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Chimpanzee Distribution around the Northern Boundary of the Mahale Mountains National Park, Tanzania

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INTRODUCTION

The Mahale Mountains National Park in Tanzania, established in 1985 (Government Notice 262 1985), conserves wildlife including chimpanzees (*Pan troglodytes*) (Itoh *et al.* 2012). An analysis of satellite images suggested that the area inside the northern park boundary had been deforested, but the situation was ambiguous because the boundary on the map did not reflect the location of landmarks in this area (*ibid.*). Based on a park policy to make the boundary known to local people, a 20-m wide strip along the boundary has been cleared of trees and beacons and park signs have been placed on the border (Figure 1). The aim of this study was to clarify the distribution of chimpanzees and other large mammals inhabiting the area around the northern park boundary.

METHODS

This study was conducted in the Mahale Mountains National Park, which is located on the eastern shore of Lake Tanganyika (Nishida 1990). The northwest side of the Mahale Mountains is covered by forest (the Kasoje

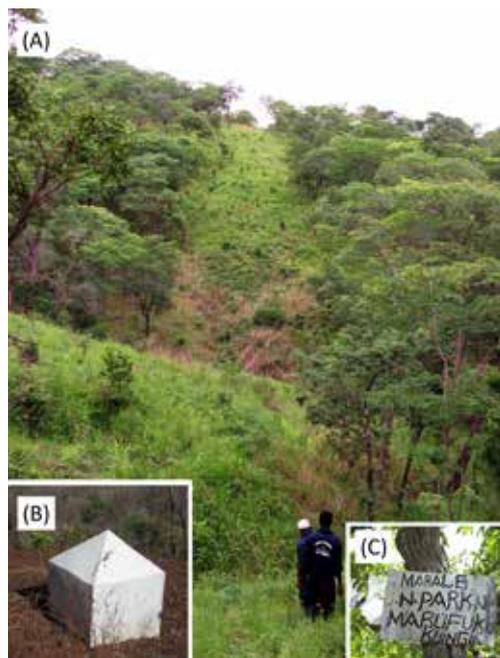


Figure 1. Park boundary. (A): A 20-m wide strip along the park border, (B): A white beacon about 1 m in height, and (C): A park sign.

Forest), which is the main habitat of the Mahale study unit-groups (*ibid.*). However, most of the area in and around the park is covered by miombo woodland and bamboo bush (Kano 1972; Figure 2). There are several rivers in the woodland and bush, and riverine forests are found along some rivers. The Karobwa Hills, which are located to the east of the park, are also covered with miombo woodland, bamboo bush, and forest and are known chimpanzee habitat (Kano 1972; Ogawa *et al.* 2006).

From 2008 to 2014, we conducted surveys around the northern boundary of the park (Figure 3A). The survey distance was measured by GPS (Garmin GPSmap60Cx), and the total distance was 100.7 km (inside the park: 17.2 km, along the park border: 25.5 km, outside the park: 58.0 km; Table 1).

We recorded the numbers and the positions of chimpanzee beds and large mammals observed during our surveys. When we found animal feces, we identified the species based on the shape and size of the droppings. The positions of beacons were also measured using GPS.

We adopted Kano's method to estimate the population density of chimpanzees: density ($/\text{km}^2$) = (number of beds detected)/(survey distance [km]) (width of survey route [0.14 km]) (detectability [70%]) (bed duration [180 days]) (Kano 1972). Although two studies have been conducted to measure the bed decay rate at the west side of the Mahale Mountains (Ihobe 2005; Zamma & Makelele 2012), no data regarding bed decay rates are available for the remainder of Mahale. To compare the results of the present study with those of the previous study (Kano 1972), we used 180 days for our measure of bed duration.

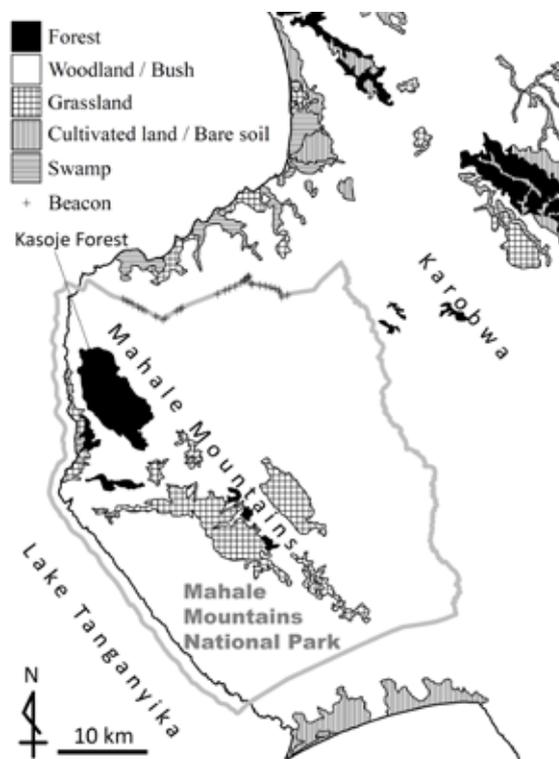


Figure 2. A vegetation map around the Mahale Mountains National Park based on "Land-cover and land-use" maps (Ministry of Natural Resources and Tourism, The United Republic of Tanzania 1996). The border of the park is drawn based on the positions of beacons and the border measured in this study.

RESULTS

We found a total of 88 chimpanzee beds during our surveys (Table 2). The beds were distributed continuously from inside to outside the park, and the beds around the boundary were found near the riverine forests of the Kabesimto, Kalungu, Lagosa, and Lukusu Rivers (Figure 3B). The estimated population densities of chimpanzees were 0.078/km² along the boundary and 0.046/km² inside the park. The estimated density outside the park was 0.038/km², but the density around Karobwa (route c: 0.13/km²) was higher than that around the other routes at the north of park boundary (0.0027/km²).

We observed yellow baboons, bushbucks, bush duikers and bats inside the park and on the park boundary, and red colobus, red-tailed monkeys, vervet monkeys, and bushbucks outside the park (Figure 3B, Table 3). We also confirmed several species of mammals used the habitat based on the fecal evidence (Table 3).

DISCUSSION

We estimated the chimpanzee population around the northern park boundary to be similar to that in Ugalla (0.08/km² [Kano 1972]; 0.10/km² [Yoshikawa *et al.* 2008]). This similarity is understandable because both the study area and Ugalla is covered with miombo woodland, and the availability of food in these two areas is considered similar. In contrast, the estimated density inside the park is lower than that on the park boundary. This may have been affected by the selection of our survey routes. Ogawa *et al.* (2013) noted that chimpanzees inhabiting miombo woodland preferred to make beds around forests and/or slopes. The survey routes on the boundary consisted of straight-lines crossing valleys with riverine forests and ridges with slopes, but flatter routes were selected for our surveys inside the park to facilitate walking. Thus, we may have underestimated the population density inside the park.

