Chimpanzees (*Pan troglodytes*) modify grouping and vocal behaviour in response to location-specific risk

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Summary

Chimpanzees have hostile intergroup relations and are reported to use two strategies to reduce risk in the territory periphery: travelling in larger subgroups ('parties'), and travelling silently. We examined data from the Kanyawara chimpanzee community, Kibale National Park, Uganda to test for evidence of these strategies. We compared behaviour in the territory core with two potentially dangerous contexts: the periphery and croplands. Parties that visited the periphery had over twice as many adult males as parties that remained in the core. Analysis of vocal production rate of 249 parties revealed that, controlling for time of day and party composition, chimpanzees produced fewer pant-hoot calls in croplands than in the core. Pant-hoot production varied in different sectors of the periphery, being reduced in three sectors, unchanged in one, and increased in one. Focal follows of 12 males found results similar to party follows, but with rank-related individual variation. Overall, these results indicate that chimpanzees have the ability to modify grouping and vocal behaviour to reduce risk in areas with a high risk of detection. However, rather than consistently remaining silent in the periphery, chimpanzees in this population sometimes increased their vocalization rate, perhaps to advertise territory ownership and coalition strength.

Keywords: territorial behaviour, chimpanzee, *Pan troglodytes*, grouping behaviour, vocal regulation.

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Introduction

In species that defend group territories, the boundaries between neighbouring groups may represent areas of increased risk. The risk associated with border zones should be greatest in species with lethal intergroup aggression, such as humans (*Homo sapiens*, Manson & Wrangham, 1991), wolves (*Canis lupus*, Mech, 1994) and various species of ants (Wilson, 1971). The risk of encountering hostile neighbours may result in what are variously called 'buffer zones', 'war zones', or 'no-mans-lands', areas avoided by individuals on both sides of a boundary. Such border zones may have important effects on behaviour and ecology (Martin & Szuter, 1999). For example, the risk of encountering hostile neighbours affected the behaviour of men and women along the frontier between the Sioux and Chippewa tribes in Wisconsin and Minnesota (Hickerson, 1965). Women avoided the intertribal zone altogether. Men entered this zone only in war parties or larger hunting parties of 15 to 20 men, and did not set trap lines, as trapping required men to work alone or in pairs (Hickerson, 1965). Avoidance of buffer zones by territorial predators may lead to increased concentrations of prey along territory boundaries. White-tailed deer (*Odocoileus virginianus*), for example, have been reported to occur in higher densities in the buffer zones between hostile human societies (Hickerson, 1965; Martin & Szuter, 1999) and between hostile wolf territories (Mech, 1994). Likewise, groups of red colobus monkeys (*Colobus badius*) were about 50% larger in the buffer zones between territories of their major predator, chimpanzees (*Pan troglodytes*, Stanford, 1998).

Chimpanzees live in multi-male, multi-female groups called unit-groups (Nishida, 1968) or communities (Goodall et al., 1979), in which adult males defend a group territory. Intergroup encounters are routinely hostile and sometimes result in injury or death, especially in cases in which many males can isolate a lone victim in a gang attack (Wilson & Wrangham, 2003). Chimpanzees have been reported to employ two strategies to reduce the risk of being attacked in border zones. First, chimpanzees may travel in parties with more males when visiting the periphery of their territory (Bauer, 1980). Parties with more males are more likely to win intergroup fights, and individuals in such parties are presumably less likely to fall victim to gang attacks (Manson & Wrangham, 1991). Second, chimpanzees may refrain from producing loud vocalizations in the periphery, in order to reduce the risk of being

detected by hostile neighbours (Goodall et al., 1979; Nishida, 1979; Boesch & Boesch-Achermann, 2000; Mitani & Watts, 2005).

Regulation of party size and vocal production in relation to location-specific risk represent intriguing examples of animals modifying their behaviour in response to the possible actions of other individuals. A growing body of research in animal communication has focused on 'audience effects', in which signallers modify their behaviour based on the identity of individuals within range of detecting the signal (Seyfarth & Cheney, 2003; McGregor, 2005). The silence of chimpanzees during border patrols has become a widely cited example of an audience effect (Grinnell & McComb, 2001; Deecke et al., 2005; Aureli et al., 2006). Such silence stands in striking contrast to the behaviour of other group territorial species, which increase their loud call production when in border zones, presumably to advertise territory ownership (Harrington & Mech, 1979; Robinson, 1979; Mitani, 1988; East & Hofer, 1991; Gese & Ruff, 1998). However, while regulation of party size and vocal production in border zones are widely reported as being typical of chimpanzee behaviour, few studies have provided systematic data.

The most systematic data for party size in border zones come from an unpublished Ph.D. thesis (Bauer, 1976, cited in Bauer, 1980). Bauer reported that for chimpanzees in Gombe National Park, Tanzania, both adult male and anoestrous female chimpanzees travelled in larger parties when in the periphery than when in the core of their territory. However, while this finding is intriguing, the analysis suffers from several shortcomings. Bauer did not provide explicit criteria for distinguishing core from periphery, making it difficult to assess the validity of this distinction. Bauer also reported his findings only in terms of total number of independently travelling individuals, without distinguishing between males and females. Because adult males are the most active participants in intergroup fights, it is important to analyze party composition as well as overall size.

Mitani & Watts (2005) found that chimpanzees were more likely to conduct boundary patrols when in parties with more males, but did not explicitly compare boundary patrols with other possible categories of visit to the range periphery.

Likewise, while chimpanzees are regularly described as maintaining silence during boundary patrols, no systematic study has compared rates of vocal production during boundary patrols and other contexts.

In this study we, therefore, collected systematic data to answer two questions related to the behaviour of chimpanzees in border zones. First, do chimpanzees travel in parties with more males when visiting the periphery of their range? Second, do chimpanzees reduce their rate of loud call production when in the periphery of their range?

Chimpanzee social structure and vocal communication

Chimpanzees live in communities of up to 150 individuals (Mitani et al., 2002) but spend most of their time in smaller parties of varying size and composition. Males defend a group territory from other chimpanzee communities by patrolling boundaries and responding aggressively to foreign males (Nishida & Kawanaka, 1972; Goodall et al., 1979; Goodall, 1986). Chimpanzees produce a variety of different calls, but most studies have focused on the most conspicuous of these, the pant-hoot. Pant-hoots are individually distinct (Marler & Hobbett, 1975; Mitani et al., 1996) and can be recognized by other chimpanzees (Kojima et al., 2003). Pant-hoots are produced by both males and females, but most commonly by high-ranking males (Clark, 1993; Mitani & Nishida, 1993). They are produced in a variety of contexts, especially upon arrival at rich food sources (Wrangham, 1977; Clark & Wrangham, 1994) and before and after travelling (Mitani & Nishida, 1993).

One hypothesized benefit of calling is advertising the location of abundant, high quality food, either to benefit other community members (Reynolds & Reynolds, 1965), or to benefit the caller by attracting mates and allies (Wrangham, 1977). Captive studies have found that chimpanzees are more likely to call when foods are abundant and divisible (Hauser et al., 1993). Chimpanzees are also sensitive to social context, and are less likely to produce food-associated calls upon discovery of a small amount of food if they have an audience of conspecifics (Brosnan & de Waal, 2003), presumably to avoid feeding competition.

