.49
Cordia	21.9	1.73	18.5	25.3
Uvariopsis	5.42	0.796	3.92	6.98
Linociera	1.65	1.14	−0.595	3.89
C. durandii	6.20	1.30	3.66	8.74
F. saussureana (*daweii*)	−2.88	0.914	−4.67	−1.09
Mimusops	−8.13	0.615	−9.34	−6.93
F. natalensis	−4.36	0.533	05.41	−3.32
F. sansibarica (*brachylepis*)	−3.28	0.628	−4.51	−2.04
C. africana (leaves)	0.0823	1.22	−2.32	2.48
F. sur (*capensis*)	−0.391	1.36	−3.05	2.27
Procolobus (meat)	−4.01	2.41	−8.74	0.72
Teclea	−11.9	1.22	−14.2	−9.44
Herbs	1.14	0.676	−0.190	2.46
F. exasperata (fruit)	−8.74	0.772	−10.3	−7.22
F. exasperata (leaves)	−7.35	2.19	−11.7	−3.05

See Table 1 for parameter descriptions.

* Models 1 and 2 were used to calculate model averaged parameters.

range centre, the more low-ranking males tended to drop out instead of travelling all the way with the rest of the party.

Intergroup Encounters: Spatial Factors

Multiple linear regression found that the three food categories that were temporally associated with the occurrence of intergroup encounters (*Musa* stems, *Pseudospondias* and *Uvariopsis*) were also spatially associated with intergroup encounters (Table 9). The model with the lowest AIC score included all three species. However, this model was only 1.3 times more probable than Model 2, which included only the two drupe fruits, *Pseudospondias* and *Uvariopsis* ($\Delta AIC = 0.6$, $w_i = 0.43$). Moreover, the 95% confidence interval for *Musa* included zero, indicating that this effect was not statistically significant (Table 10). *Uvariopsis* had the strongest spatial association with intergroup encounters, with an estimated partial regression coefficient of $\beta = 0.011$ (Fig. 7), which was 2.75 times the size of that of *Pseudospondias* and 4.8 times larger than that of *Musa* (Table 10).

Factors Affecting Responses to Foreign Chimpanzees

Parties that contained more males were more likely to give a vocal response upon hearing calls from another community (Tables 11, 12; Fig. 8a). Food value was negatively associated with the probability of giving a vocal response ($\beta = -0.067$). The number of oestrous females and infants, and distance from the centre did not affect the probability of a vocal response (Table 11).

Table 7
Multiple linear regression of factors predicting the southernmost point visited by chimpanzee groups during a follow

Model no.	No. of males	No. of oestrous females	Top 17 foods	Obs. time	K	AIC	ΔAIC	w_i
1	•	•	•	•	21	92359	0.0	0.99
2	•		•	•	20	92369	10	0.01
3			•	•	19	92382	23	0.00
4		•	•	•	20	92382	23	0.00
5	•	•		•	4	94465	2106	0.00
6	•			•	3	94470	2111	0.00
7		•		•	3	94576	2217	0.00
8				•	2	94581	2222	0.00

See Table 1 for parameter descriptions.
• Indicates parameter included in model.

Table 8
Parameter estimates for the best model for predicting the southernmost point visited by chimpanzee groups during a follow

Parameter	Estimate	SE	95% CI	
			Lower	Upper
No. of males	−30.1	5.96	−41.8	−1.84
No. of oestrous females	84.9	25.1	35.7	134
Obs. time	−10.0	−0.923	−11.8	−8.17
Pseudospondias	−28.3	1.27	−30.7	−25.8
Uvariopsis	−26.3	1.16	−28.5	−24.0
Musa (stems)	−15.2	1.85	−18.8	−11.6
Mimusops	−13.0	0.898	−14.8	−11.3
Procolobus (meat)	−3.19	3.52	−10.1	3.70
Teclea	−5.9	1.78	−9.37	−2.37
F. exasperata (fruits)	−2.13	1.13	−4.34	0.07
F. exasperata (leaves)	−1.78	3.19	−8.04	4.48
Herbs	4.10	0.945	2.17	6.03
F. natalensis	5.77	0.777	4.25	7.30
F. sansibarica (*brachylepis*)	8.30	0.916	6.50	10.1
F. sur (*capensis*)	10.0	2.00	6.17	13.9
C. africana (leaves)	13.3	1.79	9.76	16.8
F. saussureana (*daweii*)	12.2	1.33	9.60	14.8
C. durandii	26.2	1.89	22.5	29.9
Linociera	16.2	1.67	13.0	19.5
Cordia	36.3	2.52	31.4	41.2

