RESEARCH ARTICLE

Spatial Cohesion of Adult Male Chimpanzees (*Pan troglodytes verus*) in Taï National Park, Côte D'Ivoire

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Group living animals can exhibit fission–fusion behavior whereby individuals temporarily separate to reduce the costs of living in large groups. Primates living in groups with fission–fusion dynamics face numerous challenges in maintaining spatial cohesion, especially in environments with limited visibility. Here we investigated the spatial cohesion of adult male chimpanzees *(Pan troglodytes verus)* living in Taï National Park, Côte d'Ivoire, to better understand the mechanisms by which individuals maintain group cohesion during fission–fusion events. Over a 3-year period, we simultaneously tracked the movements of 2–4 males for 4–12 hr on up to 12 consecutive days using handheld GPS devices that recorded locations at one-minute intervals. Analyses of the male's inter-individual distance (IID) showed that the maximum, median, and mean IID values across all observations were 7.2 km, 73 m, and 483 m, respectively. These males (a) had maximum daily IID values below the limits of auditory communication (<1 km) for 63% of the observation time, (b) remained out of visual range (≥ 100 m) for 46% of observation time, and (c) remained within auditory range for 70% of the time when they were in different parties. We compared the observed distribution of IIDs with a random distribution obtained from permutations of the individuals' travel paths using Kolmogorov–Smirnov tests. Observation IID values were significantly smaller than those generated by the permutation procedure. We conclude that these male chimpanzees actively maintain cohesion when out of sight, and that auditory communication is one likely mechanism by which they do so. We discuss mechanisms by which chimpanzees may maintain the level of cohesion observed. This study provides a first analysis of spatial group cohesion over large distances in forest chimpanzees using high-resolution tracking, and illustrates the utility of such data for quantifying socio-ecological processes in primate ecology. Am. J. Primatol. 77:125–134, 2015.
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INTRODUCTION

Living in a group provides several costs and benefits to group members [Wrangham, 1979; Krebs & Davies, 1997; Majolo et al., 2008]. Individuals may profit from the frequent association with conspecifics and the establishment of enduring and equitable social bonds [Langergraber et al., 2009; Mitani, 2009], the dilution effect can reduce their risk of predation [Delm, 1990; Jeschke & Tollrian, 2007] and a social environment can increase offspring survival rates [Gaston, 1978; Longino, 1984; Schaik et al., 2000; Boesch et al., 2010; Klemme & Ylönen, 2010; Schülke et al., 2010]. In group living species, like carnivores or primates, group members may also benefit from cooperation during inter-group conflicts [Grinnell, 2002; Crofoot and Wrangham, 2010; Boesch et al., 2008] or hunting [Caraco and Wolf, 1975; Grinnell et al., 1995; Boesch and Boesch, 1989]. However, group living can also be costly, and group members may face increased competition over food [Symington, 1988;

Wittig & Boesch, 2003] or mating partners [Deschner et al., 2004], attraction of predators [Bruce et al., 2001] and transmission of diseases [Leendertz et al., 2004].

To maximize access to food, which is best achieved in small groups, while maintaining the benefits associated with living in large groups, individuals may separate and reunite repeatedly in so called subgroups or parties, resulting in fission–fusion

grouping dynamics [Krebs & Davies, 1997]. Changing socio–ecological conditions like the distribution or abundance of food [Stevenson et al., 1998; White, 1998; Newton-Fisher et al., 2000; Mitani & Amsler, 2003], or group-based tasks including cooperation during boundary patrols [Watts & Mitani, 2001] or hunting [Boesch & Boesch, 1989] can influence the formation and structure of parties which therefore can vary in size, composition and duration [Chapman et al., 1993; Lehmann & Boesch, 2004]. Primate species with fission–fusion dynamics do show considerable flexibility in the spatial and temporal grouping patterns of their members [Aureli et al., 2008] e.g. baboons [Kummer, 1968], spider monkeys [Chapman, 1990], bonobos [White & Burgman, 1990; Hohmann & Fruth, 2002], chimpanzees [Nishida, 1968; Goodall, 1986; Boesch, 1996], and humans [Marlowe, 2005].