Pant-hoots appear to play an important role in territorial behaviour. Chimpanzees attend closely to pant-hoots and other calls from foreign chimpanzees (Goodall, 1986; Watts & Mitani, 2001). Pant-hoot choruses likely provide an honest signal of group size, much as the roars of lions (McComb et al., 1994) or howls of howler monkeys *Alouatta* spp. (Kitchen, 2004), in that it is impossible to fake the sound of overlapping calls of multiple individuals. Consistent with this prediction, chimpanzees appear to base their

response to foreign pant-hoots mainly on numerical assessment (Watts & Mitani, 2001; Wilson et al., 2001), much like female lions and male howler monkeys (McComb et al., 1994; Kitchen, 2004). Chimpanzees in parties with many males responded to playback of recorded pant-hoots with a loud vocal response and rapid approach to the speaker, whereas chimpanzees in parties with only one or two males almost always remained silent and were less likely to approach the speaker (Wilson et al., 2001).

Study design

To gain a better understanding of how chimpanzees modify grouping behaviour and vocal production in relation to location-specific risks, we collected data on vocal behaviour and other relevant variables in wild chimpanzees. To determine which areas chimpanzees appeared to perceive as boundary areas, and whether chimpanzees travelled in larger parties in these areas, we collected data on ranging behaviour, party composition, and intergroup encounters. To control for other factors likely to affect vocal production, we collected data on feeding behaviour. In addition to quantitatively comparing vocal production rates between the core and periphery of the territory, we examined another potentially dangerous spatial context in which silence may be advantageous: raiding crops on village land.

Ranging and grouping behaviour

Chimpanzees live in large home ranges, but concentrate much of their activity within a central core of the range (Herbinger et al., 2001). Based on previous studies at other sites finding larger party size in boundary areas (Bauer, 1980) and larger male party sizes on days with boundary patrols (Mitani & Watts, 2005), as well as predictions that chimpanzees should attempt to minimize risk from intergroup aggression (Manson & Wrangham, 1991), we predicted that parties visiting the periphery would have more males than parties that stayed in the core of their range.

Loud call production

We attempted to control for the various factors that may influence vocal production in chimpanzees, including individual differences, time of day, feeding context, and location, including border visits and crop raiding.

Individual variation

The benefits of producing loud calls may vary among individuals. If the benefits of producing loud calls in border areas are largely related to defending mates from extra-group males, and if high-ranking males monopolize fertilizations, high-ranking males should be more likely to produce loud calls (Nunn, 2000; Kitchen et al., 2004). High-ranking males do obtain more fertilizations in chimpanzees (Constable et al., 2001), suggesting that they should be more willing to pay the costs of territorial defence. We, therefore, examined the effect of dominance rank on vocal behaviour in different locations.

Temporal variation

We expected pant-hoots to be given most often in the early morning, when transmission conditions are most favourable (Waser &Waser, 1977). Chimpanzees at Gombe produced pant-hoots most often in the early morning (Wrangham, 1975).

Feeding context

Previous studies have found that chimpanzees frequently pant-hooted at abundant food sources (Reynolds & Reynolds, 1965; Wrangham, 1977; Clark & Wrangham, 1994; Hauser et al., 1993). We, therefore, expected pant-hoot rate to be higher when chimpanzees fed on highly preferred foods, such as fruits, than when feeding on less preferred foods, such as terrestrial herbaceous vegetation (Malenky et al., 1994).

Border visits

Chimpanzees visiting borders face both costs and benefits of calling. The primary cost of calling in border areas is the risk of being detected by neighbours. Neighbours detecting callers might either attack the callers, or (if outnumbered) flee, thereby reducing the callers' chances for conducting a surprise attack (Manson & Wrangham, 1991). The main benefits of calling in border areas would be to maintain contact with allies and associates, and to advertise territory ownership. Goodall (1986) distinguished between patrols, during which chimpanzees search for evidence of neighbours, and

excursions, in which chimpanzees visit border regions to feed. During excursions, if chimpanzees are in sufficiently large parties, they may be expected to maintain or even increase their rate of loud call production, to announce their presence to neighbours, claim territorial space and advertise coalitionary strength (Clark, 1993).

Crop raiding

Crops planted by people provide abundant and attractive resources, but animals raiding crops face a number of potential costs, from being chased away to being killed. Few studies have tested whether animals modify their vocal behaviour when crop-raiding. Anecdotal studies report that vervet monkeys (*Cercopithecus aethiops*) are unusually quiet when crop-raiding (Kavanagh, 1980; Horrocks, 1986). Vervet monkeys in sentinel positions during crop-raids remained silent on 26 of 28 occasions, vocalizing only when surprised at close range by a person (Horrocks, 1986). Whether sentinels were unusually silent is unclear, as the authors did not provide comparable data for vocal behaviour in other contexts.

Experiments with captive chimpanzees (Hare et al., 2000; Melis et al., 2006), as well as intriguing anecdotes from the field (Goodall, 1986) indicate that chimpanzees are sensitive to the risks of being detected by competitors for food and are able to modify their behaviour to avoid detection. Chimpanzees would normally be expected to produce many pant-hoots and other food associated calls upon arrival at an abundant, high quality food source such as bananas, sugar cane or other crops. However, the costs of calling when crop-raiding are likely to be high. Farmers who detect crop-raiding chimpanzees routinely chase them out of their crops. Although chimpanzees and other wildlife are legally protected, villagers sometimes injure or kill crop-raiding animals. During the study reported here, a villager killed an adult female from the study community when she raided bananas (MLW, unpubl. data). Chimpanzees appear sensitive to the costs of crop-raiding in that they rarely raid crops unless natural food supplies are low (Naughton-Treves et al., 1998).

Summary

In summary, based on previous studies, we expected that many factors would affect pant-hoot production. Factors producing an increase of pant-hoot rate

should include individual male rank (with high-ranking males calling more), time of day (with more frequent calling early in the morning), and feeding context (with more frequent calling when eating fruit than lower quality foods). We predicted that, controlling for all of these factors, pant-hoot rate in the periphery would either be lower than in the core of their range (if most boundary visits involved silent boundary patrols), or higher (if boundary visits mainly involved advertising numerical strength and territory ownership). Finally, we predicted that chimpanzees should remain quiet when raiding crops, to avoid being chased or killed by humans.

Methods

Study population

We studied the Kanyawara community of chimpanzees living in Kibale National Park, Uganda (Figure 1). This community contained 49–51 individuals during the study period (June 1997–November 1998), including 10–11 adult males, 1–2 adolescent males, 15–16 adult females and 2–5 adolescent females, all of which were individually recognized. Isabirye-Basuta initiated the systematic study of this community in 1983 (Isabirye-Basuta, 1988), and the community has been studied continuously since 1987 (Wrangham et al., 1992, 1996). The study site, described in detail elsewhere (Struhsaker, 1997), includes a mosaic of evergreen forest, swamp, and exotic softwood plantations within the park and smallholder farms, forest patches and tea plantations outside the park.