See Table 1 for parameter descriptions.

The probability of moving towards the source of the calls increased when more adult males were in the party (Fig. 8b) and decreased when more oestrous females were present (Tables 13, 14). Model 1, which had the lowest AICc, included only males and oestrous females. Model 2, which also included infants, distance from centre and food value, also received strong support ($\Delta AICc = 1.3$, $w_i = 0.25$), indicating that these three parameters also influenced the probability of approaching. The number of infants had a positive effect on approaching, while the distance from range centre and food value both had a negative effect; the 95% confidence intervals for all three of these included zero, indicating that their effects were not statistically significant (Table 14).

Impact of Range Contraction

The Kanyawara community's range contracted from a peak of 29.5 km^2 in 1998 to 13.8 km^2 in 2006, a mere 47% of its peak size (Fig. 1b). This contraction included a shifting of the southern boundary a full kilometre north from 2004 to 2006.

DISCUSSION

During the 15-year study period intergroup encounters occurred relatively infrequently, and when they did occur, they mainly involved vocal encounters between parties separated by hundreds of metres. Nevertheless, when males from rival communities came within sight of each other, they were invariably hostile to each other, and sometimes inflicted severe injuries, including at least two fatalities. Encounters were spatially and temporally correlated with feeding behaviour, particularly with food species located along the southern periphery.

Factors Leading to Intergroup Encounters

Intergroup encounters were observed most often during longer follows, when chimpanzees travelled further from the range centre and further south, and when they spent more time eating foods

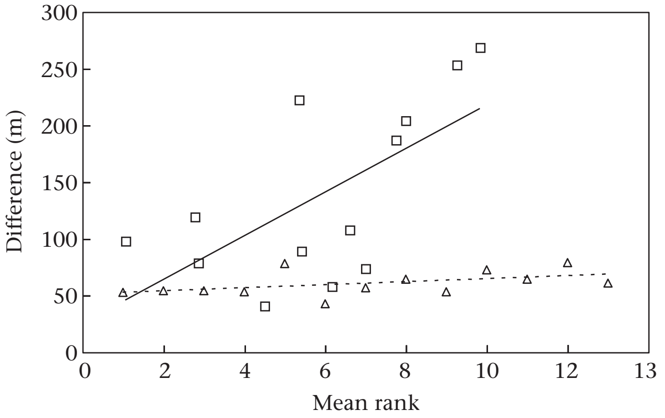

Figure 6. Effect of male chimpanzee dominance rank on travel towards the periphery. For each male, the mean difference between the party's maximum difference from the range centre and the male's own maximum distance from range centre is plotted against that male's mean rank, for days on which the party travelled extremely far (≥2 SD more than the mean daily maximum) from the range centre (squares, fitted with solid regression line) and on all other days (triangles, fitted with dashed line).

located in the southern part of their range. Neither of the party composition variables (number of adult males or females with sexual swellings) directly affected the probability of an intergroup encounter occurring. Instead, intergroup interactions occurred most often when Kanyawara chimpanzees travelled closer to their neighbours, especially their southern neighbours, and when the southern border areas had abundant food, which presumably attracted chimpanzees from both sides of the border.