Individuals of primate groups that show fission–fusion dynamics can actively maintain cohesion by (a) remaining in visual range, (b) remaining in auditory contact, or (c) using a mental representation of the location of other group members when not in visual or auditory contact [Noë & Laporte, 2014]. The cohesion of groups can be quantified with different measurements, e.g. using the association time and nearest neighbor distance of individuals within one party [Cowlishaw, 1999] or spatial measures of inter-individual distances (IID) between group members [Byrne, 2000]. By comparing spatial measures of cohesion to the individuals' visual and auditory range, it is possible to make inferences about mechanisms that determine group cohesion and mechanisms by which individuals reunite.

Group cohesion influences the communication among group members and the possibility of collective decision making needed for coordinated activities [Conradt & Roper, 2005]. Here, we distinguish between group cohesion and group coordination. Studies of group cohesion often involve some overall measure of group spread and relate this to environmental context [Byrne, 2000]. In contrast, measuring group coordination (e.g. in studies of fish [Strandburg-Peshkin et al., 2013]) involves retaining measures of both when and where individuals move in reference or in response to each other. In this study, we focus on three measures of group cohesion (see below) rather than on (dyadic) coordination, deferring to the discussion how members might coordinate their movements to maintain group cohesion. A few studies of non-human primates investigated spatial group cohesion or coordination by GPS tracking of individual movements and analyzed inter-individual distances between group members [Ramos-Fernández et al., 2011; Sugiura et al., 2011; Otani et al., 2013]. Ramos-Fernández and his colleagues found no evidence of coordination between different subgroups of spider monkeys *(Ateles geoffroyi)*. The size of observed spider monkeys' territories range from 0.5 to1 km^2, and their long-distance calls can be heard for up to 1 km. The observed parties of spider monkey groups were almost always within auditory range.

Groups of wild chimpanzees *(Pan troglodytes verus)* living in Taï National Park (TNP), Côte d'Ivoire, occupy territories of about 25 km^2 [Boesch & Boesch-Achermann, 2000]. Living in a densely forested habitat, they have a maximum visual range of 50 m, but their loudest communication modality, the drumming on buttresses, has a range of approximately 1.0–1.5 km [Boesch, 1991a; Arcadi et al., 1998]. In this study, we investigated how often Taï chimpanzees maintain group cohesion by remaining within auditory range, especially while they are outside each other's visual range. We simultaneously followed several males to record their locations with GPS devices, and used this high-resolution spatiotemporal tracking data to determine the proportion of time individuals remained within different spatial thresholds (i.e. visual and auditory range) by analyzing three measures of group cohesion: daily maximum IID, daily median IID, as well as minute-by-minute IID distributions. Our analyses provide a quantitative scale of the cohesiveness, facilitating the discussion about the mechanisms that drive cohesion and by which individuals coordinate their movements.

METHODS

Statement of Ethical Treatment of Non-Human Primates

All research was conducted with permission of the local communities, the Centre Suisse de Recherches Scientifiques in Côte d'Ivoire (CSRS), the Ministère de la Recherche Scientifique and the Ministère de l'Environnement et des Eaux et Forêts in Côte d'Ivoire, complied with protocols approved by the Max Planck Institute in Germany, and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates.

Study Group

We collected movement and behavior data from the adult males of the Taï Chimpanzee Project's East group between November 2007 and November 2010 [Boesch et al., 2010]. The East group at Taï occupies a territory of approximately 27 km^2 (Fig. 1). Habituation of the East group started in 2000, and all adult males were fully habituated by the beginning of this study. Although observers could follow all adult females when they associated with other group members, some avoided being tracked when they moved alone or only with their offspring. Therefore, we excluded all females from the individual track-log data collection to reduce observation pressure. When we began our study, East group had 46 members: 6 adults and

Territory use of East group
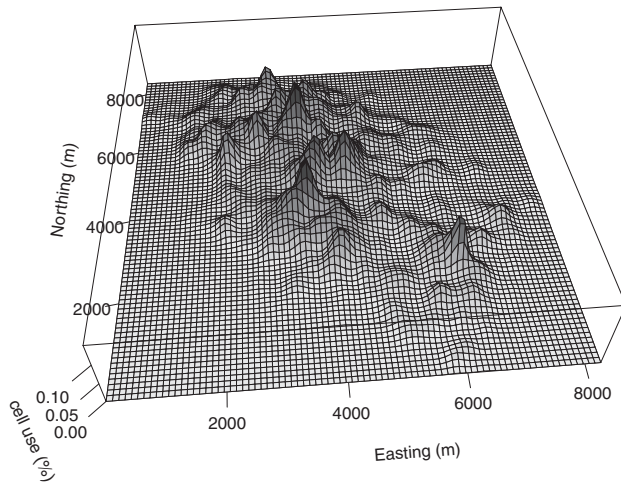**(November 2007–November 2010)**

Fig. 1. Territory use of East group based on a kernel density estimator (grid cells 100×100 m) calculated from all individual travel paths observed on 232 days of the study. The territory is approximately $27 \, km^2$.