Range use

Range analysis relied both on locations obtained from a Global Positioning System (GPS) unit (Garmin 12 XL, accurate to 15 m RMS) and on maps of the trail system overlain with a 500×500 m grid. As part of the long-term study (Wrangham et al., 1996), observers followed a focal party of chimpanzees each day, recording the party's location on a map of the trail system at 15-min intervals. For purposes of analysis, we recorded the grid cell for each map location. We used GPS locations of trail intersections and other landmarks and a digitized topographic map (1:50 000 Y732 Series map, 1960, Department of Overseas Surveys) to align the trail map and the
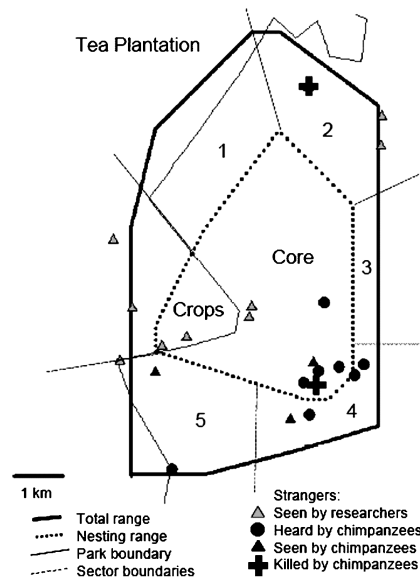
Figure 1. Kanyawara community range and location of intergroup interactions and sightings of stranger chimpanzees, 1996–1998, showing the park boundary (solid grey line), nesting range (inner polygon with dotted line), total range (outer polygon with solid black line), and the locations of Core, Crops and Periphery, including the five different sectors of the Periphery (separated by dashed lines), Grey triangles indicate sightings of stranger chimpanzees seen by researchers when Kanyawara chimpanzees were not present. Black circles indicate locations in which Kanyawara chimpanzees appeared to hear and respond to the calls of stranger chimpanzees. Black triangles indicate the locations where Kanywara chimpanzees saw stranger chimpanzees. Crosses indicate locations of chimpanzees killed during intercommunity conflict in 1991 (in the south) and 1998 (in the north).

associated grid to standardized map coordinates (UTM). We then determined the UTM coordinates for the center of each grid cell.

We used Biotas home range software (Ecological Software Solutions, 2000) to calculate minimum convex polygons (MCPs) enclosing the centers of all grid cells occupied during the study, and the locations used for night nests. Because border visits and intergroup interactions were relatively rare, we used ranging and intergroup data from the entire three-year period (1996–1998) to provide sufficient observations to identify likely borders with neighbouring communities. The MCP method has been criticized for shortcomings such as estimates of home range size being sensitive to outliers and sample size (Börger et al., 2006). For the purposes of this study, though, it provides a useful means of identifying the extent of the range, and is widely used

in other studies for this purpose (e.g., wolves, Mech, 1994; spotted hyenas (*Crocuta crocuta*), Boydston et al., 2003; chimpanzees, Chapman & Wrangham, 1993; Herbinger et al., 2001; Lehmann & Boesch, 2003; Williams et al., 2004).

We sought to identify border regions systematically, using ranging data, night nest locations, and the locations of interactions with and sightings of stranger chimpanzees. Unhabituated chimpanzees live on all sides of the Kanyawara community, except perhaps on the northwest where the park borders a large tea plantation (Figure 1). The precise number and geographic extent of these communities remains unknown, but based on sightings, we believe there is one community to the west, one community to the north, one or two communities to the east, and one community to the south and southwest.

To identify boundaries with neighbouring communities, we used a GPS unit to record the location of all cases in which Kanyawara chimpanzees encountered strangers or heard calls that appeared to be given by foreign chimpanzees, based on the location of the calls (i.e., towards the periphery) and the distinctive responses elicited by those calls (e.g., fear grimaces, embracing, mutual mounting, and responding with loud calls and rapid movements towards the distant calls if in a large party), as well as any other cases in which observers saw foreign chimpanzees (Figure 1). We also recorded the locations of one known intergroup killing, in which Kanyawara chimpanzees were found displaying around the body of a recently killed adult male in the north of their range (Muller, 2002), and a likely intergroup killing, in which a Kanyawara male was found dead in the area of a recent intergroup interaction in the south (Wrangham, 1999).

Because chimpanzee territories generally include large areas of overlap with neighbouring communities (Herbinger et al., 2001), and because the relatively small number of intergroup interactions recorded provided only poor resolution of the boundary area, we used ranging data and a map of the park boundary to divide the study community's range into three regions: Core, Periphery and Crops. We designated all locations outside the park boundary as Crops. Although this area includes other habitat such as villages, tea plantations, swamps and forest patches, chimpanzees from the study community were not observed to leave the park except to raid crops. Following a previous analysis of ranging behaviour for this population (Wilson et al., 2001), we used night nest locations to identify the Periphery. Chimpanzees sleep

in trees, usually in a new location each night, with each individual building a simple nesting platform from branches. We assume that chimpanzees will only nest in relatively secure areas. We, therefore, defined the Core as all locations within both the park boundary and the nesting range, defined as the minimum convex polygon enclosing all points used for night nests. Periphery consisted of all points outside the nesting range but within the park.

To determine whether our definition of Periphery was consistent with an elevated level of risk of intergroup encounter, we tested whether the number of intergroup encounters observed in the Periphery was greater than expected, based on the amount of time spent observing chimpanzees in that area. For each location, we used ArcView GIS (Environmental Systems Research Institute, 1997) to measure the distance to the nearest boundary with the nesting range, and whether the point was inside (positive values) or outside (negative values) the nesting range. We then conducted a chi-squared test, using the percent of observation time (1996–1998) in the Core and Periphery to generate expected values.

For each of the parties followed for collection of vocalization data (see below), we tested whether parties that visited Periphery contained more males than parties that remained in the Core.

Because chimpanzees are unlikely to perceive the Periphery as homogeneous, we conducted a spatially-explicit analysis, dividing the Periphery into sectors of similar size (3–5 km along the perimeter). These sectors are somewhat arbitrary, but are based on likely locations of neighbouring communities and ecologically salient features. At the time of the study, Sector 1 included large areas of papyrus swamp, cypress and pine plantation bordering the tea plantation, separated from Sector 2 by the trail leading to the village of Kitabumbwa. Sector 2 consisted of a large expanse of forest, selectively logged in previous decades (Struhsaker, 1997). Sector 3, to the east, bordered a series of hills that are mainly covered in pine plantations, grassland, and regenerating forest. Sector 4, in the southeast, consisted of high quality lowland forest, separated from Sector 5 by Nyakajojo Ridge, which was covered in pine plantations. Sector 5 consisted mainly of forest and swamp along the Dura River.

Sampling protocol

Unbiased estimates of behaviour rates generally require focal follows of individuals (Altmann, 1974). However, focal follows are difficult to conduct

when subjects are feeding in crops and other areas of dense vegetation, resulting in under-sampling for those conditions. Additionally, since chimpanzees visit border areas infrequently (Herbinger et al., 2001), few samples per individual can be obtained during border visits. Because pant-hoots are loud enough to be heard even when individuals are out of view, all occurrences of pant-hoots can be recorded even when focal follows are impractical. We, therefore, collected two complementary sets of data: party follows and individual focal follows. As described below, we used party follows to examine temporal patterns and to test for the effects of party composition and location in range. We used focal follows to examine individual variation in vocal production in different locations.

