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Savanna Chimpanzees (*Pan troglodytes schweinfurthii*)
 Consume and Share Blue Duiker (*Philantomba monticola*)
 Meat in the Issa Valley, Ugalla, Western Tanzania

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INTRODUCTION

Meat eating is pervasive across chimpanzee populations in Africa, with red colobus monkey (*Piliocolobus* spp.) being the most common prey (Boesch & Boesch 1989; Stanford *et al.* 1994a; Watts *et al.* 2012, Hosaka 2015) if sympatric in the same habitat. Besides colobus monkeys, chimpanzees consume a variety of other primates, including olive and yellow baboons (*Papio* spp.) and bushbabies (*Galago* spp.). In the forest habitats of western Tanzania chimpanzees have been reported to consume numerous different mammalian species: 18 at Mahale Mountains National Park (Uehara 1997; Hosaka 2015) and eight at Gombe National Park, whilst in the miombo woodland dominated Ugalla Region no direct observations have been recorded to date (Table 1). In West Africa, chimpanzees from Tai Forest, Ivory Coast consume eight different mammal species, all primates (Boesch & Boesch 1989). Wherever chimpanzees consume meat, it is almost always via hunting, as they rarely scavenge (Watts 2008).

Table 1. Species hunted at Gombe and Mahale, and whether they are present and hunted at Issa, modified from Goodall (1986) and Newton-Fisher (2014).

Common name	Species	Gombe	Mahale	Ugalla	
				Present	Hunted
Primates					
Red-tailed monkey	<i>Cercopithecus ascanius</i>	X	X	X	
Blue (Sykes) monkey	<i>Cercopithecus mitis</i>	X	X	X	
Vervet monkey	<i>Chlorocebus pygerythrus</i>		X	X	
Red colobus monkey	<i>Piliocolobus tephrosceles</i>	X	X	X	
Senegalese bushbaby	<i>Galago senegalesnsis</i>		X	X	
Human	<i>Homo sapiens</i>	X		X	
Greater galago	<i>Otolemur crassicaudatus</i>	X		X	
Chimpanzee	<i>Pan troglodytes</i>	X	X	X	
Baboon	<i>Papio</i> spp.	X	X	X	
Ungulates					
Warthog	<i>Phacochoerus aethiopicus</i>		X	X	
Blue duiker	<i>Philantomba monticola</i>	X	X	X	X
Bushpig	<i>Potamochoerus larvatus</i>	X	X	X	
Bushbuck	<i>Tragelaphus scriptus</i>	X	X	X	
Carnivora					
African civet	<i>Civettictis civetta</i>		X	X	
White-tailed mongoose	<i>Ichnuemia albicauda</i>		X	X*	
Afrotheria					
Elephant shrew	<i>Rhynchocyon</i> sp.		X	X**	
Yellow spotted hyrax	<i>Heterohyrax brucei</i>		X	X**	
Rodentia					
African striped squirrel	<i>Funisciurus</i> sp.	X		X*	

* The genus is present at Issa, but it is uncertain whether the species is similar across Tanzanian sites.

** Other genera of the same Family exist at Issa.

Habitat and wildlife diversity clearly influence potential prey for chimpanzees. In Fongoli, Senegal for example, chimpanzees live in a mosaic savanna landscape and prey on patas monkey (*Erythrocebus patas*) (Pruetz & Marshack 2009), a species that is rarely sympatric with otherwise mostly forest-dwelling chimpanzees. In Ugalla, two recent studies on the diet of wild chimpanzees each found only a paucity of animal tissue in over 1,200 combined samples. Yoshikawa and Ogawa (2015) reported a single case of bird bones and another of unidentified mammalian tissue in over 450 samples analyzed between 1995–2011 from the Nguye area, whilst Piel *et al.* (under revision) reported no mammalian tissue in

over 800 samples collected from 2009–2014 from the Issa Valley. A reliance of faecal analysis to infer dietary behavior has well-discussed limitations (Boesch & Boesch 1989; McGrew *et al.* 2009; Phillips & McGrew 2013) and so direct observations are critical to revealing items that may be otherwise fully digested or rarely consumed.