1 sub-adult male, 16 adult females with 16 offsprings, 3 nulliparous females and 5 juvenile orphans. The smallest group size occurred in March 2009 after an outbreak of anthrax disease, during which several individuals died, leaving only 35 group members. At the end of this study, the group consisted of 43 individuals: 5 adult males, 12 adult females with 15 offsprings, 4 nulliparous females and 7 orphans.

Data Collection and Calculation of Inter-Individual Distance Values

The author NE and six field assistants collected all data following the research and hygiene protocol of the Taï Chimpanzee Project [Boesch, 2008]. All observers were trained for at least six months prior to data collection. We followed all adult males of the East group and alternated our choice of focal subjects to ensure similar observation time for each male and each pair (dyad) of males (Table I). During the study, the males Porthos and D'Artagnan died, while Triton reached maturity. We therefore collected most observations for the dyads including Lakini, Marc, Freddy, and Athos.

We carried out simultaneous focal follows [Altmann, 1974] of 2–4 males in series of 2–12 consecutive days. On the first day of each series of consecutive daily follows, we searched for the intended focal subjects. We encountered them during the day in the same or in different parties and conducted data collection until they had built their night nests (usually between 6 and 7 p.m.). On the following days, we began focal follows when the males left their night nests (usually around 6 a.m.) and finished data collection when they built their new night nests.

Each observer followed one focal subject at a time, carrying a handheld GPS device (Garmin 60csx) to track its daily travel path by recording the focal subject's locations automatically every 60 sec (Fig. 2). Spatial coordinates were recorded in UTM units, WGS84 coordinate system [Garmin International Inc., 2007]. We expect the recorded GPS position to be accurate to the actual location of the focal subject within ± 25 m (observation inaccuracy), including the observer's distance of ± 10 m to the focal subject (see hygiene rules of the TCP [Boesch, 2008]) and a mean GPS inaccuracy of ± 14.2 m (calculated for comparable GPS devices in the same region and habitat [Normand & Boesch, 2009]). We interrupted the individual tracking of the focal subjects for only two reasons: (a) when an observer was unable to see the focal subject or (b) when the GPS device did not receive satellite readings. The lead author NE conducted random

TABLE I. Observation Time for Each Male and Male-Male Dyad. Data Collection Occurred Over 232 Days From November 2007 to November 2010

Male	Observation days (hours) per male	Days (hours) of observation per male-male dyad						
		Ath	Dar[a]	Fre	Lak	Mar	Por[b]	Tri[c]
Athos	125 (1195)		8 (41)	72 (470)	45 (245)	57 (335)	6 (23)	11 (81)
D'Artagnan[a]	26 (231)			9 (69)	10 (65)	4 (25)	4 (23)	2 (9)
Freddy	132 (1294)				39 (180)	64 (421)	7 (39)	15 (115)
Lakini	100 (1206)					44 (197)	8 (54)	9 (57)
Marc	128 (797)						4 (18)	23 (211)
Porthos[b]	17 (156)							0 (0)
Triton[c]	35 (473)							