The chimpanzee density in the area outside the northern park boundary was estimated to be lower than that of Karobwa. In western Tanzania, the human population is concentrated to the shore of Lake Tanganyika, and the northern area has been affected by human activity such as deforestation (Itoh *et al.* 2012). The position of chimpanzee beds along the Lukusu River outside the northern park boundary (Figure 3B) was about 10 km from the shore, and Karobwa is located about 26 km from the shore. Outside the protected area, more chimpanzees are thought to inhabit the area distant from the lakeshore, where human activity is low.

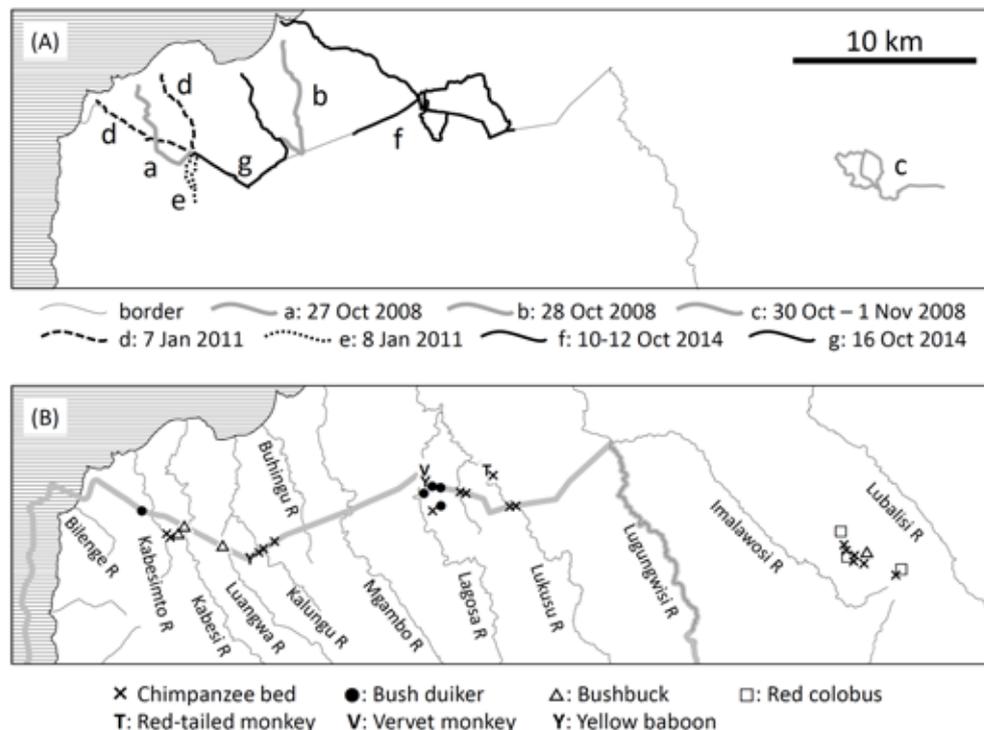


Figure 3. (A): The location of the survey routes, and (B): The water system and the locations of chimpanzee beds and mammals observed during the survey.

Table 1. The length of the survey routes (km).

route	inside ¹	border ²	outside ³	total
a	3.2		3.4	6.6
b			8.0	8.0
c			16.1	16.1
d		7.3	5.0	12.3
e	8.6			8.6
f	5.4	10.6	19.3	35.3
g		7.6	6.2	13.8
total	17.2	25.5	58.0	100.7

1: Inside the park. 2: Along the park border. 3: Outside the park.

Table 2. The locations and numbers of chimpanzee beds.

route ¹	inside/outside ²	position ³	altitude (m)	N
a	inside	6°02'50.4" S, 29°47'07.0" E	911	1
a	inside	6°02'56.9" S, 29°47'12.5" E	928	7
c	outside	-	-	37
f	outside	6°01'05.4" S, 29°56'41.6" E	905	2
f	boundary	6°01'36.0" S, 29°55'47.1" E	891	12
f	boundary	6°01'38.9" S, 29°55'56.9" E	950	14
f	inside	6°02'04.3" S, 29°57'23.7" E	950	4
f	inside	6°02'03.6" S, 29°57'13.0" E	924	1
f	inside	6°02'11.2" S, 29°54'58.0" E	895	1
g	boundary	6°03'24.3" S, 29°49'49.7" E	998	1
g	boundary	6°03'17.3" S, 29°49'58.0" E	1000	7
g	boundary	6°03'06.0" S, 29°50'16.9" E	1108	1
total				88

*1: See Table 1 and Figure 3 in detail. *2: Inside or outside the park or along the park boundary. *3: Based on the geodetic datum Arc 1960.

It was thought that chimpanzees did not reside between the Mahale Mountains and the Karobwa Hills (Kano 1972). The results of the present study suggest that the riverine forests between these two sites are also suitable habitat for chimpanzees. Thus we assume that the two populations, *i.e.* those in the Mahale Mountains and the Karobwa Hills, can be connected by chimpanzees inhabiting the stepping-stone-like riverine forests, but 18 km between the Karobwa Hills and the riverine forest on the Lukusu River remain unexplored (Figure 3B). As Nakamura & Fukuda (1999) found chimpanzee beds around the middle part of the eastern park boundary, the connection of the two populations will be clarified by more information about the area around the eastern park boundary.

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Table 3. Mammals observed or confirmed by fecal evidence on each survey route.

English name	species name	direct observation		fecal evidence	
		inside the park & boundary	outside the park	inside the park & boundary	outside the park
yellow baboon	<i>Papio cynocephalus</i>	f		f	
red colobus	<i>Procolobus rufomitratus</i>		c	g	
red-tailed monkey	<i>Cercopithecus ascanius</i>		f		
vervet monkey	<i>Chlorocebus pygerythrus</i>		f		
bushbuck	<i>Tragelaphus scriptus</i>	a, g	c	f, g	b
bush duiker	<i>Sylvicapra grimmia</i>	d, f		f, g	f
buffalo	<i>Syncerus caffer</i>				c
roan antelope	<i>Hippotragus equinus</i>			f, g	c, f
waterbuck	<i>Kobus ellipsiprymnus</i>			f	f
bushpig	<i>Potamochoerus larvatus</i>			a, b	c, d
elephant	<i>Loxodonta africana</i>			f	
leopard	<i>Panthera pardus</i>			a	g
civet	<i>Civettictis civetta</i>			f	
hyena	<i>Crocuta crocuta</i>				f
bat	unidentified		f		

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Ogawa H, Moore J, Kamenya S 2006. Chimpanzees in the Ntakata and Kakungu Areas, Tanzania. *Primate Conserv* 21:97–101.

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<NOTE>

Elementary Technology Correlates with Lifetime Reproductive Success in Wild Chimpanzees, but Why?