For collection of vocal behaviour data, teams of two observers joined the regular long-term study field assistants in following chimpanzees throughout their range, all day when possible. The first observer conducted party follows, noting the time to the nearest minute for all occurrences of pant-hoot bouts produced by members of the focal party. A bout was defined as either a single or chorused pant-hoot separated from other bouts by silence or non-pant-hoot calls. In practice, a median of 4 min separated successive bouts, with only 3% of bouts occurring within the same minute. At 15-min intervals, the observer recorded the map location and the identity of all individuals known to be travelling with the party.

Pant-hoots are highly variable calls, consisting of a series of introduction, build-up, climax, and let-down elements. Pant-hoots grade into other calls such as hoots, which lack a climax element. Precise determination of call type by ear in the field can be difficult, especially when many individuals are calling. Some of the calls recorded by observers as 'pant-hoots' may, therefore, include closely related calls. However, because the focus of this study relates to loud calling and the risks of detection, to be conservative, when in doubt we erred towards including calls that observers judged to be close to pant-hoots in their acoustic structure and loudness.

The second observer conducted focal follows throughout the day, choosing subjects randomly from the available individuals. To reduce dependence in the data, a minimum of 30 min separated the start time of samples on the same individual. Each focal follow consisted of a series of five point-samples at 2-min intervals, noting the behavioural state (feed, groom, be-groomed, rest, move, other) and map location of the subject, concurrent with continuous sampling of the time and category of all vocalizations made by

the focal subject. Vocalization categories included bark, waa-bark, grunt, food grunt, nest grunt, pant-grunt, pant-hoot, scream, copulation scream and laughter (Marler & Tenaza, 1977; Clark, 1993). Pant-hoots can be heard at a greater distance than other calls (1–2 km) (Ghiglieri, 1984), though barks and screams are also loud. The various grunts are soft and can only be heard within tens of meters.

MLW trained and supervised two field assistants, D. Muhangyi (DM) and J. Barwogeza (JB), who collected the majority of observational data while MLW focused on recording vocalizations for acoustic analysis. To ensure reliability among observers, we conducted trials in which a pair of observers recorded 10 min of focal follow data from a single target. We conducted a total of 28 trials on three separate days, with 16 different chimpanzees serving as focal targets. Estimates of vocalization rate were closely correlated, both for the two field assistants (e.g., for pant-hoots, Spearman rank correlation, $r_s = 0.93$, $N = 19$ trials, $p < 0.0001$) and between DM and MLW (pant-hoot rate: $r_s = 0.85$, $N = 8$ trials, $p < 0.05$). Formal trials were not conducted between MLW and JB, but data collection was regularly supervised to ensure accurate and consistent recording of events.

Thus, three observers contributed to the data for party follows (DM: 732 h; JB: 538 h; MLW: 143 h) and focal follows (DM: 138.9 h, JB: 57.5 h, MLW: 3.6 h). The overall estimates of pant-hoot rate did not differ among these observers for either party follows (Kruskal–Wallis test: $H = 4.26$, df $= 2$, NS) or for focal follows (Kruskal–Wallis test: $H = 0.935$, df $= 2$, NS).

Feeding data

Because pant-hoots may be elicited by arrival at food sources, we recorded feeding behaviour for both party follows and focal follows. During party follows, as part of the long-term study, field assistants recorded whether party members were feeding at 15-min intervals, and if so, the species and part being eaten (e.g., ripe fruit or terrestrial herbaceous vegetation (THV)). For each focal follow, the observer recorded whether the subject was feeding or engaged in some other behaviour state at 2-min intervals and, if feeding, the species and part.

Data analysis

Party follows

To identify spatio-temporal patterns in vocal behaviour, and to determine the effects of party composition and feeding behaviour, we analyzed party follow data as follows. First, for each party, we limited data to hours in which data were recorded for the entire hour (four 15-min samples and continuous data throughout). For each hour observed, we calculated the total number of pant-hoot bouts produced by that party. We then calculated the mean number of adult males, adult females, and females with sexual swellings present during each hour, as well as the per capita pant-hoot rate (total pant-hoot rate divided by the mean number of adult males and females). For each hour, we also calculated the number of 15-min points for which party members were observed feeding, and if feeding, the type of food (e.g., ripe fruit or THV). Because parties sometimes occupied more than one grid cell during a given hour, for each hour we calculated the mean location (in UTM coordinates). Using the mean location for the hour, we determined the grid cell occupied for the majority of the hour, and whether the hour was spent mainly in the Core, Crops, or Periphery. Taking the average location for each hour seemed appropriate given the rather coarse-grained measures available from the grid cells as well as the likelihood that chimpanzees in this population do not perceive these boundaries to be abrupt (due to the overlap in ranges among communities as well as the lack of obvious landmarks, such as ridges or streams, separating community ranges). For each hour, we also determined the mean distance to the nearest boundaries of the park and nesting range.

In analyzing the party follow data, we sought to identify patterns on both a broad and fine scale while avoiding problems of pseudo-replication and inter-dependence that would arise from treating each hour of data as a statistically independent sample. We, therefore, plotted values spatially and temporally to identify overall patterns in the raw data, then conducted two statistical tests designed to control for the various factors likely to affect vocal production.

To visualize the spatial patterning of range use, party composition, and vocal behaviour, for each grid cell we determined the following from party follows: the total number of observations, the mean number of adult males, and the mean number of pant-hoots per hour, plotting these values with ArcView. To visualize temporal patterns, we plotted the mean rate of pant-hoot production versus time of day for all parties, separated by location. To

visualize the effects of party composition, we plotted the mean rate of pant-hoot production versus the number of adult males, rounded to the nearest whole number.

We then conducted two statistical tests designed to control for factors identified in these visualizations: First, considering each party as unit of analysis, we conducted stepwise regression to determine which of the following factors affected the overall rate of pant-hoot production: the mean number of adult males, the mean number of adult females, the mean number of females with sexual swellings, the percentage of feeding time spent eating fruit, and the number of hours spent during the day in each of the three locations: Core, Crops and Periphery.

Second, we conducted an analysis of matched pairs to control for the time of day, party composition, and presence of the alpha male. Because females rarely pant-hoot unless in mixed-sex parties (Clark, 1993) we limited analysis to parties with at least one adult male. We searched the dataset to identify matched pairs based on time of day and party composition, blind to the number of pant-hoots that were produced. For each hour that a test party spent in Crops or Periphery, we identified a control party that was observed in Core with the same number of males as the test party. If multiple parties met these criteria, we used a single party, to ensure an equal number of parties in each sample, choosing the control party that was observed closest in time to the test party and that provided the greatest overlap in time. Hours that could not be matched were discarded from the analysis. To control for the possible influence of rank effects on party follow samples, we limited this analysis to samples in which the alpha male was present. We then used Wilcoxon signed-rank tests to test whether parties observed in Crops and Periphery pant-hooted less often than when in Core.