Each of the 7 males of East group was a focal subject for 17–132 days. Four males were observed for >100 days and 7 male-male dyads for >20 days during the entire study period (grey cells). The dyad Porthos-Triton was not observed because Porthos died before Triton reached maturity.
[a]died in April 2009.
[b]died in March 2008.
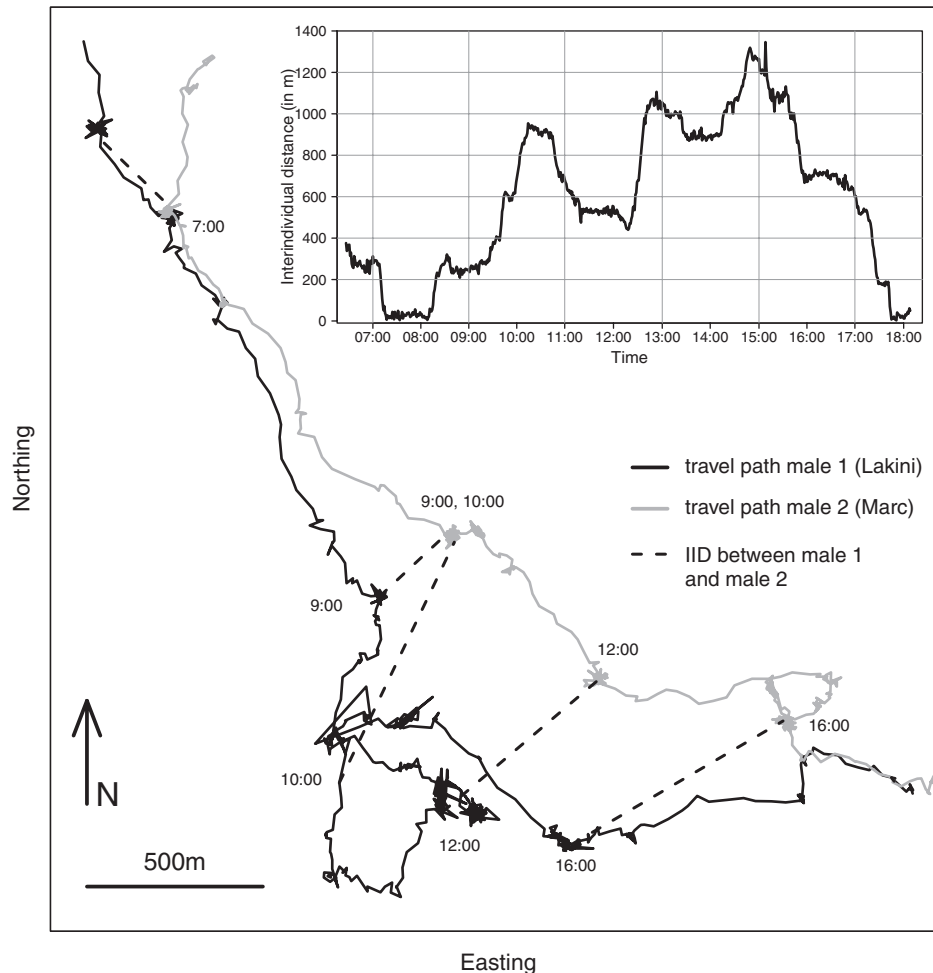[c]adult since July 2009.

Fig. 2. Individual travel paths of two adult male chimpanzees (Lakini and Marc on May 16th, 2009). They illustrate the spatiotemporal scale of fission-fusion events throughout the observation. The dotted straight lines exemplify five inter-individual distances (IID) between the focal subjects at 07:00, 09:00, 10:00, 12:00 and 16:00. The embedded graph shows all IID values calculated for the entire day on a minute-byminute sampling interval.

inter-observer reliability tests with the field assistants and verified GPS device accuracy by randomly assigning two GPS devices per observer.

We used the statistical software R (version 2.14.1, [R Core Team, 2013]) to calculate straight line distances between the coordinates of the GPS locations of all focal subjects to obtain the IID values in meters for every minute we observed at least two males (Fig. 2). In addition, we calculated the daily median IIDs and maximum IID values for each dyad to reduce the effect of autocorrelation in the data on the spatial analysis.

Boesch and Boesch-Achermann [2000] defined individuals as belonging to different parties when they are not in visual range (50 m). Here, we defined two focal subjects as belonging to different parties whenever their calculated IID value was $\geq 100\,\text{m}$ (the sum of both 25 m observation inaccuracies and the 50 m maximum visual range). Our conserva-

tive threshold ensures that two males satisfying this criterion are extremely likely to be in different parties.