Factors Promoting Travel Towards the Periphery

Given that chimpanzees were more likely to encounter their neighbours in the periphery, especially the southern periphery, what induced them to travel there? We found that travel to the periphery depended most strongly on a combination of follow duration, the number of adult males in the party and the percentage of feeding time devoted to foods located towards the periphery. Not surprisingly, chimpanzees travelled further from the range centre during longer follows. Observers generally attempted to follow chimpanzees throughout their range, but were more successful in sampling the full range of travel during longer follows. Parties with more males travelled further from the range centre and in all directions, especially to the south, the area with the highest risk of encountering neighbours. This is consistent with earlier studies from this site and elsewhere showing that chimpanzees are more likely to visit the periphery of their range (Gombe: Bauer 1980; Kanyawara: Wilson et al. 2007) and to conduct boundary patrols (Ngogo: Mitani & Watts 2005) when in parties with more males. Consistent with the previous finding that males with higher mating success participate more often in boundary patrols (Watts & Mitani 2001), high-ranking males travelled further than low-ranking males on days when parties travelled extremely far from the range centre.

Parties with more fecund females travelled less far to the south. This finding provides partial support for the prediction that males travel towards borders when their access to fecund females is restricted. However, this factor appeared to affect travel only towards the south, rather than general travel away from the range centre. Presumably, if males visited the periphery mainly to search for fecund females (either from other communities, or for those females of their own community with more peripheral individual core areas), a shortage of fecund females would induce males to travel further in all directions. An alternative explanation is that females avoided the increased risk of intergroup aggression associated with travelling south. The distribution of females in different ‘neighbourhoods’ in Kanyawara supports this view. During the 1990s, females ranged within three overlapping neighbourhoods: northern, central and southern (Wrangham et al. 1996; Emery Thompson et al. 2007). Data from feeding behaviour and endocrine sampling indicated that the southern females had access to the highest-quality habitat, and the northern females, the lowest-quality habitat (Emery Thompson et al. 2007). Despite the higher-quality habitat in the south, most females ranged in the north or central neighbourhoods, and by 2001, the southern neighbourhood disappeared, when the one remaining southern female shifted her range to the centre (Emery Thompson et al. 2007).

In addition to social factors, feeding behaviour explained much of the variation in daily travel patterns. Some foods, especially figs and herbs, were widely available throughout the year and throughout the range, whereas other foods, particularly drupe fruits, were more spatially and temporally restricted in their

Table 9
Multiple linear regression of factors predicting the number of chimpanzee intergroup encounters per 500 × 500 m grid cell

Model no.	BAN	PSD	UVA	*K*	AIC	ΔAIC	w_i
1	•	•	•	4	524.6	0.0	0.57
2		•	•	3	525.2	0.6	0.43
3	•		•	3	550.2	25.6	0.00
4			•	2	550.4	25.8	0.00
5		•		2	616.7	92.1	0.00
6	•	•		3	618.1	93.5	0.00
7		•		2	693.0	168.4	0.00

See Table 2 for parameter descriptions.
• Indicates parameter included in model.

Table 10
Model averaged* parameter estimates predicting the number of chimpanzee intergroup encounters per 500 × 500 m grid cell

Parameter	Estimate	SE	95% CI	
			Lower	Upper
Uvariopsis	0.011	0.0010	0.0094	0.013
Pseudospondias	0.0043	0.00080	0.0027	0.0059
Musa (stems)	0.0023	0.0015	−0.00055	0.0052

* Models 1 and 2 were used to calculate model averaged parameters. See Table 2 for parameter descriptions.