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INTRODUCTION

In evolutionary ecological terms, if females ‘convert’ resources into offspring, then accessibility and utilizability of resources must be essential to female reproductive success. Acquiring and processing resources depends on a multitude of factors, from competition (inter- and intra-specific, contest *vs.* scramble, *etc.*) to technique (discerning, disarming, extracting, *etc.* prey). For chimpanzees (*Pan troglodytes*), much is known about these factors in a general sense: Chimpanzee females compete mostly indirectly by occupying core home ranges within neighbourhoods within group territories (Pusey *et al.* 1997; Williams *et al.* 2002; Emery Thompson *et al.* 2007). Key

variables, such as rank, season, sociality, activity budget, diet quality, foraging effort, are interlinked in explaining variation in female fitness (Murray *et al.* 2006, 2007, 2009). Of these variables, social rank seems likely to be the most important, as manifest in priority of access to resources via scramble competition in core areas of individual female ranging.

Most analyses of dietary impact rely on general measures, such as 'diet quality', which may equal fruit availability (Murray *et al.* 2009), or 'habitat quality', which may equal average plot productivity (Murray *et al.* 2006). In faunivory, most dietary analyses have been limited to generic meat consumption, with invertebrates sometimes ignored altogether (Tennie *et al.* 2009), but recent studies confirm the nutritional value of termites (O'Malley & Power 2014). Outcome analyses of reproductive success rely on incomplete and usually contemporaneous records (*e.g.* fertility, Jones *et al.* 2010), rather than on lifetime fitness over the whole reproductive lifespan. We know of no previous attempt to relate elementary technology to reproductive success, in any species of primate.

Termite fishing is one of the most widespread pattern of technical extractive foraging in chimpanzees, ranging across Africa from Senegal to Tanzania (McGrew *et al.* 1979; Goodall 1986; Sanz & Morgan 2011). It is the best-known and longest-studied type of elementary technology in the species, having been first observed at Gombe (Goodall 1963, Lonsdorf 2006). We compare females from the Gombe population in terms of their frequency of using vegetative probes to 'fish' for *Macrotermes* termites. We relate the females' success in this primary extractive foraging technique in their early lives to their eventual lifetime reproductive success (LRS) achieved, on a variety of measures. We combine data on tool use from a 3-year period in the 1970s with later (2012) data on LRS: age at first birth, offspring survivorship, inter-birth interval, and age at death. We hypothesise positive correlations between frequency of termite fishing and rank and LRS.

METHODS

Data set

We focussed data analysis on all 14 parous females of the Kasekela community in Gombe National Park, for whom from 1972–75 we had observational data. One female, NP, then was excluded, as she had only 6 hr of observation. The remaining 13 females in the community at Gombe were studied by focal-subject sampling (Martin & Bateson 2007) by various researchers over 'follows' of varying duration. We extracted data on bouts of termite fishing (of 5 min duration or longer) from the feeding column of the standard Gombe data-collection instrument, the Travel & Group chart (T&G). Frequency here means total duration of bouts of termite fishing per total feeding time, so the proxy measure for intake of termites was time spent fishing. McGrew & Marchant (1999) showed that time spent fishing and number of soldiers obtained by fishing were highly positively correlated at Gombe.

However, two outlier females were excluded from further analyses, for different reasons: GG fished for termites but was sterile (Pusey *et al.* 1997), so she had zero direct fitness (as per Gilby *et al.* 2006). FF was fecund but never fished for termites during the study. Despite having more observation hours (175.5) than all but two of the other females, she was not seen to eat termites during the period, although she ate termites at other periods in her life: for example, she ate termites in 1998–2001, but no comparable frequency data were presented (Lonsdorf 2006). We have no explanation for this abstinence over 1972–75; a lengthier, more detailed analysis from the entire Gombe database is needed. Furthermore, FF was the most reproductively successful female in Gombe's history, having given birth first at 13 yr and lived to 46 yr. Seven of her offspring survived to more than 5 yr. As there were no reproductive data for GG and no termite fishing data for FF, we did analyses on the 11 remaining females.

Variables

Fishing bouts and observation hours were taken from all available T&G records of females as focal targets, to-

Table 1. Termite feeding rates, demographic data, and reproductive success measures in female chimpanzees at Gombe.

ID	% feeding time spent termite feeding	Total observation time (hours)	Age in 1973	Dominance rank	Age at 1st birth (years)	Offspring survived over 2 years	Offspring survived over 5 years	Mean Inter-birth Interval (months)	Age at Death (years)
PI	11.0	113.9	12	3	18	5	4	61.0	44
MF	9.6	167.1	17	2	13	4	4	60.0	31
ML	8.01	196.3	24	2	15	3	3	152.0	37
PS	8.00	108.8	24	1	15	3	3	74.5	33
AT	7.9	107.5	21	3	15	3	3	71.3	35
GK	6.7	92.9	13	4	14	0	0	n/a	19
PL	5.7	113.0	21	4	22	2	1	n/a	30
SW	6.3	126.4	15	4	15	5	4	64.3	n/a
NV	2.7	258.0	20	4	17	1	1	n/a	22
LB	1.4	55.5	13	4	17	2	2	79.0	27
WK	0.4	52.0	15	3	14	2	2	73.0	30

ID: Initials of individual female names. PI = Patti; MF = Miff; ML = Melissa; PS = Passion; AT = Athena; GK = Gilka; PL = Pallas; SW = Sparrow; NV = Nova; LB = Little Bee; WK = Winkle. Age at 1st birth: age at which the female gave birth to her first live offspring. Mean inter-birth interval: see Methods. n/a = not available. SW is still alive (aged 56 years). Three individuals had too few surviving offspring to calculate inter-birth interval.

Table 2. Correlations between termite fishing and reproductive success.

Variables of reproductive success	<i>n</i>	<i>rho</i>	<i>p</i> (one-tailed)
Age at first birth (yr)	11	-0.12	0.35
Offspring survived over 2 yr	11	0.65	0.02
Offspring survived over 5 yr	11	0.64	0.02
Mean inter-birth interval (mo)	8	-0.41	0.16
Age at death (yr)	10	0.73	0.01

talling 1391 hr and 343 focal follows. This sample is only a fraction of the total T&G data set, which has been collected over decades (see Strier *et al.* 2010); thus our study should be considered preliminary. Ages were estimated only to the nearest year, as subjects were born before habituation was achieved at Gombe, or were immigrants of unknown origin. Data on (live) births and deaths (to the nearest month) came from the Gombe database. Age at death was taken as last sighting, as most deaths were unobserved. Inter-birth intervals were based on completed birth intervals only, that is, when the next birth followed that of an infant who survived at least 5 yr (to weaning). Criterion for offspring survivorship to 5 yr follows Pusey *et al.* (1997), but we also added a less stringent criterion of 2 yr (survival through infancy). Scaled ranks for females could not be calculated, given the scarcity of contest competition; instead we assigned categorical ranks (top, high, middle, low), according to published directionality of pant-grunting in dyads (Goodall 1986; Pusey *et al.* 1997).