Evaluating a Possible Bias of IID Values

Because of the way we located focal subjects (see above), the data could include a selection bias influencing the IID values we had to search for the males and encountered them during the first day, whereas we began tracking them on the second and following days right from their nests. We compared the first IID value from each first and second day of 81 follows in 2010 to test for this possible selection bias and found no significant difference (Wilcoxon signed rank test: $N_{\text{day1}} = N_{\text{day2}} = 81, V = 44{,}570{,}110, P = 0.075$). In this sample, focal subjects were members of the same party (IID $< 100\,\text{m}$) at the start of the observations on 72% of the first days and on 69% of the second days. We also

compared the IID values for the first three hours of observation on the first and second day for the same 81 follows and found no significant differences (Wilcoxon signed rank test: $N_{day1} = N_{day2} = 14{,}502$, $V = 43{,}039$, 130, $P = 0.088$). We concluded that our method of searching for the focal subjects did not cause any significant bias in the IID values. Consequently, we retained all data for the spatial cohesion analyses.

Determining the Auditory Range and Calling Rate

Estimates for the auditory range of chimpanzees in TNP range from 1.0 to 1.5 km [Boesch, 1991a; Arcadi et al., 1998]). Drumming on buttresses is the chimpanzee's loudest communication modality and consists of frequencies <20 Hz [Crockford & Boesch, 2005]. Kojima [1990] showed that the hearing abilities of chimpanzees and humans have only slight differences across the audible spectrum, with chimpanzees being less sensitive to frequencies below 250 Hz, while both species show a similar resonance frequency and gain of the external ear. Based on these findings, we can determine the upper bound of the auditory range of chimpanzees using data collected by human observers. Each observer carried a GPS device to record the focal subject's location and in addition, during a period of 11 months (January-November 2010), noted the exact time and type of each call and drumming emitted by the focal subject, as well as those heard from any chimpanzee in another party (including those from neighboring groups).

We found that the focal subjects signaled (calling or drumming) on average twice per hour (mean time between signals $= 25.8 \pm$ SD 46.0 min, range: 0–499 min, $N = 2819$), but sometimes remained silent for extended periods (up to 8 hr). With notes from the observers, we were able to match signaling events to the different focal subjects and calculated their IID at the time of signaling. Here, we included only observations where all signals within one minute were produced by one focal subject (i.e. no chorused signals), and these signals were detected by an observer following another focal subject within a different party (IID ≥ 100 m). IIDs at the time of signaling averaged $316.7 \pm$ SD 181.4 m (range: 101–953 m, $N = 272$). Considering the slight differences in hearing abilities of humans and chimpanzees and the observation inaccuracies (see above), we determine 1.0 km to be the threshold for the largest distance at which chimpanzees in Taï forest could detect auditory signals from conspecifics.

Inter-Individual Distance Analyses

We applied two complementary approaches to analyze the inter-individual distance data. In the first approach, we obtained the daily maximum IID for each dyad for all days with at least four consecutive hours of observation. This first analysis allows for broadly characterizing the observed separation distances. However, this analysis does not quantify the spread of IIDs during the day, i.e. it does not reflect the variability in fission–fusion grouping patterns. To measure this variability, we computed the cumulative distribution function of the minute-by-minute IIDs. In addition, we designed a nonparametric bootstrap test to evaluate whether this distribution differed from a null model without spatial cohesion. This analysis is described in the next section.

Permutation Tests as the Null Model for Spatial Group Cohesion

To evaluate the extent of spatial cohesion between males, we compared the distribution of the empirical IID values to IID values that we obtained from an intra-dyadic permutation of observed daily travel paths. We kept the order of the recorded locations, so that each travel path of the males remained intact. We permuted the daily travel paths within each dyad across all days of observation and calculated the minute-by-minute and daily median IID values for these permutations. The permutation procedure removed any spatial cohesion in collective movements of the males, while keeping all other aspects of individual movement intact e.g. speed, turning angles, proportion of time spent moving or resting, and potential dyadic affinities that can override spatial proximity in determining cohesion [Polansky & Wittemyer, 2011].

We based the permutation tests on 7 dyads for which we had more than 20 days of observation (Table I) and included only those days with at least four consecutive hours of observation (mean time of observation per day $= 8.45 \pm$ SD 2.09 h, range: 4.07–12.5 h, $N = 327$). We obtained IID values from 1,000 permutations of travel paths for each dyad to build up a null distribution of IID values.