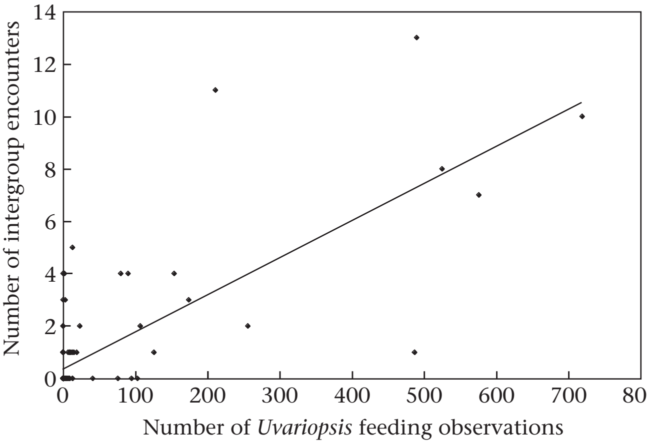

Figure 7. Spatial association between chimpanzees' feeding on *Uvariopsis* and intergroup encounters. Number of intergroup encounters observed per 500 × 500 m grid cell ($N = 166$ grid cells) as a function of the number of feeding observations for *Uvariopsis*; the line is fitted with simple linear regression.

Table 11
A priori logistic regression models predicting the probability of chimpanzees giving a vocal response following the start of an intergroup encounter

Model no.	No. of males	No. of oestrous females	No. of infants	Food value	Dist. from centre	K	AICc	ΔAICc	w_i
1	•			•		3	130.1	0.0	0.70
2	•					2	133.8	3.7	0.11
3	•	•	•	•	•	6	135.2	5.1	0.05
4	•	•				3	135.5	5.4	0.05
5	•				•	3	135.6	5.5	0.05
6	•		•			3	135.9	5.8	0.04

See Table 1 for parameter descriptions.
• Indicates parameter included in model.

occurrence. Previous studies of this population have found that the amount of feeding time on drupe fruits is negatively correlated with time spent eating figs (Wrangham et al. 1996; Emery Thompson & Wrangham 2008) and nonfruit foods such as leaves and stems (Wrangham et al. 1998), indicating that chimpanzee prefer drupe fruits over these other foods. We found that chimpanzees stayed closer to the range centre the more they ate figs, leaves and herbs as well as two drupe fruits, *Mimusops* and *Teclea*, whose groves were centrally located, but they travelled away from the range centre when they spent more time eating other drupe fruits and banana stems.

While these results are based on feeding data, rather than direct sampling of the environment, results from three more direct measures support the view that the feeding records provide an adequate assessment of the abundance and distribution of foods in the environment. First, the close correspondence between feeding data and phenology data indicate that feeding records provide an accurate sample of what is available to eat (at least for preferred, seasonally available foods). Second, the seeds collected from dung samples revealed a strong correspondence between what observers saw chimpanzees eating and what actually passed through the chimpanzees' digestive tracts (Wrangham et al. 1991). Third, vegetation transects found that the spatial distribution of food species generally corresponded with the locations revealed through observations of feeding behaviour. Indeed, while phenology and vegetation transects are important for providing unbiased sampling of the environment, we conclude that the feeding records provide an even better indication of food availability, at least for preferred foods, given that chimpanzees spend much of every day searching for food, and regularly search throughout their range, rather than the limited number of trees on the phenology trails or the few hectares sampled in transects.

Based on these results, we conclude that chimpanzees travelled to the periphery when food was more abundant there, and tended to do so in parties with a sufficient number of adult males to provide safety against neighbours.

Responses to Neighbours

Consistent with previous experimental findings (Wilson et al. 2001), chimpanzees were more likely to give a vocal response and approach foreign chimpanzees when in parties with more adult males. In a series of playback experiments simulating a single male intruder to chimpanzees at Taï, Herbinger et al. (2009) found that the number of males in the listening party affected the response to the calls of unfamiliar intruders, but not to the calls of males from immediately neighbouring communities. Herbinger et al. (2009) therefore suggested that the strong effect of male number on the response of Kanyawara chimpanzees to playback experiments (Wilson et al. 2001) resulted from experimenters playing back calls of completely unfamiliar chimpanzees. However, our current observational data show that the response to actual intruders closely resembled the response to simulated intruders, in that it depended mainly on numerical strength. This indicates that the difference in response between Kanyawara and Taï

Table 12
Model parameter estimates for the best model for the probability of chimpanzees giving a vocal response following the start of an intergroup encounter

Parameter	Estimate	SE	95% CI	
			Lower	Upper
No. of males	0.34	0.075	0.19	0.48
Food value	−0.067	0.029	−0.12	−0.0093

See Table 1 for parameter descriptions.