All statistical tests were done with SPSS Statistics 19. As data were not normally distributed, all tests used were non-parametric. Level of statistical significance (α) was set at 0.05, one-tailed.

RESULTS

Table 1 gives the results of percentage of feeding time spent in termite fishing by individual, as well as their data on five measures of reproductive success. When the ter-

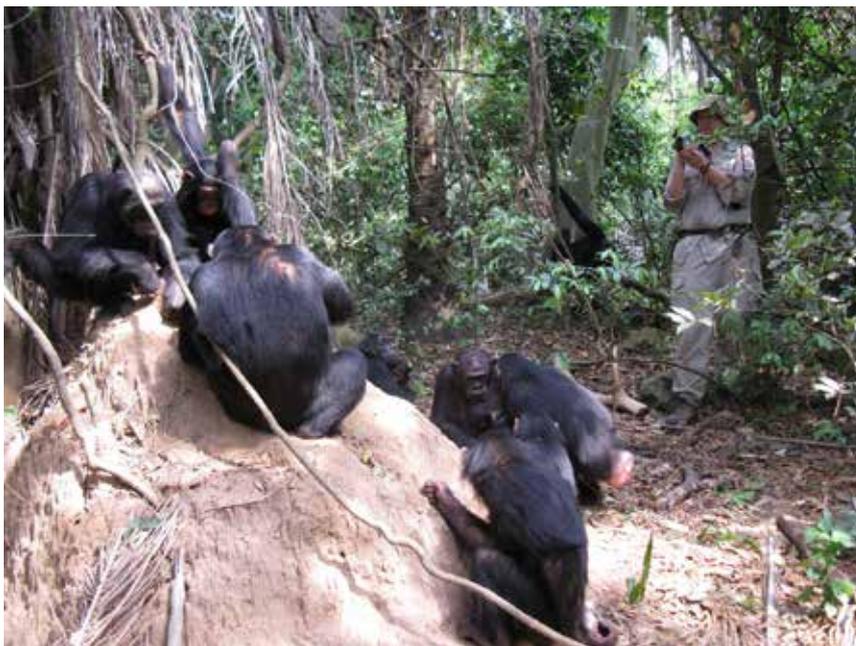


Figure 1. Members of three Gombe matriline (ML, PI, SW) fish together at termite mound in 2009 (Photo by Samson Pindu).

mite fishing data were collected, females were 17–18 yr old on average, and most (6 of 11) had had their first live birth at 15–16 yrs of age. The eventual median number of offspring surviving to both 2 yr and 5 yr was 3 (ranges: 0–5, 0–4). Median IBI was 72.2 mo, but three subjects had too few surviving offspring to calculate IBI. Median age of death was 31 yr (range: 19–54+). All of these life history norms resemble other, larger data-sets from Gombe (Goodall 1986).

Table 2 gives results of correlations (Spearman's *rho*) between percentage of observation time spent eating termites and the five dependent variables reflecting LRS. All five variables are in the expected direction of greater LRS. Three of the five measures are individually significantly correlated. Thus, more frequent termite fishers have higher LRS by rearing more surviving offspring and living longer. Social rank also was positively correlated with reproductive success ($n = 11$, $rho = 0.63$, $p = 0.04$, one-tailed).

DISCUSSION

Females who did more termite fishing during their early years of reproductive life had higher reproductive success over their lifetimes. They lived longer and raised more offspring successfully through infancy and through weaning. They tended to have shorter inter-birth-intervals. This may be the first demonstration in a primate species of enhanced reproductive success as a payoff related to elementary extractive technology.

Why this correlation occurs is beyond the scope of this pilot study, but it seems most likely to be a matter of individual, differential access to resources (hence the positive correlation with social rank) than a matter of differential skill in termite fishing. It is hard to imagine self-serving technical proficiency in an individual foraging task being linked to dominance status. If access to resources is the key, then a further next step would be to evaluate the abundance, distribution and productivity of *Macrotermes* mounds in the core ranges of individual females, plus competitive behavior among females. Dominance rank influences use of space by chimpanzee females (Murray *et al.* 2007) and use of higher quality core areas, at least in terms of fruiting productivity, results in enhanced reproductive success (Emery Thompson *et al.* 2007). However, termite fishing (a renewable resource) is often done socially, without obvious contest competition (see Figure 1).

If social rank is the primary causal variable that determines reproductive fitness, this may be expressed in a variety of ways. Individual variation in efficiency and extent of termite fishing also should be assessed (e.g. McGrew & Marchant 1999; Lonsdorf 2006). Similarly, differential motivation (appetite) for termites, phenotypic

quality (Jones *et al.* 2010), or even general competence at foraging could account for our results. None of these alternative hypotheses can be tested with our data in this preliminary study. However, rank is a constructed attribute, not a behavioral variable. How dominance ‘acts’, whether generally or specifically, can be elucidated only through focussed studies such as this one. Future studies should make use of comprehensive data-bases that include such variables (*e.g.* Strier *et al.* 2010); a more comprehensive study of termite fishing and rank over lifetimes might resolve the correlation/causation quandary.

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<NOTE>

Is Chimpanzee (*Pan troglodytes schweinfurthii*) Low Population Density Linked with Low Levels of Aggression?

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INTRODUCTION

Observations have shown intraspecific aggression to be a common behavior in chimpanzee society (van Lawick-Goodall 1968; Muller 2002). Both sexes are characterized by an array of aggressive behaviors, varying in severity from non-directed displays to lethal attacks. Forces driving intragroup agonism range from male–male competition to increase status within a linear dominance hierarchy to maintaining access to estrous females (Watts 1998). Recently, Wilson *et al.* (2014) surveyed 18 chimpanzee intercommunity rates of lethal aggression, and showed population density to be a significant predictor. Yet, it remains unknown if this pattern can be generalized to rates of aggression within communities as well.

Although intracommunity aggression is often less brutal than between community aggression, it may be driven by the same ecological forces. The goal of this study was to document the rates of aggression for the savanna-gallery forest Semliki chimpanzee (*Pan troglodytes schweinfurthii*) community and compare them with known rates at Kanyawara and Gombe. We test the hypothesis that population density is related to intraspecific group aggression. We predict that Semliki chimpanzees will be more peaceful than Kanyawara and Gombe chimpanzees, given Semliki has the largest of all recorded home ranges, and lowest population density among observed chimpanzee communities.

METHODS

Study area

Chimpanzees have been studied in the Toro-Semliki Wildlife Reserve (TSWR) in western Uganda since 1996 (Samson & Hunt 2012). Their community home range is the largest known at 72.1 km² (Samson & Hunt 2012), with the second and third largest home ranges being the dry-habitat sites of Fongoli at 64 km² (Pruetz 2006) and Assirik at 50 km² (Tutin *et al.* 1983). There are estimated

Table 1. Inter-site comparison of intra-group aggression.