We used a two-sample Kolmogorov–Smirnov (KS) test (ks.test function in the R software environment [R Core Team, 2013]) to test whether the empirical cumulative IID distribution function (IID values ≥ 100 m) rose more quickly than the null distribution, which would indicate more cohesion than expected by chance. We also compared daily median IID values between the empirical and permuted datasets to remove any influence of fine-scaled behavioral variation, e.g. if the individuals remained in one spot for several hours and then traveled to a new location, this could bias the description of IID values in times of no movement. This practice also allowed us to ensure that results were robust given the variation in sample sizes.

In the permutation test, we randomized across days. We were concerned that in particular the

permuted IIDs tended to be much larger than the observed ones what may simply be a result of changes in territory use through time. The potential for such bias in the analysis is intuitive in a thought exercise, but also borne out by observations of overall territory size and the density distribution map of space use by chimpanzees within their territory (Fig. 1). To address this potential shortcoming of the permutation study, we checked home range overlap statistics based on a partition of the data according to rainfall (but not at a finer scale such as month). Rainfall may influence chimpanzee movement behavior, as the plants they feed on have seasonal fluctuations often matching those of rainfall [Anderson et al., 2005; Polansky & Boesch, 2013]. We calculated the Bhattacharyya's affinity (BA) index (maximum of 1, [Fieberg & Kochanny, 2005]) on the empirical data to estimate the overlap in territory use between dry and wet seasons. We computed the BA index using the adehabitatHR package [Calenge, 2006] in the R software environment [R Core Team, 2013]. Our data produced a BA index of 0.96 indicating substantial overlap in territory use between wet and dry seasons. This measure shows a low impact of seasonality for this study, so we permuted travel paths over all seasons. Given the high overlap in range use by season and the fact that observation days were not consistently and regularly spaced through time, we chose to control for any dyad effects (by sampling within dyads) rather than to try to control for systematic territory use changes.

RESULTS

Tracking Data

Over a three-year period (November 2007 and 2010), we simultaneously tracked the movements of at least 2–4 males on 232 unique days. In total, we tracked the daily travel paths of 441 male–male dyads (dyad days) and collected over 5,300 hr of focal subject observation (mean daily observation time per dyad: $7.06 \pm SD\ 3.27$ h, range: 0.27–12.5 h, $N = 441$) (Fig. 2). Days with short observation time occurred when we began new focal follows or lost contact with a subject because he travelled rapidly through dense, swampy or flooded areas. In total, we recorded more than 429,000 GPS locations of all focal subjects and calculated 214,545 inter-individual distances between males.

Inter-Individual Distances Between Male Chimpanzees

We observed 330 dyad days with at least 240 simultaneously recorded locations for both males. Of these 330 dyad days, 7 dyads had a daily maximum IID less than 100 m, 202 dyads had daily maximums between 100 m and 1 km, and 121 dyads had daily maximums greater than 1 km. From the 121 dyads with a daily maximum IID greater than 1 km (which in total consist of 60,876 minute-by-minute IID values), 38% of the minute-by-minute IIDs were greater than 1 km. The largest IID measured between any two males across all observations was 7,272 m.

Based on the minute-by-minute samples, males were outside their visual range (IID $\geq$ 100 m, i.e. not in the same party) for 45.9% of the time (arrow 1 in Fig. 3), and they were beyond the auditory communication threshold (IID values > 1 km) for only 13.6% of the time (arrow 3 in Fig. 3). With the focus of this study on spatial cohesion between males outside their visual range, we carried out further analyses on the subset of the data with the IID $\geq$ 100 m (dotted curve in Fig. 3). We found that focal subjects having no visual contact with each other remained within their auditory range for 70.4% of the time (arrow 2 and corresponding box plot in Fig. 3).

Non-Random Distribution of Inter-Individual Distances

To evaluate if the empirical IID distribution was non-random, we compared it to a null distribution of IID values obtained by permuting the daily travel paths. The procedure we used to obtain data suitable for the permutation test retained 149,848 empirical minute-by-minute IIDs, whereas the permutation produced 5,003,803 such values. The empirical observations showed that focal subjects were within auditory range 68.7% of the time, whereas the permuted data showed only 16.9% of the values within this range (arrow 1 and 2 in Fig. 4, Panel A). The cumulative distribution function of the empirical IID rose more rapidly than the null distribution, allowing us to reject the null hypothesis that the two distributions were the same (KS test, $D^+ = 0.60$, $P < 0.001$).