Where chimpanzees do capture prey, researchers have long been interested in meat-sharing (reviewed in Mitani & Watts 2001). Initial hypotheses described how males monopolized meat and used it as currency, trading it for mating opportunities either on a short or long-term basis, dubbed “meat for sex” (Stanford *et al.* 1994a, 1994b; Gomes & Boesch 2009). Others have argued that rather than sharing with females, meat-holders share preferentially instead with other males, using meat to build alliances with other males (Nishida *et al.* 1992; Mitani & Watts 2001). Finally, a third hypothesis suggested that individuals share meat to reduce the number of beggars, who are otherwise energetically expensive to continuously avoid (Gilby 2006).

We report here on an opportunistic observation of chimpanzee consumption of blue duiker (*Philantomba monticola*) and subsequent acquisition of meat by party members in the Issa Valley, Ugalla, Tanzania. On 4 September, 2015 we observed multiple members of the Issa community feeding on the duiker carcass. We describe here this observation in the context of meat-eating of savanna chimpanzees and also the reliability of macro-analysis of faecal samples to infer dietary consumption.

METHODS

The Issa Valley is located in the Ugalla region, almost 100 km east of Lake Tanganyika (Figure 1) in western Tanzania. The study area extends over 85 km². The region is characterized by extreme seasonal variation: Annual rainfall averages 1,240 mm (range: 955–1,537) and the rainy season typically lasts from October to April, whilst the dry season (months with less than 100 mm of rainfall) lasts for five to six months, from April/May to September (Piel *et al.* 2015). The mosaic vegetation structure of the study area is dominated by miombo woodland (*Brachystegia*, *Julbernardia*, and *Isobertinia*) interspersed with riverine forest, grasslands, and swamps. Russak (2014) recorded 42 mammal and 12 frugivorous bird species including lion (*Panthera leo*) and leopard (*Panthera pardus*). Most recently, researchers observed wild dog (*Lycan pictus*) (McLester *et al.* unpublished data) in the area.

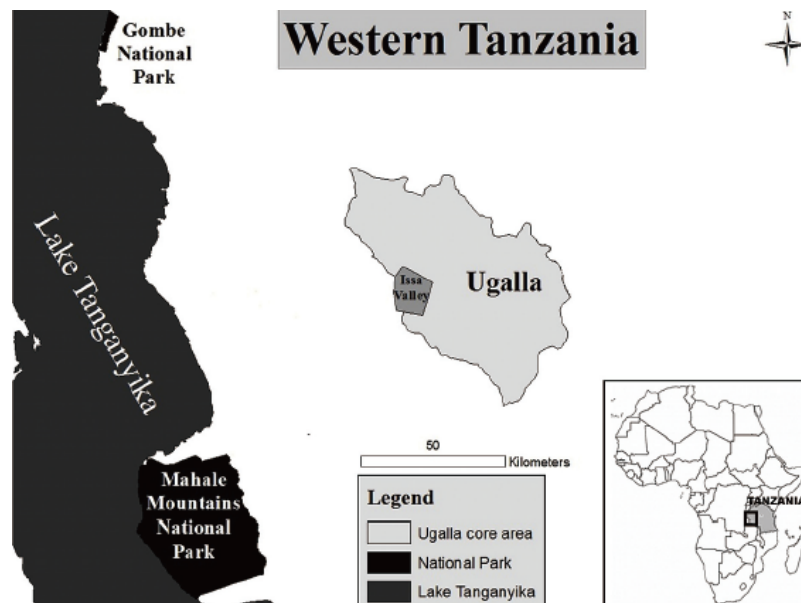


Figure 1. A map of western Tanzania, with the Issa study area as well as Gombe and Mahale Mountains National Parks identified (credit: L. Pintea, Jane Goodall Institute, USA).

Since 2008, there has been a continuous research presence at Issa, and chimpanzees continue to show increased comfort with human presence, rarely fleeing approaching observers (Piel *et al.* unpublished data). All individuals are considered to be part of one community with an estimated home range of between 100–200 km² (Rudicell *et al.* 2011). As of September 2015, researchers had individually identified 14 different chimpanzees.