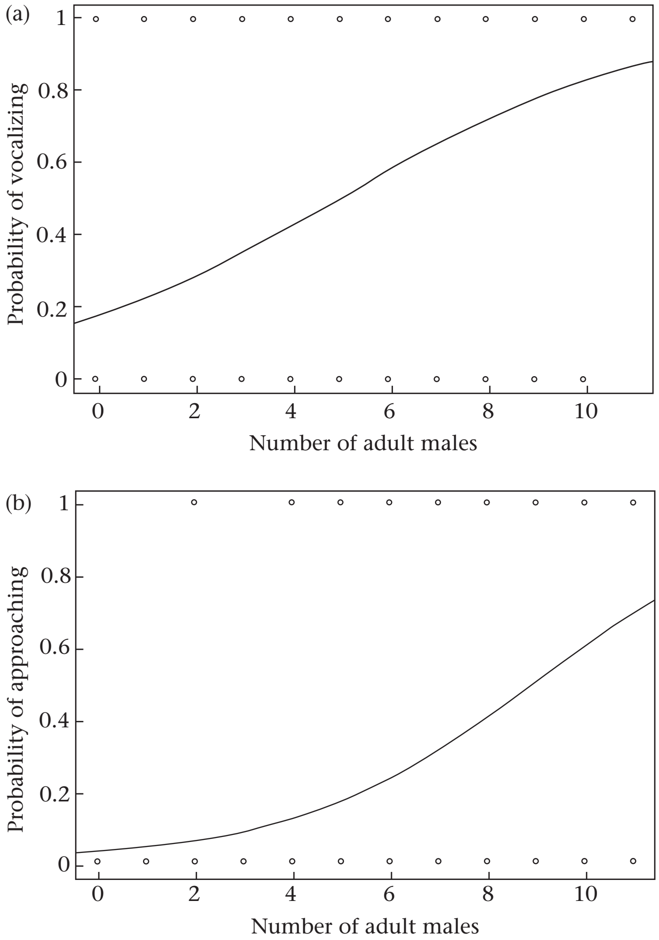

Figure 8. Logistic regression curves fitted to the probability of chimpanzees giving (a) a vocal response and (b) approaching foreign chimpanzees after the start of an intergroup encounter.

Table 13
A priori logistic regression models predicting the probability of chimpanzees approaching strangers following the start of an intergroup encounter

Model no.	No. of males	No. of oestrous females	No. of infants	Food value	Dist. from centre	K	AICc	ΔAICc	w_i
1	•	•				3	121.9	0.0	0.49
2	•	•	•	•	•	6	123.2	1.3	0.25
3	•			•		2	125.2	3.3	0.09
4	•					2	125.3	3.4	0.09
5	•				•	3	127.0	5.1	0.04
6	•		•			3	127.3	5.4	0.03

See Table 1 for parameter descriptions.
• Indicates parameter included in model.

Table 14
Model averaged* parameter estimates for the probability of chimpanzees approaching strangers following the start of an intergroup encounter

Parameter	Estimate	SE	95% CI	
			Lower	Upper
No. of males	0.49	0.12	0.25	0.72
No. of oestrous females	−0.54	0.22	−0.94	−0.070
No. of infants	0.061	0.039	−0.028	0.13
Dist. from centre	−0.00015	0.00010	−0.00033	0.000062
Food value	−0.014	0.011	−0.034	0.010

* Models 1–6 were used to calculate model averaged parameters. See Table 1 for parameter descriptions.

chimpanzees is a population difference, rather than an artefact of different experimental methods. Such population differences are to be expected, given the variation in social and ecological factors that result in different payoff structures. For example, while female lions, *Panthera leo*, in the Serengeti responded to intruders based on numerical assessment (McComb et al. 1994), female lions in Ngorongoro Crater always responded to simulated intruders, probably because in their more densely populated habitat, it always paid to threaten intruders, even when the odds of winning were low (Heinsohn 1997).