For matched pairs analyses, we were able to find control parties for all of the parties except for one that visited Crops in the late evening (1900–2000). Because hours that could not be matched were discarded from the analysis, the final sample consisted of 77 h recorded from 33 parties in Crops and 147 h from 55 parties in Periphery. Preliminary analyses showed that discarding unmatched hours did not affect the results.

Focal follows

For focal follows, we plotted the location of the focal subject at the start of each follow onto a digitized trail map. We used ArcView to determine

whether the location was in Core, Crops or Periphery. For each focal sample in Crops and Periphery, we identified the Core sample for the same individual that was nearest in time ($\pm$3 h or less) and had the most similar number of males in the party ($\pm$2 males or less). We also attempted to match feeding context. For each Periphery sample, we chose a Core sample that fit the above criteria and also matched the type of food eaten during the sample (fruit, THV or none). For Crops, the appropriate feeding context for comparison was less clear. Chimpanzees sometimes ate high-quality foods in Crops, such as sugar cane and ripe banana fruits, but most of their time was spent eating banana stems. We, therefore, chose three matches for each, based on type of food eaten during the sample: fruit, THV or none. Matches were chosen blind to the rate of pant-hoot production.

We calculated dominance rank from the direction of agonistic wins and losses using a probabilistic method that permits ranking of individuals with few observations (Jameson et al., 1999). We conducted statistical tests using StatView (SAS Institute, 1998). Because sample sizes were small and data were not normally distributed, we generally used nonparametric procedures. All tests for significance were two-tailed with the criterion of significance set at $p < 0.05$.

Results

Ranging behaviour

From 1996–1998, observers recorded 7385 h of range location and party composition. During this time, the Kanyawara chimpanzees ranged over an area enclosed by a minimum convex polygon covering 37.8 km^2 (Wilson et al., 2001), with night in nests located inside a 15.8 km^2 subset of the total range. Land outside the park covered 2.2 km^2 of the nesting range and another 6.9 km^2 beyond the nesting range. The area defined as Core – that part of the nesting range within the park, – thus, covered 13.6 km^2 (36.0% of the total), Crops covered 9.1 km^2 (24.1%) and Periphery 15.1 km^2 (39.9%). Although the Core was, thus, smaller than the Periphery, chimpanzees spent the vast majority (85%) of observation time in the Core, compared to 11% in the Periphery and 4% in crops (Figure 2).
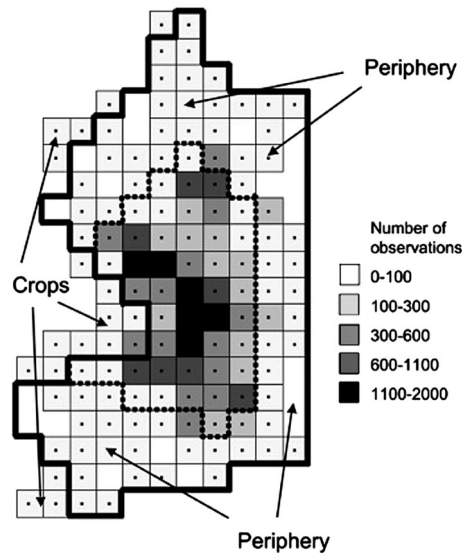
Figure 2. Observation density (number of 15-min scans obtained in each location, 1996–1998). Grid cells with at least one observation are outlined with a square and marked with a black dot in the centre. Grid cells with no observations are left blank. The solid black polygon encloses grid cells whose centres are within the park. The dotted black polygon encloses grid cells whose centres are within the nesting range.

Intergroup encounters

A total of 12 intergroup encounters were observed from 1996–1998. These encounters took place a median 148 m outside the nesting range (range 753 m within to 2188 m outside the nesting range). Seven encounters took place in the Periphery, more than expected based on the number of observation hours in that location (chi-squared test, $\chi^2 = 6.99$, df $= 1$, $p < 0.01$).

Party follows

During 238 observation days (June 1997 to November 1998), three observers followed a total of 249 different parties, recording a total of 1413 h of party follow data in which at least one male was present for more than half of the hour. The majority of parties (149) stayed within Core for the duration of the follow. Forty-one parties spent at least one hour in Crops, of which 36 visited both Crops and Core on the same day. Of the 62 parties that spent at least 1 h in Periphery, 41 were observed in both Periphery and Core on the same day.

Observers obtained a total of 92 h of vocalization data in Crops and 198 h in Periphery.

Range location and party size

Parties observed in Periphery and Crops had more males than parties observed in Core (Figure 3). Parties that remained in the Core the entire day ($N = 149$) had a median 2.2 males, whereas parties that travelled to the Periphery ($N = 62$) had a median 5.9 males (Mann–Whitney U test, $U = 2786$, $p < 0.0001$) and parties that travelled to Crops ($N = 41$) had a median 4.8 males (range $= 0.0$ to 9.0 males; Mann–Whitney U test, $U = 1580.5$, $p < 0.0001$). For the 41 parties that were observed at both the Core and Periphery on a single day, the number of adult males was higher at the Periphery (median $= 6.0$ males) than when they were in the Core (median $= 5.3$ males; Wilcoxon signed-rank test, $z = -1.994$, $N = 41$, $p < 0.05$). The 36 parties that were observed at both Core and Crops on a single day did not differ in the number of adult males when at these two locations (Core: median $= 4.8$ males, range $= 0.0$ to 8.6 males; Crops:
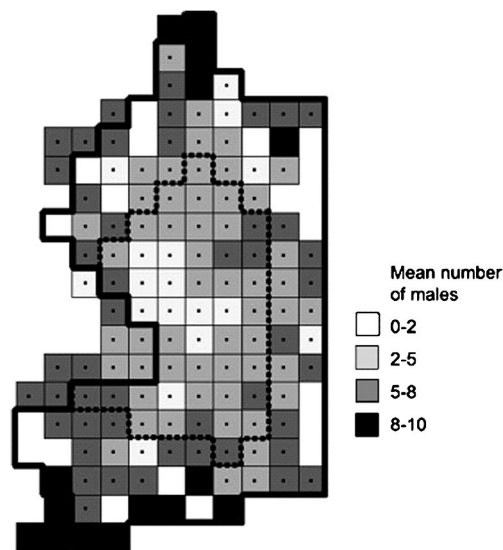
Figure 3. The mean number of males per 500×500-grid cell for all observations, 1996–1998. Shadings indicate cell values grouped by frequency of occurrence, from the first quartile (white) through the fourth (black).

median $= 5.0$ males, range $= 0.0$ to 9.0 males; Wilcoxon signed-rank test, $z = -0.865$, N $= 36$, NS).

