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.

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

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

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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	*n*	*rho*	*p* (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 (alpha) 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-

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

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

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