	Observation time (hr)	Total aggressive acts	Rates of aggression	Population density	Territory km ²	Number of individuals	Poisson rate ratio
Semliki	34.7	6	0.17	1.4	72	104	--
Gombe	1570	319	0.20	2.5	24	60	0.85
Kanyawara	1428.3	442	0.31	3.3	15	50	0.56

Note: Gombe data are from Goodall (1986). Kanyawara data are from Muller (2002) except for territory size cited from Chapman & Wrangham (1993). Rates of aggression are per hour of observation. Population density is calculated as the number of individuals per km². The Poisson rate ratio is for all sites are compared to Semliki.

to be 30 males, which suggests a community size of approximately 104 (estimated using the average sex ratio across *P. t. schweinfurthii* sites) (Stumpf 2007).

Data collection

Data were collected between the months of August 2010–January 2011. When chimpanzees were observed, we used 40-min group focal follows to generate rates of aggression for individuals (Altmann 1974). All-occurrence sampling was possible given the conspicuous nature of chimpanzee agonism. If a party could not be observed for the full 40-min period, then the data was not used. Party composition was recorded every 10 min during focal follows. Behavioral categories followed those of Goodall (1986) and methods follow general protocols applied to characterize group and individual levels of aggression by other researchers at chimpanzee field sites (Muller 2002). Charging displays, chases and all incidents of contact aggression were considered as aggression.

Data analysis

All analyses were conducted in R (R Development Core Team 2014). Average rates of aggression per hour were calculated. Pearson's correlation coefficient (r) was used to assess relationships between group size, intercom-

munity population density (among the sites at Semliki, Gombe and Kanyawara) and agonism. A Poisson test was used for inter-site comparison. Given small sample sizes, power analysis was performed to predict ideal sample sizes required to achieve greater power properties. All statistical tests were two tailed.

RESULTS

Overall, a total of 34.7 hr of observation were conducted. Semliki male chimpanzees were the only sex observed performing aggressive behaviors. Number of aggressive acts was significantly correlated with party size ($r = 0.43$, $p = 0.001$) and the average party size during an aggressive event ($N = 6$, mean = 6.17) was larger than the average party size when no aggressive event occurred ($N = 46$, mean = 3.61). Six instances of aggression were observed from the total sample ($N = 52$) of 40-min group focal follows. Three instances (50%) of aggression occurred under the context of reunion. Adult males at Semliki are characterized by 0.17 aggressive acts per observation hour (see Table 1). A comparison of rates by way of a Poisson test reveals that the Semliki sample was almost half as likely to show aggression than the Kanyawara sample (rate ratio = 0.56), although the result only trends towards significance. Averaged rates of aggression showed a strong, positive relationship with community population density ($r^2 = 0.93$, $p = 0.26$; see Figure 1); power analysis revealed an n of 6 (sites) would achieve a power level of 0.8 and significant results at the current r^2 .

DISCUSSION

To our knowledge, this study is the first to directly compare within group aggression between a large home range, low population community with that of smaller, more population dense communities. Overall, the hypothesis that population density is linked with intraspecific aggression was not rejected (due to small sample sizes further research is necessary to support the hypothesis). Male chimpanzees at Semliki seem to experience less frequent aggression (charging displays, chases and attacks) than do males at other communities (see Table 1 & Figure 1).

Interesting patterns emerge from these data, which suggest that not only is intercommunity aggression a function of population density (Wilson *et al.* 2014), but this effect also helps explain the rates of intracommunity aggression. The adaptive benefits for intercommunity aggres-

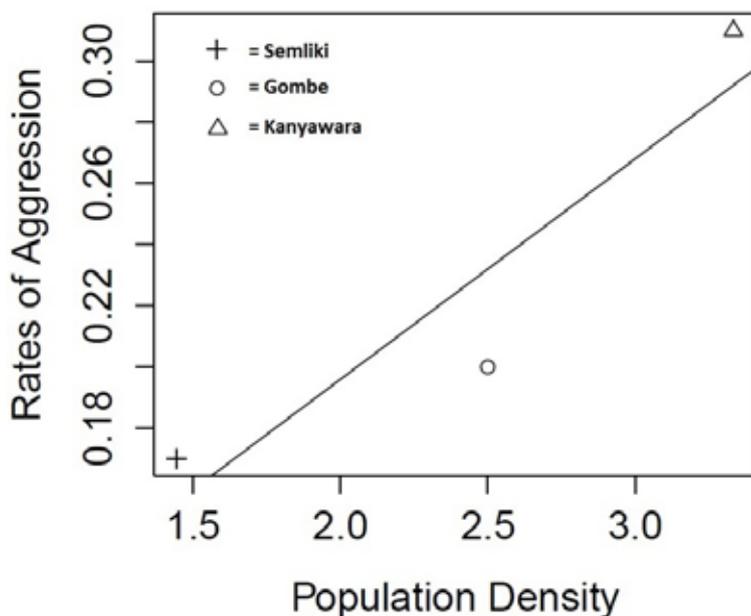


Figure 1. Semliki chimpanzees are more less aggressive when compared to Gombe or Kanyawara chimpanzees. Hourly rates of aggression were averages among sites. Population density was measured as the number of individuals per km². The black line indicates a simple linear regression for illustrative purposes only.

sion has been well documented as coalitionary behavior may be an evolved tactic by which chimpanzees increase their fitness through increased access to territory, food and mates (Watts & Mitani 2001; Wilson & Wrangham 2003; Watts *et al.* 2006; Wrangham *et al.* 2006). That the pattern holds for intracommunity aggression suggests that ecology and territory size is a key predictor of violent behavior in general. Chimpanzees avoid costly encounters when possible, and a greater home-range size permits less frequent contact, and therefore less need for violent behavior. These data are preliminary, and future research should calculate rates of aggression within communities to robustly test trends suggested by this research.

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<NOTE>

Hidden Risk of Arboreality?: An Arboreal Death of an Infant Chimpanzee at Mahale

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INTRODUCTION

We humans are terrestrial animals, basically staying on the ground for most of our daily activities. On the other hand, chimpanzees' activities take place both on the ground and in trees (*e.g.* Takemoto 2004). They typically use the ground when traveling long distances but often feed arboreally because their main foods (*i.e.* fruits and leaves) are produced by trees.

Being on the ground is generally more dangerous than being in trees: for example, mid- to large-sized carnivores that can potentially prey upon infant chimpanzees are often terrestrial (although some can climb trees, they usually walk at ground level). Thus, some authors have proposed that chimpanzees' arboreal beds may have an antipredatory function (Pruetz *et al.* 2008; Stewart & Pruetz 2013). In addition, a chimpanzee may get involved in aggressive intimidation displays by conspecific males that usually take place on the ground. Thus, when females and immature chimpanzees see a displaying male approaching, they usually climb up trees to avoid the risk. Such potential dangers of being attacked by predators or conspecifics may be more fatal to smaller-bodied infant chimpanzees than adults.