Effects of time of day and party composition

The per capita rate of pant-hoot production followed similar temporal patterns in both Core and Periphery, peaking early in the morning (0700–0800) and decreasing until about noon, after which calling continued at a low rate (Figure 4a). Per capita pant-hoot production was lower in Periphery than in Core for most (9 of 14) hours of the day, with the exception of the early morning (0700–0800) when it was noticeably higher in the Periphery. For the 12 days on which parties were observed in the Periphery at this hour, pant-hoots
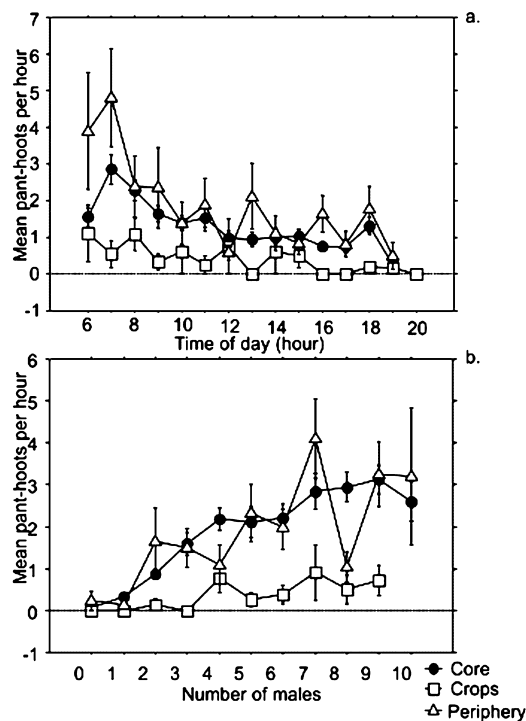
Figure 4. Variation in pant-hoot rate with (a) time of day and (b) number of adult males in Core, Periphery or Crops. Symbols indicate (a) the mean number of pant-hoots produced each hour for all parties and (b) the mean rate of pant-hoot production for parties with a given number of males (rounded to the nearest whole number), with error bars indicating $\pm$ one standard error. To clearly show data points that fall directly on the *x*-axis, the *y*-axis is shown continuing to -1, although negative call rates are obviously impossible.

were recorded on 9 days (range: 3 to 18 pant-hoots per hour), suggesting that this peak was not simply the result of a few influential samples. In contrast to both Core and Periphery, the rate of pant-hoot production for parties in Crops remained low throughout the day (Figure 4a). The raw number of pant-hoot bouts recorded per hour increased steadily with the number of males for parties in Core and Periphery but not for parties in Crops (Figure 4b).

Spatial patterning

Plotting the mean hourly pant-hoot rate observed for each 500×500-m grid cell gives some indication of spatial patterning (Figure 5). While controlling for time and party composition is essential for statistical testing, it is clear from these raw data that chimpanzees were not always silent when visiting the Periphery. However, a tendency towards quieter behaviour is evident near the edges of some areas of the Periphery, especially in the southwest, southeast, and northeast, and in Crops.
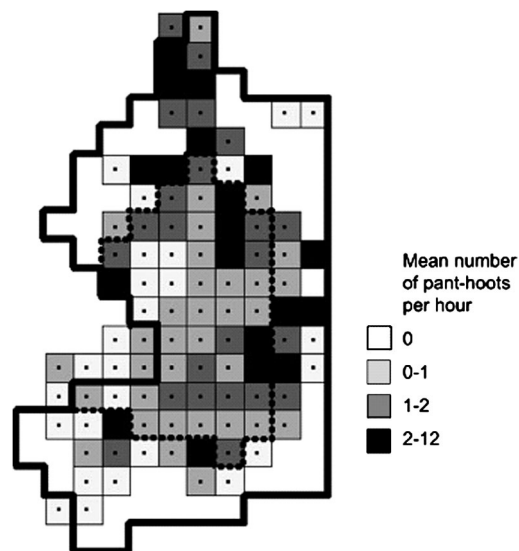
Figure 5. The mean number of pant-hoots per hour per 500×500-grid cell for all observations, 1997–1998. Shadings indicate cell values categorized by quartile, from the first quartile (white) through the fourth (black). Pant-hoot rate is not adjusted for time of day, party composition, or other factors known to be important. Because vocal behaviour data collectors were not present for a proportion of days for which party composition data were collected, some cells shown with data in the previous figure are blank here.

Effects of location

Party follows – stepwise regression

Considering all parties, a stepwise regression revealed that the mean rate of pant-hoot production during the day depended most strongly on the mean number of adult males (coeff. = 0.33, F-to-Remove = 60.75), the mean number of females with sexual swellings (coeff. = 0.47, F-to-Remove = 6.35), and the number of hours spent in Crops (coeff. = -0.23, F-to-Remove = 7.9; $R^2 = 0.26$, $F_{3,248} = 28.53$, $p < 0.0001$). Variables that failed to enter the model included the number of adult females, the number of hours spent in Periphery, the number of hours spent in Core, and the percentage of feeding time spent eating fruit.

Party follows – matched pairs

Parties observed in Crops pant-hooted a median 0.0 pant-hoots per hour (range = 0.0 to 5.0), compared to a median 1.0 pant-hoots per hour for their matched pairs in Core (range = 0.0 to 8.0; Wilcoxon signed-rank test: $z = -2.87$, $N = 33$, $p < 0.01$). Parties observed in Periphery produced a median 1.0 pant-hoot per hour (range = 0.0 to 10.7), compared to 1.67 pant-hoots per hour for their matched pairs observed in Core (range = 0.0 to 10.5). This difference was not statistically significant (Wilcoxon signed-rank test, $z = -1.394$, $N = 55$, NS). Of the 55 parties observed, 25 showed a reduction in pant-hoot rate at the Periphery, with the difference between Periphery and Core ranging from -9.0 to -0.25 pant-hoots per hour. Thirteen parties showed no change in pant-hoot rate (difference = 0.0), and 17 showed an increase in pant-hoot rate (range in difference = 0.25 to 9.7). Twenty parties observed at Periphery did not produce any pant-hoots (58 h of observation) compared to 15 such parties observed in Core (37 h of observation).

Vocal behaviour in the Periphery varied among the different sectors (Figure 6; Kruskal–Wallis, $H_4 = 11.1$, $p < 0.05$). Specifically, compared to parties observed in Core, parties observed in Periphery pant-hooted less frequently in Sectors 1, 2, and 5, more frequently in Sector 3, and at an unchanged rate in Sector 4.

Focal follows

We obtained 1470 focal samples for 12 males in Core (1253 samples), Crops (61 samples), and Periphery (156 samples). For each male we obtained a
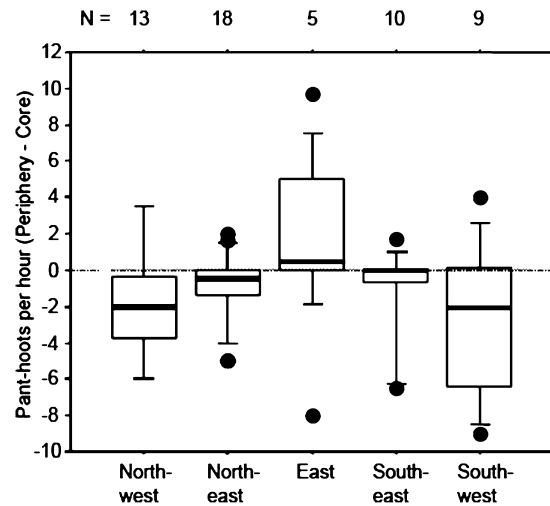
Figure 6. Box plots illustrating the variation among different sectors of the Periphery in the difference in pant-hoot rate between parties observed at the Periphery and the parties observed in Core matched for time of day and party composition. Horizontal lines indicate the 10th, 25th, 50th, 75th and 90th percentiles. Boxes enclose the inter-quartile ranges, and medians are emphasized by bold lines.

median 112.5 focal samples in Core (range: 44 to 177), a median 5 samples in Crops (range: 1 to 15) and a median 16 samples in Periphery (range: 4 to 22).