To better understand chimpanzee dietary patterns, researchers collected faecal samples opportunistically and sluice samples in a near-by river.

OBSERVATIONS

At 0816 h EM and a field assistant encountered a party of at least five individuals who were foraging *Julbernardia globiflora* fruits in miombo woodland. Researchers followed the party into a riverine forest, with individuals periodically in and out of sight, when they

heard a cacophony of chimpanzee vocalizations, including alarm barks. When researchers arrived, they encountered a party of nine chimpanzees and were able to approach within 10 m, although the chimpanzees were obscured in the canopy vegetation. Through a hole in the canopy, they identified an adult male climbing up whilst holding the carcass of a blue duiker in one of his hands (Figure 2). Six other individuals that clustered within 2 m around him followed him. At this time the carcass had already been dismembered, with only a portion remaining with the male in sight. The meat holder fed on and picked at the carcass whilst simultaneously allowing at least one other adult male as well as an adult female and her dependent offspring to feed from the meat by taking some pieces. Selectively, he chased and denied other individuals access to the meat.

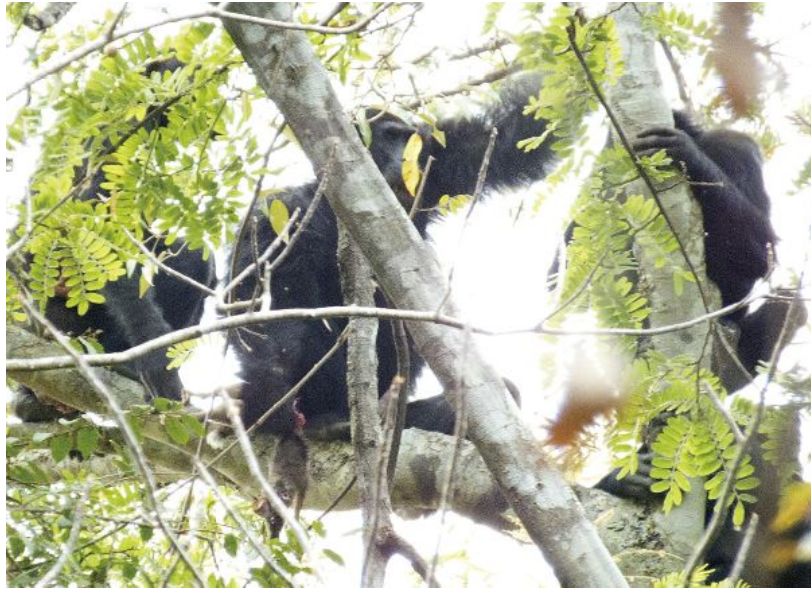


Figure 2. An adult male chimpanzee at Issa holds the blue duiker carcass (credit: E. McLester).

After 10 min the meat holder left the tree, with some individuals in pursuit of him, whilst others remained in the tree. Researchers then saw the male climb an adjacent tree and disappear into the canopy, after which a chorus of pant hoots and screams were heard. There was a period of silence, and at 1015 h, researchers approached the location near the source of the vocalizations and identified three individuals consuming scraps of meat. By 1031 h, the chimpanzees had dispersed and researchers began searching for tissue remains and faecal samples in the surrounding area. None were recovered.

The following day, researchers tracked a chimpanzee party for over 8 h. In that time they collected six faecal samples, three of which contained vertebrate remains: either hair or bone (tooth), or both (Figure 3).



Figure 3. Mammalian (likely blue duiker) remains from chimpanzee faeces collected the day after the observed meat consumption (credit: S. Ramirez-Amaya).

DISCUSSION

Wild chimpanzees consume at least 40 different species of vertebrates across Africa (Newton-Fisher 2014) and numerous studies have addressed the role that meat might play as a nutritional resource (Boesch & Boesch-Achermann 2000), as a social tool to build alliances (Nishida *et al.* 1992), recruit mates (Stanford *et al.* 1994b) and to reciprocate meat sharing (Mitani & Watts 2001). For savanna-woodland chimpanzees in the Issa Valley our observations represent the first direct observation of mammalian consumption and expand the number of communities that are known to consume meat.