In light of these events, a mother chimpanzee with a small infant looks more protective on the ground than in trees. For example, on the ground, a one-year-old infant is almost always carried by the mother when she travels, and is usually within arm's reach when the mother is engaged in grooming or resting. Should anything untoward occur, the mother will immediately retrieve the infant. On the other hand, in a tree, an infant of the same age may meander farther away. In this instance, the mother appears less worried, probably because she can better monitor any potential danger.

Here we report a rare observation of an infant's death,



Figure 1. A dorsal view of the dead body of the female infant chimpanzee. An arrow shows where the intestine is protruded out of the anus.

which may have resulted from independent arboreal activity.

OBSERVATION

A dead body of a female infant chimpanzee, assumed to be TE13 (a yet unnamed one-year-old infant daughter of Ternie [TE]), born between March 12 and May 12, 2013, was found within Mahale M group's home range (Mahale Mountains National Park, Tanzania) on July 13, 2014. When TE13 was last observed alive in the company of her mother on June 7, 2014, the infant looked healthy with no indication of sickness or injury. Four days later, on June 11, Ternie was observed without TE13, and there was no confirmed sighting of another individual (*i.e.* an allomother) carrying the infant. Because an infant of that age never travels away from the mother for any length of time, TE13's safety became an immediate concern. A research assistant raised the possibility that TE13 may have succumbed to infanticide because she was healthy when last seen.

On June 13, the second author, AR, found a dead infant on a *Psyrax parviflora* tree, north of the Katulu Valley where M group chimpanzees frequently visited. The dead body was pinched and stuck between two boughs that were branched just underneath. It was so tightly pinched between the boughs that AR needed to exercise some force to detach the body from the tree. No bite wounds were found on the remains, and all limbs and fingers were intact (Figure 1). Thus, the possibility of infanticide or predation was ruled out. Because the remains were lodged in a tree, there was no sign of scavenging (a dead body on the ground is easily ravaged by bush-pigs [*Potamochoerus larvatus*] or other scavengers). The body's surface was completely desiccated, but there was a strong, putrid smell suggesting that the internal organs were decomposing. From the external genital organs, the sex was judged as female. From the teeth and body size, the remains were not of a stillborn infant. Considering

the disappearance of TE13 between June 8 and June 11 (two to five days before the dead body was found) and the confirmed presence of all the other infants around that age, it appeared likely that the remains were those of TE13.

It is significant to note that a part of the intestine was found outside the anus (see Figure 1). Because the body was tightly pinched between two tree boughs, we assume that the infant was accidentally caught between them, which caused a visceral cleft.

DISCUSSION

Judging from the circumstantial evidence, we envisioned the occurrence as follows: TE13's mother (or another chimpanzee) may have pushed against one of the two boughs while feeding on the tree's fruits. The bough may then have bounced sharply back as she changed her position. Tragically, at that moment, her infant may possibly have been trapped between the boughs.

Ternie had already successfully weaned her first child (TE13's older sister), and there was no indication that her childrearing skills had somehow degraded. Therefore, we did not believe TE13's death was due to any inappropriate child-handling by the mother. All the evidence showed it was rather an unfortunate accident.

This observation may imply that even an arboreal environment, which is thought to be safer than a terrestrial one, can sometimes be dangerous. If mothers protected their infants by always holding them, even in trees, as they do on the ground, such an accident could be prevented. However, carrying a one-year-old infant may impede the arboreal activity of mothers, and may not be ideal for infants' locomotor development. Thus, there should be some trade-offs.

Arboreal accidents do cause the deaths of healthy chimpanzees. It was reported that two Gombe chimpanzees (Williams *et al.* 2008) and one Tai infant chimpanzee (Boesch & Boesch-Achermann 2000) died after falling from trees. Although there have been no direct observations of falls from trees causing any chimpanzee deaths at Mahale (Nishida *et al.* 2003), Nakai *et al.* (2004) inferred from the skeletal trauma of an adult female named Gwakakumo that she may have died from such a fall. At a Japanese zoo, a two-year old male chimpanzee died by accidentally hanging himself from a rope (Yoshida 1994). Our report definitively adds another cause of deaths in relation to arboreality.

Such accidents constitute a relatively rare cause of confirmed deaths of wild chimpanzees (Boesch & Boesch-Achermann 2000; Nishida *et al.* 2003; Williams *et al.* 2008). However, this does not necessarily mean that they are *really* that rare; it is possible that such incidents are simply not noted. In TE13's case, we were lucky enough to find her remains because of two incidental conditions. First, during the period in question, M group chimpanzees repeatedly visited the same area with stands of *Psyrax*,

meaning that human observers were also there on a regular basis. Second, because *Psyrdrax* trees are relatively short with sparse canopies, it was easy for the observer to notice the dead body. We may not have been able to notice the remains if a higher and denser-canopied tree were involved or in a place less frequented by the chimpanzees. In such cases, we cannot solve the disappearances of infants. This dilemma poses the distinct possibility that arboreal deaths may be more common than we know.

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<NOTE>

Responses of Wild Chimpanzees to Fresh Carcasses of Aardvark (*Orycteropus afer*) in Mahale

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INTRODUCTION

Despite more than 50 years of research on wild chimpanzees, there has been no record of encounters between them and aardvarks (*Orycteropus afer*). The habitats of aardvarks are distributed widely in sub-Saharan Africa and cover most of the narrower habitats of chimpanzees (Lindsey *et al.* 2008). However, aardvarks are typically nocturnal, foraging for termites, ants, and larvae at night, while chimpanzees are typically diurnal, hence the lack of recorded encounters between the two species.

This study reports the first two recorded observations of the rare event of chimpanzees encountering aardvark carcasses, which occurred within 1 month. This provides valuable insight on two topics.

The first topic is the reaction of chimpanzees to non-conspecific carcasses. The observations provide a variety of clues about chimpanzees' emotional traits and their cognition of potential dangers such as predation and illness. Several studies (Teleki 1973; Boesch 1991; Hosaka *et al.* 2000) reported that chimpanzees showed intense emotions of fear and confusion toward dead bodies of mature members belonging to the same unit-group. Early, harsh "wraa" calls and late, feeble "huu" calls (Goodall 1986) seem to be typically expressed during such encounters. The same calls are emitted when chimpanzees see or hear large carnivores such as leopards (*Panthera pardus*) and lions (*Panthera leo*) (Hiraiwa-Hasegawa *et al.* 1986; Tsukahara 1993).