We verified the robustness of these results by also comparing daily median IID distributions. This analysis produced similar results, with 83.6% of the empirical median IIDs and 19.0% of the permuted values within auditory range (arrows 1 and 2 in Fig. 4, Panel B). The KS test similarly rejected the null hypothesis ($D^+ = 0.68$, $P < 0.001$, $N = 396$ empirical values, $N = 190,000$ permuted values).

DISCUSSION

For wild chimpanzees living in the Taï forest where the visual range is limited, it is likely challenging to maintain group cohesion while employing fission–fusion grouping patterns. We found that any two adult males of our study group were in different parties almost half the time (46%). Given that they were in separate parties, however, they remained within auditory range (1 km) for more than two thirds of the time (70%). Together with the analysis of daily
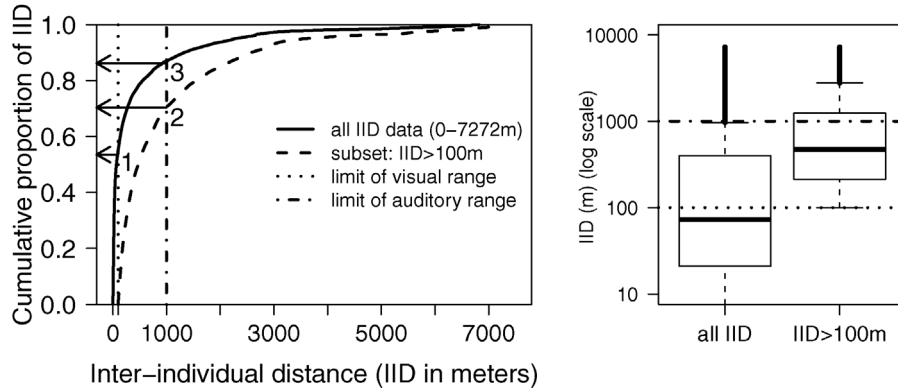
Fig. 3. Cumulative distribution plot and box plot for all observed IID values of wild adult male chimpanzees in Taï forest (continuous curve). The males remained in different parties 45.9% of the time (IID = 100 m) (arrow 1). During the time of separation in different parties, where the focal subjects had no visual contact with each other (subset of data represented by the dotted curve), they remained within auditory range 70.36% (IID = 1,000 m) (arrow 2). The males separated farther than the auditory range only infrequently, for 13.1% of the entire time (IID > 1,000 m) (continuous curve, arrow 3).