Considering all focal samples that were obtained, males produced a median hourly pant-hoot rate of 0.76 in Core (range = 0.14 to 1.7), 0.19 in Periphery (range = 0.0 to 6.3), and 0.0 in Crops (range = 0.0 to 2.5). Other loud calls, such as screams and waa-barks, were rarely observed in any context. When in Crops, chimpanzees rarely vocalized, but five out of 11 males gave soft food grunts. Males produced food grunts at the following rates: a median 0.4 per hour in Core (range = 0 to 1.3), 0.0 in Periphery (range = 0.0 to 3.5) and 0.0 in Crops (range = 0.0 to 3.8).

Data from focal follows in Core revealed that high-ranking males pant-hooted more often than low-ranking males (Kendall rank correlation: $\tau = -0.545$, $N = 12$, $p < 0.05$; Figure 7). This difference was most pronounced in Crops and Periphery, where the alpha male pant-hooted far more often than any other male (Figure 8).

Considering just the matched pairs of focal samples, males produced a median 0.0 pant-hoots per hour when in Crops ($N = 8$, range = 0.0 to 2.5),
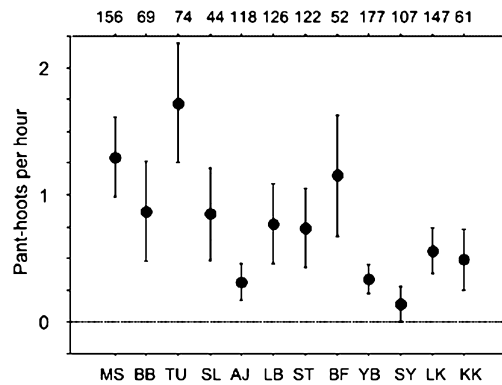
Figure 7. Mean pant-hoot rate ($\pm$ SE) from all Core focal follows versus mean rank from all observations at Core. Males are ranked from left (high) to right (low), based on their mean rank for samples obtained in this location. The number of samples for each individual is shown at the top.

compared to the following feeding contexts in Core: 0.42 pant-hoots per hour when feeding on fruit (range = 0.0 to 8.75), 0.0 pant-hoots per hour when feeding on THV (range = 0.0 to 7.5), and 0.0 when not feeding (range = 0.0 to 1.5). The difference in pant-hoot rate between Crops and feeding on fruit in Core falls short of statistical significance (Wilcoxon signed rank test, $N = 8$, $z = -1.83$, $p = 0.07$; Figure 8a).

Controlling for time of day and feeding context, males did not differ significantly between Core and Periphery (Wilcoxon signed rank test, $z = -0.89$, $N = 12$, NS). The median pant-hoot rate was 0.19 in Periphery (range = 0.0 to 5.8) and 0.21 in Core (range = 0.0 to 1.5). The alpha male, MS, pant-hooted more frequently in Periphery than Core (Figure 8b).

Seven of 12 males stayed quiet or reduced their call production in Periphery compared to Core. Of the 5 males who increased their pant-hoot rate in Periphery, 3 were current or former alpha males (MS, BB and SY). The highest-ranking male, MS, showed the greatest increase: 1.5 per hour in Core compared to 5.8 per hour in Periphery (Figure 8). MS pant-hooted in six of 15 samples in Periphery, with these samples being distributed across five different months of a fifteen-month period, indicating that this high rate is not the result of a single unusual sample. In addition to pant-hooting at a high rate in Periphery, MS was the only individual observed pant-hooting in Crops, though he did so in only one of six samples in Crops.
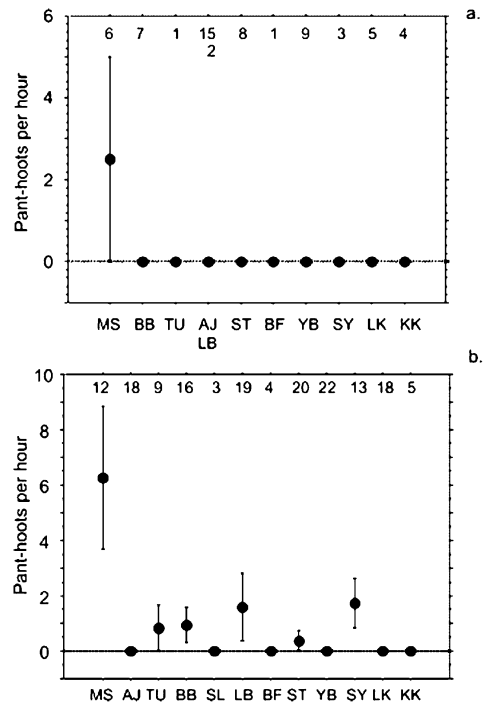
Figure 8. Mean pant-hoot rate (± SE) from focal follows in (a) Crops and (b) Periphery versus mean dominance rank for each male in each of those conditions. Males are ranked from left (high) to right (low), based on their mean rank for samples obtained in each location. The number of samples for each individual is shown at the top of each graph. Because some males changed in rank, and samples were not evenly distributed over time for each location, the ordering of the males differs between the two graphs.

Discussion

Range location and party composition

Parties that visited Periphery and Crops contained more males than parties that stayed in Core. The larger number of males in parties visiting Periphery is consistent with predictions that males visiting border areas should travel in larger subgroups to reduce risks of lethal attack by neighbouring groups (Manson & Wrangham, 1991). The rarity of travelling in border areas except in parties with many males suggests that even if the probability of encountering neighbours is low, the risks of meeting neighbours when outnumbered are potentially high – a likelihood borne out by the occasional intergroup killings observed in this population (Wrangham, 1999; Muller, 2002).

Why chimpanzees should travel in larger parties when visiting Crops is unclear. At least four explanations are possible. First, given the difficulty of following small parties in Crops, a sampling bias may exist. Second, the abundant food of Crops may reduce the costs of feeding competition, enabling large parties to travel together. Third, most or all of the Crops area is used to some extent by a neighbouring chimpanzee community ('Gusaziire's'). Though Gusaziire's community appears to be small (perhaps two adult males, one adolescent male, and two to four females), the risk of encountering neighbours may increase the incentive for traveling in larger parties. Fourth, travelling in larger groups could reduce the costs of vigilance. To choose among these hypotheses, additional observations would be required, perhaps accompanied by experiments that simulate detection by farmers in crop areas.