The second topic is the scavenging tendency of chimpanzees. Watts (2008) reviewed published cases of scavenging by wild chimpanzees and argued that chimpanzees avoid scavenging because fresh carcasses are rare in the forest and chimpanzees may not recognize certain species as potential prey, whereas Mahale chimpanzees sporadically scavenged fresh carcasses of their prey species, such as bushbuck (*Tragelaphus scriptus*), killed and cached by leopards (Hasegawa *et al.* 1983; Hosaka *et al.* 2001). In contrast, several reports (*e.g.* Boesch & Boesch 1989; Hirata *et al.* 2001) suggest that the western chimpanzees do not eat mammals absent from their prey species list at the respective study sites; they did not consume a blue duiker (*Cephalophus monticola*) or a western tree hyrax (*Dendrohyrax dorsalis*) accidentally captured and killed, but only toyed with them.

METHODS

Observations of wild chimpanzees (M-group) were





Figure 1. The carcass of an aardvark found on August 17, 2005. Claw wounds on the body surface and a large bloody laceration on the chest were so fresh that it was presumed to have been killed by a leopard a couple of hours earlier.

made in the Mahale Mountains National Park, Tanzania, on August 17 and September 4, 2005. Audiovisual data from video tapes and field notes taken by the authors were analyzed to obtain a sequence of events.

Sympatric aardvarks have never been studied in detail but their nocturnal activities were observed in some camera-trap studies (Moyer 2006; Nakamura, personal communication).

OBSERVATIONS

1. August 17, 2005.

At approximately 0930 h, just before moving to forage, a group of chimpanzees encountered a dead aardvark that appeared to be a subadult female (>30 kg) in the leafy bush near the river junction of the Manya and the Kasoje. Initially, several individuals, including OR (adolescent male) and SY (adult female), emitted “wraa” calls so harshly that others going eastward turned back westward to reach the site. All 21 individuals in the foraging group gathered at the site.

Although there was a diversity of responses among individual chimpanzees, there were some tendencies observed for age–sex classes (Table 1). Adolescent males showed the highest intensity and ambiguity in their responses. OR, who emitted “wraa” calls most often, would not approach the carcass and remained still on a tree approximately 20 m distant. Three other adolescent males, PR, CD, and MC, boldly approached the carcass, and inspected it thoroughly, sometimes touching it. Similar explorative behaviors were rare among other age–sex individuals, although three adult/adolescent females touched the carcass. Other individuals, including four adult males, approached to watch the carcass and stayed for a while without emotional confusion.

At approximately 1030 h, their emotional reactions gradually subsided, with a sporadic production of “huu” calls. At 1045 h, the last remaining individual, GW (old female), left the site.

Evidently, not a single individual attempted to taste the carcass meat.

The aardvark was presumed to have been freshly killed by a leopard, a couple of hours before being encountered. There were many fresh claw wounds on the surface of the body (Figure 1). A large fatal open wound was observed on the chest and some meat had been eaten by the killer. Fresh blood remained wet. Only a few flies had reached the body. Later in the afternoon, one of the authors (E.I.) went back to the site to find that the carcass had disappeared. We presume that the leopard had returned to the carcass after the chimpanzees and researchers had left the site, and removed it. According to Bailey (1990), a leopard will not move far from a cached carcass, often concealing itself and resting in the vicinity, so as to return to feed when its appetite is renewed.

2. September 4, 2005.

At approximately 1300 h, in arid bush near the sun-exposed, dry bed of the Ikola River, chimpanzees encountered another aardvark carcass; this one was foul-smelling and putrid. There was no indication as to the cause of death. It appeared to have been dead for 4 or 5 days. No “wraa” calls were heard (Table 1). Several individuals emitted “huu” calls as they walked in single file toward the carcass, but most of them passed the carcass without close inspection. Only three of 26 individuals— CD, OS (juvenile male), and LZ (juvenile female)—made a detour to inspect the carcass. Only CD touched the carcass. The two juveniles (OS and LZ) showed intense, ambiguous emotions, reflecting curiosity and fear toward the carcass, repetitively approaching and retreating.

Threatening behaviors toward the carcass were observed in this case only. The chimpanzees sometimes approached the carcass to inspect it and attempted to repel flies by shaking their hands (Table 1). The two juveniles would rush away each time they threatened the carcass.

Neither of them attempted to bite the carcass or eat any meat.

DISCUSSION

As Hosaka *et al.* (2000) have suggested, there is no

substantial difference in chimpanzee responses when they encounter conspecific or non-conspecific dead bodies. They show emotions by emitting “wraa” calls or “huu” calls. They approach, watch, sniff, and touch the carcass for inspection, while they are ready to run away from the carcass with a slight stimulus or none. It seems plausible that these behaviors reflect “general curiosity” in wild chimpanzees. Unusual or unfamiliar objects often motivate an animal’s explorative behavior, since it may be adaptive in learning of risks and dangers. Fear arises at the same time and motivates the animal’s retreat because the explored objects may be risky or dangerous to it.

However, two differences may be noticed in chimpanzees’ responses when they encounter the carcasses of either familiar conspecific or non-conspecific mammals. First, chimpanzees did not show as much curiosity about the putrid non-conspecific carcass (this study) as they showed about a putrid conspecific carcass (Hosaka *et al.* 2000). The identity of the carcass and the long-term relationships with the dead individual may have affected their responses to a certain degree. Second, chimpanzees showed more curiosity about the fresh non-conspecific carcass (this study) than they showed about the fresh carcass of a conspecific animal that died from a respiratory disease (Hosaka *et al.* 2000). Cause of death may have motivated different responses. If chimpanzees find a carcass freshly killed by a leopard, this may motivate them to be alert and to explore it for more information about the predator.

Finally, this study provided valuable information as to the stenophagous nature of chimpanzee meat-eating habits. Ihobe (1993) insisted that chimpanzees are stenophagous meat-eaters in contrast to humans, who have evolved as euryphagous meat-eaters after acquiring a “prey image” for any type of mammal meat and beginning to rely on a “scavenging life” in savannah (Speth 1989).

It is likely that chimpanzees did not eat the fresh aardvark carcass simply because they had no prey image for this nocturnal mammal that they would not normally encounter during their ranging in the daytime. It seems easier for chimpanzees to develop a prey image for diurnal mammals (*e.g.* arboreal monkeys), with which they have a high encounter rate (Uehara 1997; Hosaka *et al.* 2001).

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<NEWS>

A survey of the savanna vegetation in Bossou, Guinea

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At Bossou, located 4 km west of the Nimba Mountains representing the only World Natural Heritage site (UNESCO/MAB) in Guinea, a group of chimpanzees has been studied for the past 39 years (Matsuzawa *et al.* 2011). The Bossou chimpanzees, which currently number nine individuals, have coexisted over many generations with the local Manon people in the village. Due to the lack of female immigration since the beginning of

the field study and a flu-like epidemic (Matsuzawa *et al.* 2004) that occurred in November 2003, this isolated local population is in ongoing danger of extinction. The Green Corridor project (Hirata *et al.* 1998), a tree plantation effort in the savanna, was started in 1997 to promote individual interchanges between the wild chimpanzee groups at Bossou and the Nimba Mountains. We developed the arbor procedure (Ohashi *et al.* 2008) at a sapling nursery in the savanna using chimpanzee feces after struggling to protect fragile saplings in the savanna with HEXATUBES (Phytoculture Control Co., Ltd.). The arbor procedure provides saplings with similar conditions to those of the nursery after transplantation to the savanna. We had constructed 47 arbors for plantings by 2012.