Panel A: minute–by–minute IID values

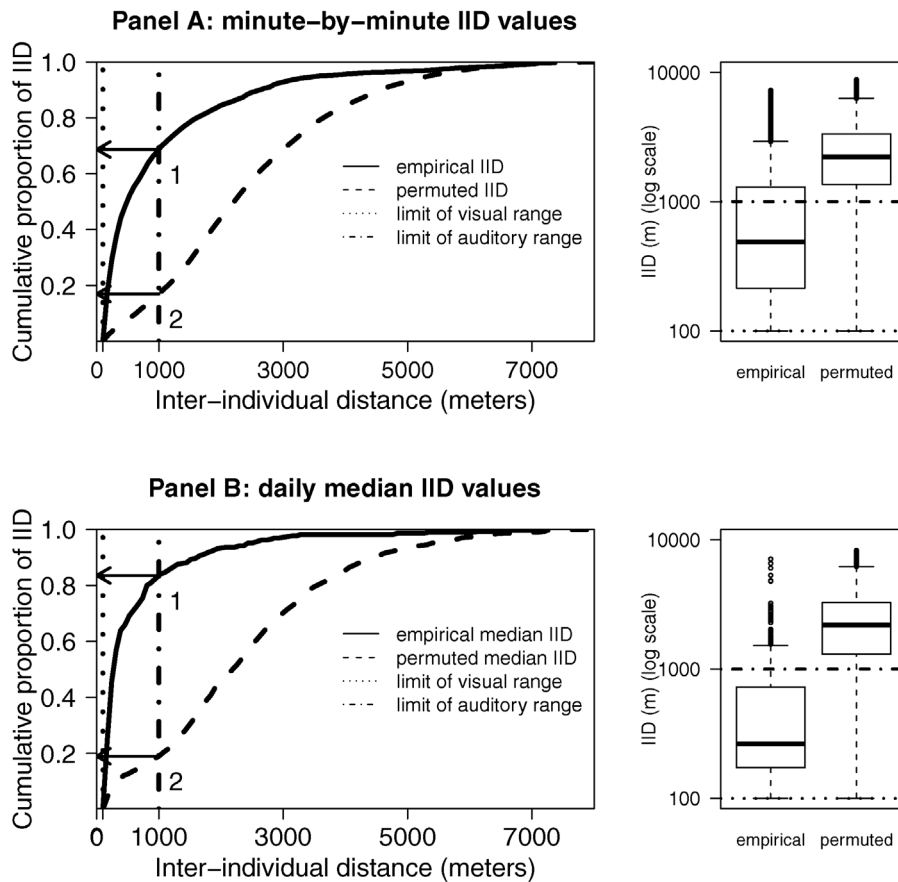**Panel B: daily median IID values**

Fig. 4. Cumulative distribution plot and box plots for the IID values (>100 m based) on empirical (continuous curves) and permuted data (dotted curves). Panel A shows the distributions with the minute-byminute sampling intervals. Panel B shows the distributions using the calculated daily median IID values. The box plots illustrate the significant difference between the distributions of both data sets.

median and maximum IID values, these findings suggest that male chimpanzees at Taï maintain spatial cohesion even when visually separated.

Since individuals can and do use most of their territory during the year (the maximum observed IID was approximately 7.2 km, e.g. during mate guarding [Boesch & Boesch-Achermann, 2000]), and therefore have the potential to separate farther than their auditory range, this raises the question as to what might be determining the scale of cohesion observed

here. Based on (a) a low percentage of observed IIDs outside auditory range and (b) the comparison with randomly permuted travel paths showing lower IIDs than expected by chance, we conclude that male chimpanzees in TNP actively limit their IIDs to be within auditory range.

Chimpanzees may face dangerous, potentially fatal situations when they encounter other chimpanzee communities or predators [Krebs & Davies, 1997; Cheney, 1987; Watts et al., 2006; Boesch et al., 2007]. These situations require the cooperation of all group members to defend the territory [Watts & Mitani, 2001; Boesch et al., 2008] or to chase predators away [Boesch, 1991b]. When Taï chimpanzees encounter invading neighboring groups, they emit loud calls and drum on buttresses and then remain silent for some minutes waiting for other group members to join before attacking the intruders [Boesch & Boesch-Achermann, 2000]. Such cooperation requires that group members, that may be dispersed, are able to reunite quickly. Males that generally remain within auditory range of each other (no matter if they were moving, feeding or resting) can thus retain the benefits of living in large groups when needed.

Many primates use auditory signaling to maintain group cohesion and intensify communication when group members are outside visual range, suggesting that they exchange information about their positions and movements, e.g. squirrel monkeys [Boinski, 1991], capuchin monkeys [Boinski, 1993], sifakas [Trillmich et al., 2004], golden brown mouse lemurs [Braune et al., 2005], and other neotropical primates [Boinski, 1996; Boinski & Garber, 2000]. Chimpanzees regularly use vocalizations and drumming to communicate over long distances [Clark, 1993; Uhlenbroek, 1996]. In this study, we also found that the observed males communicated approximately twice per hour, but individuals also remained silent for extended periods or moved beyond auditory range. These observations suggest that individuals may employ more complex cognitive tools to maintain cohesion, such as remembering where food was and anticipating where others will likely be feeding [Normand & Boesch, 2009; Janmaat et al., 2013]. Alternatively, it is possible that spatiotemporal fluctuations in food availability could explain cohesion in a cognitively simpler way, e.g. individuals depleting food resources and moving incrementally in the direction of most food at a regional scale. Further research may help to clarify the behavioral, ecological and cognitive drivers of group cohesion and coordination of chimpanzees in the Taï forest. Disentangling and quantifying the many socio–ecological mechanisms shaping group cohesion and collective movement in wild primates in general remain difficult challenges [Boinski & Garber, 2000]. Opportunities to advance our understanding of primate social systems by using large amounts of high-resolution data show much promise

[Krause et al., 2013]. With the emerging technologically driven improvements in the resolution of individual movement data such as those presented here, combined with aerial and satellite based data on detailed resource distributions at a landscape scale, primatologists will increasingly be able to quantify the cognitive, social and ecological mechanisms shaping the collective movement of their subjects.

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