

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-

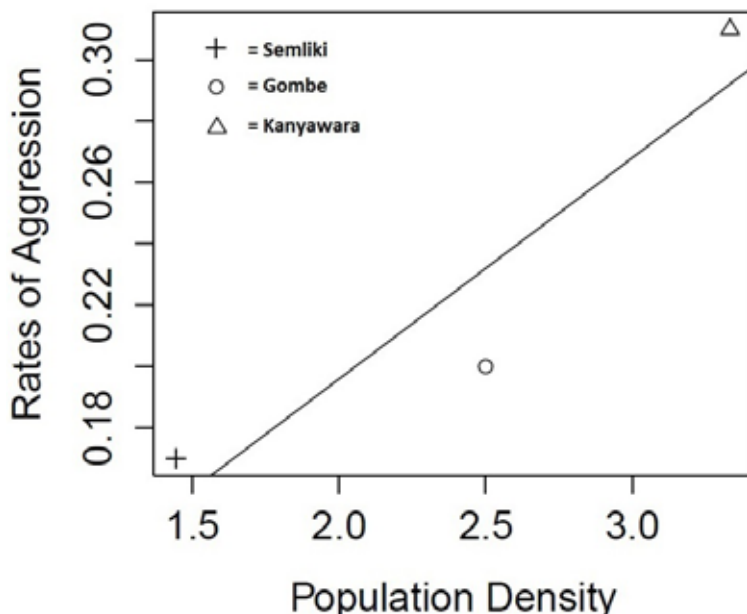


Figure 1. Semliki chimpanzees are more less aggressive when compared to Gombe or Kanyawara chimpanzees. Hourly rates of aggression were averages among sites. Population density was measured as the number of individuals per km². The black line indicates a simple linear regression for illustrative purposes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