The arbor procedure is well suited for promoting plant growth in the savanna to greater than 4 m in height. In brief, the procedure involves the following steps: (1) growing *Uapaca heudelotii* saplings in chimpanzee feces (Matsuzawa 2007), (2) planting the saplings under arbors in the savanna during the rainy season, and (3) cutting the grass in the area surrounding the grown saplings to protect them from bush fires, especially during the dry season. Theoretically, regular use of the arbor procedure will construct a plantation corridor connecting the forests of Bossou and the Nimba Mountains. Currently, we must refine a strategy for connecting each arbor to create this tree plantation corridor. The trees grown in a plantation can provide similar condition as the arbor by shadowing over the new natural and/or artificial saplings that surround rotten arbors during strong sunshine. Expanded grass cutting is expected to maintain these saplings by facilitating sapling growth in the rainy season and increasing the resistance of the plantation to bush fires in the dry season (Morimura *et al.* 2011). We place plantation arbors only where necessary, in places where saplings cannot grow naturally. The combination of arbor sapling plantation and grass cutting may allow us to extend the plantation area into a belt over 1 km in length while controlling the

labor force and financial costs. We began cutting the grass between the plantation points at current and former arbors to create plantation strip areas in January 2014.

It is unclear, however, what plant species can grow naturally in the savanna around Bossou, which is dominated by elephant grass. Moreover, no information is available on whether grass cutting facilitates the growth of small natural saplings that are under the bush.

Therefore, we conducted vegetation surveys at two transects soon after grass cutting between July and August 2014. In the first transect (#1), the grass had been cut in January 2014. The elephant grass had subsequently grown up and dominated the area again by the time of the survey. In the second transect (#2), the grass had been cut for the first time at the time of the present survey. The lengths of transects 1 and 2 were 581 m (from 7°38'2.16"N/8°28'51.12"W to 7°38'12.87"N/8°29'4.42"W) and 524 m (from 7°37'59.8"N/8°28'51.54"W to 7°38'11.39"N/8°29'6.54"W), respectively, and the width of each was approximately 10 m. NM and local assistants identified the scientific names of all natural tree species below a height of 2 m and measured their heights (Figure 1).

We counted 127 and 120 natural plants in transects



Figure 1. A local collaborator measuring a sapling.

Table 1. Natural plants in each height category in transects 1 and 2.

Scientific name	Transect 1				Transect 2				Plant consumption by Bossou chimpanzees
	50>	50–100	100–150	150–200	50>	50–100	100–150	150–200	
<i>Albizia adianthifolia</i>	2		3			1	1	1	YES
<i>Albizia zygia</i>		1	1			2	4	9	YES
<i>Alchornea cordifolia</i>						1			YES
<i>Anthocleista djalonensis</i>						1	2		
<i>Bridelia ferruginea</i>			2	2			4	3	YES
<i>Chlorophora excelsa</i>								1	YES
<i>Craterispermum caudatum</i>					1				
<i>Dychrostakys glomerata</i>	2	20	3				3	4	
<i>Ficus sur</i>		1	1	1				1	YES
<i>Funtumia elastica</i>							1		YES
<i>Gbertiodendron bilineatum</i>						1			
<i>Harungana madagascariensis</i>	22	15	14	1		6	8	7	YES
<i>Morinda germinata</i>		2	1						
<i>Myrtragyna stipilosa</i>						1		1	
<i>Nauclea latifolia</i>	3	5	13	8	7	9	16	15	YES
<i>Phyllanthus discoideus</i>						2	2		YES
<i>Vismia guineensis</i>	1								
<i>Vitex micrantha</i>	1		2						YES
Unknown						2	2	1	
Total	31	44	40	12	8	26	43	43	



Figure 2. Watering the plantation trees with an engine-driven pump.

1 and 2, respectively (Table 1). A total of 18 plant species were identified, and five plants were categorized as unknown. Seven species grew in both transects. Of the 18 species, 11 were included on the plant food list of the Bossou chimpanzees (Matsuzawa *et al.* 2011). We categorized the plant heights into the following four classes: <50, 50–100, 100–150, and 150–200 cm. The number of saplings between the two transects was significantly different for each height class except for 100–150 cm (Mann-Whitney *U*-test, $U = 761.0$, $Z = 0.93$, $p = 0.35$). In transect 1, the less recently cut area, the numbers of plants were larger than in transect 2 for the <50 and 50–100 cm classes (<50 cm class: *U*-test, $U = 22.0$, $Z = 3.95$, $p < 0.01$; 50–100 cm class: $U = 167.5$, $Z = 5.04$, $p < 0.01$). In contrast, the number of plants in transect 1 was smaller than that in transect 2 for the 150–200 cm class ($U = 126.0$, $Z = 2.74$, $p < 0.01$). Thus, transect 1 was more enriched with small natural saplings compared to transect 2.

The findings of the vegetation surveys indicated that grass cutting was effective for enhancing the growth of natural saplings, because (1) few different plant species can survive naturally in the bush, (2) new natural saplings can emerge after mowing, and (3) the natural plant species in the transects mostly consisted of various food plants of the Bossou chimpanzees. A number of new natural saplings in transect 1 compared to transect 2 can be expected to become a possible food resources of fruiting trees for wild chimpanzees in the future, while most of them were too young to produce fruits at the moment. Therefore, the combination of arbor sapling plantation and grass cutting around the plants was effective, not only for improving the working efficiency of the labor force and reducing financial costs, but also for practicing reforestation by providing natural food and space resources for wild chimpanzees. Further studies on the survival of saplings at different height classes are necessary, as the present survey observed fewer tall natural saplings in transect 1 than in transect 2.

We plan to plant 20,000 saplings of *Uapaca heudelotii* in the area of the two transects in 2015. This planting is expected to illustrate the effectiveness of our combined procedure by creating plantation strips greater than 1 km in length. Additionally, in 2014, we started a pilot study on watering the grass-cutting area during the dry season with an engine-driven water pump (Figure 2). Our

empirically grounded techniques for plantations have substantially accelerated the progress of the Green Corridor project. Unfortunately, an epidemic of Ebola virus disease (EVD) is ongoing in Guinea, Liberia, Sierra Leone, and other countries (Butler & Morello 2014). Two patients with EVD were confirmed in Lola, a town located approximately 18 km from Bossou, in September 2014. Despite these circumstances, all local collaborators that have worked for the Green Corridor project remain in good health.

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