During the last three decades of research on wild chimpanzees, discussion of chimpanzee predation focused on the consequences for arboreal prey, namely colobus populations (Stanford *et al.* 1994a; Hosaka *et al.* 2001; Mitani & Watts 2001; Newton-Fisher *et al.* 2002; Gomes & Boesch 2009). More recently, however, with the first habituation of savanna chimpanzees at Fongoli, more unorthodox sources of prey are being revealed, terrestrial and nocturnal, for example *Erythrocebus* (Pruetz & Marshack 2009) and *Galago* (Pruetz & Bertolani 2007). Now at Issa, we report an observation that also suggests a terrestrial capture. Issa chimpanzees are not the only community to consume antelopes. The chimpanzees of Mahale Mountains also consume blue duikers (Takahata *et al.* 1984). What remains poorly understood is what drives prey selection and hunting frequency.

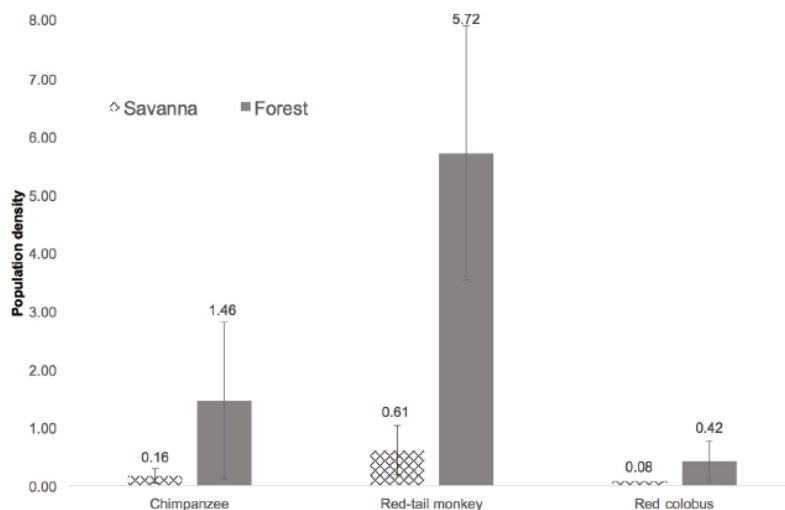


Figure 4. Population density variation between forest-dwelling and savanna

primates, with error bars indicating standard deviations (source: Plumptre & Reynolds 1996; Chapman & Lambert 2000; Moyer *et al.* 2006; Rode *et al.* 2006; Davenport *et al.* 2007; Petre *et al.* 2007; Kouakou *et al.* 2009; Moore & Vigilant 2013; Samson & Hunt 2014; Piel *et al.* 2015). A single record exists from Issa's red colobus population, hence the lack of error bars.

There are at least three potential explanations for prey selection and hunting frequency variability. First, one reason for lower prevalence of meat-eating at Issa may be the population density of both chimpanzees and potential prey (Figure 4). For example, chimpanzees and red-tailed monkeys live at very low densities, reducing the likelihood of encounters between the species. It may be that with less forest available, and subsequently lower monkey density (Figure 4), chimpanzees living in more open habitats exploit alternative prey sources. More data on prey availability and preference might resolve whether an environmental explanation is sufficient. Second, an alternative explanation in terms of culture might be explored: According to Boesch & Boesch (1989), Tai forest-chimpanzees never eat blue duikers even if they capture them, although blue duikers are fairly common in their habitat, whereas Issa chimpanzees have not been reported to capture or eat arboreal prey, despite the fact that chimpanzees and arboreal monkeys live sympatric at Issa. Third, macro-analysis may be insufficient for detecting animal tissue. Whilst it reveals much about chimpanzee diet (Phillips & McGrew 2013), Boesch & Boesch (1989) have outlined its limitations. That no mammalian tissue was observed in an analysis of over 1200 faecal samples across Ugalla suggests that either meat-eating is an extremely rare event, or else not all items that chimpanzees consume are detectable in faeces. We suspect it is the former, and as chimpanzee habituation improves in the coming months, we anticipate observing more chimpanzee predation events.

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