Vocal production

Consistent with other studies, we found that (i) chimpanzees pant-hooted most often in the morning (Wrangham, 1975); (ii) the overall rate of pant-hoot production increased with increasing numbers of males per party (Clark, 1993; Mitani & Nishida, 1993); and (iii) high-ranking males called more often than low-ranking males (Clark, 1993; Mitani & Nishida, 1993). Controlling for these factors, we found that chimpanzees called most often in the Core of their range and least often in Crops.

The abundance, quality, and divisibility of cultivated foods suggest that these resources would normally elicit pant-hoots if humans did not defend them. Despite the general tendency for parties with more males to produce more pant-hoots, parties observed in Crops produced few pant-hoots, even when many males were present. The two methods used, party follows and focal follows, yielded similar effects of location on call production, indicating that the results are not due to the biases inherent in either sampling method.

In contrast to expectations that chimpanzees should reduce loud call production when visiting peripheral areas, we found evidence of a more variable response, with a (non-significant) tendency towards decreased pant-hoot production offset by increased production of pant-hoots at certain times of day (early morning), by some individuals (mainly the alpha male) and in some locations (especially Sector 3, the eastern boundary (Figure 6)). This evidence of variability is consistent with the competing goals relating to vocal

behaviour in border areas: avoiding detection and advertising territorial ownership.

Many of parties that spent at least one full hour in the Periphery during the period of observation did decrease their call rate, and many parties produced no pant-hoots while visiting the Periphery, consistent with previous reports of border patrols in this population (Wrangham, 1999; Watts et al., 2006). However, on other occasions, chimpanzees did pant-hoot during visits to the Periphery, and in some cases substantially increased their call rate. Thus, chimpanzees were not uniformly silent in the Periphery. Whether this is random variation, or a systematic response to perceived social challenges is, presently, unclear. For example, chimpanzees may be most vocal when they are attempting to challenge neighbours, when they sense that they are particularly strong, or when the value of a bluff is high. In areas in which intergroup encounters are rare, or the neighbouring communities are known to be weak, it may be advantageous to increase call rate. Intergroup encounters occurred infrequently on the eastern boundary (Figure 1), the region with the greatest increase in loud calling in the periphery. In contrast, in the south and southwest, intergroup encounters occurred more frequently (Figure 1), and chimpanzees pant-hooted less often (Figure 5).

We are confident that our failure to find a uniform decrease in loud call production during border visits is not simply an artefact of the study design, such as insufficient sample size, or using too large an area as the Periphery. We were able to detect silence in Crops with somewhat fewer observation hours than we obtained for Periphery. The Periphery does cover a large area, but the findings that Kanyawara chimpanzees visited this area rarely, travelled in large parties when visiting the area, and were more likely to encounter strangers in this area, indicate that it does represent an area of increased intergroup threat.

Thus, controlling for party size, time of day and feeding context, we did not find a consistent change in loud call production in the Periphery. Although it is difficult to be certain in the absence of systematic data from other sites, the possibility exists that Kanyawara chimpanzees conduct silent border patrols less frequently than some other populations. This could occur if the risks of encountering neighbours are low, either because of low population density (and, thus, low probability of encountering any neighbours), or because one or more of the neighbouring groups are weak and represent little threat. Differences may occur both among populations, and within

populations over time, depending on the threat facing a given chimpanzee community. For example, the Ngogo community, located 12 km from the Kanyawara community towards the centre of Kibale National Park, lives at a much higher population density and experiences a correspondingly higher level of intergroup encounters. The approximately 145 chimpanzees of the Ngogo community (Watts & Mitani, 2006) use a range covering between 25 km^2 (Mitani & Watts, 2005) and 35 km^2 (Watts & Mitani, 2001), for a density of 4.1 to 5.8 chimpanzees/km^2. This is roughly 3 to 4 times the density of the Kanyawara community (50 chimpanzees/37.8 km^2 = 1.3 chimpanzees/km^2). Living at higher population density, the risk (and opportunity) of encountering neighbours is much higher for Ngogo chimpanzees, which encountered strangers 26 times during 23 months of observation (Watts & Mitani, 2001), for a rate of 1.1 encounters/month. This is approximately 3 times the rate at which Kanyawara chimpanzees encountered strangers (0.33 encounters/month).

In addition to variation among populations, chimpanzees may modify their vocal behaviour in border areas based on changing levels of threat from neighbouring communities. For example, at Gombe National Park, Tanzania, the Kasekela community has increased in size over the past 10 years, while the neighbouring Kalande and Mitumba communities have been severely reduced in numbers (Pusey et al., 2007). In border areas where Kasekela chimpanzees once entered cautiously and quietly (e.g., Wilson et al., 2004), Kasekela chimpanzees now enter to feed and travel noisily, accompanied by mothers and infants (MLW, pers. obs.). Likewise, at Mahale National Park, Tanzania, in the 1970s, chimpanzees from the large M-group 'called out' several times during an incursion deep into the range of the much smaller K-group (Nishida, 1979). K-group chimpanzees generally maintained silence and retreated upon hearing the larger M-group (Nishida, 1979).

In species that use loud calls in both within- and between-group contexts, the net benefits of calling must take both contexts into account. If intergroup encounters are extremely rare, then the payoffs of within-group benefits may predominate. Because Kanyawara chimpanzees encounter their neighbours infrequently, the benefits of maintaining contact with their allies may more often be greater than the risks of detection.

Rank and pant-hoot production

High-ranking males called more frequently than low-ranking males, and three of the five males who increased their call rate in Periphery were cur-

rent or former alpha males. This result is consistent with the expectation that high-ranking males have more to gain from producing loud calls in intergroup contexts (Nunn, 2000; Kitchen et al., 2004). The two former alpha males with elevated call rates in Periphery also responded vigorously to playback of intruder calls, traveling towards the front of progressions towards the speaker (Wilson et al., 2001).

Pant-hoot rate at borders is likely to be influenced by party size, just as chimpanzees are more likely to call in response to a simulated intruder when in larger parties (Wilson et al., 2001). For example, although the highest-ranking male sharply increased his pant-hoot rate in Periphery, he did so only when in parties with three or more males. Other males also appeared to remain quiet when travelling in Periphery in parties of one to two males, but the small sample sizes excluded the possibility of statistical tests.

Temporal patterning

Chimpanzees called most often in the early morning. This may have been due to advantageous atmospheric conditions at that time of day, or to 'frequency windows', times of day minimizing overlap with calls of other species using similar frequencies. Alternatively, it may be a result of socioecological factors. Chimpanzees tend to begin the day by eating their preferred food, ripe fruit (Wrangham, 1977), a context that frequently elicits pant-hoots (Hauser et al., 1993; Clark & Wrangham, 1994).

In conclusion, chimpanzees consistently travelled in parties with more males when visiting border zones. Chimpanzees reduced production of loud calls during at least one context in which calling would be costly: crop-raiding. Chimpanzees showed a tendency to produce fewer loud calls when visiting parts of the periphery, but along the eastern boundary of their range actually increased their rate of calling. Individual males consistently reduced their call rate when crop raiding, but showed more variation in their response to border areas. Individual variation was closely tied to rank, perhaps because high-ranking males gain greater benefits from calling. These findings indicate that wild chimpanzees modify their grouping and vocal behaviour in response to the risks associated with particular locations.

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