In contrast to the prediction that males would respond more aggressively in locations with higher food value, this parameter had a negative impact on probability of vocal response, as well as a negative (but not statistically significant) effect on approaching. This finding indicates that chimpanzees did not base their decision to escalate on the quality of the food resources at stake. A possible explanation for the negative relationship between food value and vocal response is that, because intergroup encounters took place in the periphery, they often occurred in grid cells that were only rarely visited, leading to a low calculated food value. Because the intergroup interactions in this area involved a community that appeared more powerful than Kanyawara, the Kanyawara chimpanzees may have been especially wary of escalating contests with this community.

The number of females with full sexual swellings negatively affected the probability of approach, suggesting that male chimpanzees face a trade-off between range defence and mate guarding. Fecund females may result in a reduction of effective numerical strength, as some males may be motivated to refrain from approaching intruders, either to ensure that these females did not mate with intruders, or to prevent males from their own community from mating with these females in their absence. This finding is consistent with that of an earlier experimental study in which the second-highest ranking male stayed behind with a fully tumescent female while the other males approached the simulated intruder (Wilson et al. 2001).

The presence of young infants had a positive, but not statistically significant effect on approach probability. The direction of this effect is consistent with the infanticide protection hypothesis; it may be that this effect was statistically nonsignificant only because of the relatively small sample size ($N = 120$). However, the estimated magnitude of this effect was 7.5 times smaller than the effect of the number of adult males, and 8.8 times smaller than the effect of the number of oestrous females, indicating that even if the effect were significant, it would be less important than other party composition effects. Distance from centre and food value both had negative, but not statistically significant, effects on the probability of approach. These findings are consistent with the failure to find an effect of location in range on response to a simulated intruder (Wilson et al. 2001), and indicate that the previous finding was not an artefact of the locations used in the experiments.

Together, these findings indicate that in this population, the decision to escalate a contest with intruders does not depend primarily on the value of resources at stake, whether these are mates, offspring, food or territory. Instead, chimpanzees appear to respond mainly to the risks associated with fighting, being more likely to approach intruders when there are more males in their own party. These findings provide further evidence that the competitive advantage enjoyed by larger groups can be a key factor in the evolution of social behaviour.

In summary, intergroup encounters in this population of chimpanzees occurred most often when abundant food sources attracted chimpanzees from both sides of a territorial boundary. Whether an aggressive response ensued depended mainly on whether the residents had sufficient strength in numbers. We expect these findings to be relevant to many species of group-territorial animals. Previous studies have demonstrated that the search for food explains a large proportion of animal movement decisions. For example, patterns of travel in gibbons, *Hylobates lar*, suggest they follow a spatial map of key food resources (Asensio et al. 2011); lions spend more time in parts of their range where prey are more abundant (Spong 2002), and a wide range of marine predators follow travel patterns that appear to maximize the chance of encountering prey (Sims et al. 2008). Given the primary importance of foraging, intergroup encounters in many species probably result from neighbouring groups being attracted to the same food resource, rather than from groups intentionally seeking to interact with rivals. When encounters do occur, numerically superior groups are more likely to respond aggressively, not only in chimpanzees but also in lions (McComb et al. 1994), black howler monkeys, *Alouatta pigra* (Kitchen 2004), and spotted hyaenas, *Crocuta crocuta* (Benson-Amram et al. 2011).

Given that the our estimate of the food value of a particular location had, if anything, a negative relationship to whether males would respond aggressively, one might conclude that such aggression is unrelated to food resources. Detailed examination of the socioecological factors leading to encounters, however, reveals the central importance of the distribution and abundance of food in causing such encounters to occur. These findings therefore draw attention to the need for caution in making inferences about the function of intergroup aggression based only on responses to encounters, without such contextual data.

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Supplementary Material

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