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New Observations of Meat Eating and Sharing in Wild Bonobos (*Pan paniscus*) at Iyema, Lomako Forest Reserve, Democratic Republic of the Congo

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Abstract

Bonobos (*Pan paniscus*) consume a variety of vertebrates, although direct observations remain relatively rare compared to chimpanzees (*Pan troglodytes*). We report the first direct observations of meat eating and sharing among bonobos at Iyema, Lomako Forest, Democratic Republic of Congo. We collected meat consumption data ad libitum from June to November 2017 over 176.5 observation hours and conducted monthly censuses to measure the abundance of potential prey species. We observed 3 occasions of duiker consumption and found indirect evidence of meat consumption twice (*n* = 5). We identified the prey species as Weyn's duiker (*Cephalophus weynsi*) in all 4 cases that we saw the carcass. This species was the most abundant duiker species at Iyema, but other potential prey species were also available. Meat sharing was observed or inferred during all 3 observations. However, the individual controlling the carcass frequently resisted sharing, and aggressive attempts to take the carcass were observed. This report contributes to a growing body of data suggesting that wild bonobos consume meat at higher rates than previously thought, female control of carcasses is frequent but not exclusive, and meat sharing in bonobos is primarily passive but not without aggression.

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The evolution of meat eating and sharing has been argued to play an important role in hominin evolution [Isaac, 1978; Aiello and Wheeler, 1995], thus prompting its study in our closest living relatives, particularly the genus *Pan* [Mitani, 2009]. Until recently, direct observations of meat eating and sharing in bonobos remained rare when compared to observations in chimpanzees (*Pan troglodytes*) [Badrian and Malenky, 1984; Ihobe, 1992; Bermejo et al., 1994; White, 1994; Hohmann and Fruth, 2008; Hirata et al., 2010; Sakamaki et al., 2016] leading to the conclusion that bonobos consumed meat less frequently than chimpanzees [Gilby et al., 2013, 2017]. Thus, most models of the evolution of cooperation via food sharing in *Homo* have focused heavily on meat eating and sharing in chimpanzees [e.g., Gilby et al., 2010, 2017; Samuni et al., 2018a; but see Yamamoto, 2015, for a discussion of the role of fruit sharing in bonobos]. Recent reports demonstrate that some bonobo populations consume meat at much higher rates than previously known [Moore et al., 2017; Fruth and Hohmann, 2018]. However, frequency of meat consumption across sites varies from 6 events across multiple decades at Wamba [Hirata et al., 2010] to 2 events per month across 2 communities at LuiKotale [Fruth and Hohmann, 2018].

Bonobos consume a variety of different vertebrate species, but available data suggest between population differences in preferred prey despite the relative consistency of available prey species [reviewed in Sakamaki et al., 2016]. While most chimpanzee populations prefer red colobus (*Piliocolobus* spp.) when available [Newton-Fisher, 2015], chimpanzees that are not sympatric with this species also exhibit variation in preferred prey [Hobaiter et al., 2017]. In both *Pan* species, group or population level prey preferences may develop via a specialized prey image based on frequency of encounters with different prey species and subsequent social learning [Boesch and Boesch, 1989; Ihobe, 1990; Sakamaki et al., 2016; Hobaiter et al., 2017], but demography and other ecological factors also play a role [Boesch and Boesch, 1989].

Notably, bonobo females frequently control the carcass during sharing events [White, 1994; Surbeck and Hohmann, 2008], whereas in chimpanzees males predominantly maintain control [Newton-Fisher, 2015; but see Pruetz et al., 2015; Hobaiter et al., 2017; Samuni et al., 2018b]. Meat sharing occurs in both species, but not necessarily for the same reasons. Among chimpanzees, sharing functions to reinforce social bonds [Mitani and Watts, 2001; Wittig et al., 2014; Samuni et al., 2018a, b], acquire future mating opportunities [Gomes and Boesch, 2009], and reduce harassment [Gilby, 2006]. Among bonobos, sharing also functions to reinforce social bonds [White, 1994; Yamamoto, 2015], but the beggar may also use the interaction to assess their social relationship with the possessor [Goldstone et al., 2016]. Here, we describe the first reported observations of meat eating and sharing in the Iyema bonobos.

Iyema is located in the Lomako Forest, Tshuapa Province, Democratic Republic of Congo (DRC) (1.015556, 21.113889) with a trail system approximately 30 km^2 in size (Fig. 1). The Lomako Forest consists primarily of primary forest with small patches of secondary forest and swamp forest [White, 1992]. As of 2017, the bonobos were semihabituated, and most were relaxed and could be followed and observed when arboreal. The exact number of bonobos and communities inhabiting Iyema remains unresolved; however, observation and preliminary genetic analyses indicate that between 26 and 66 individuals inhabit the area within the trail system, likely across two or more communities [P. Bertolani, pers. commun.; Brand et al., 2016].

This study took place from June to November 2017 for a total of 176.5 h of direct observation. We followed parties as they left their night nests or after contact while
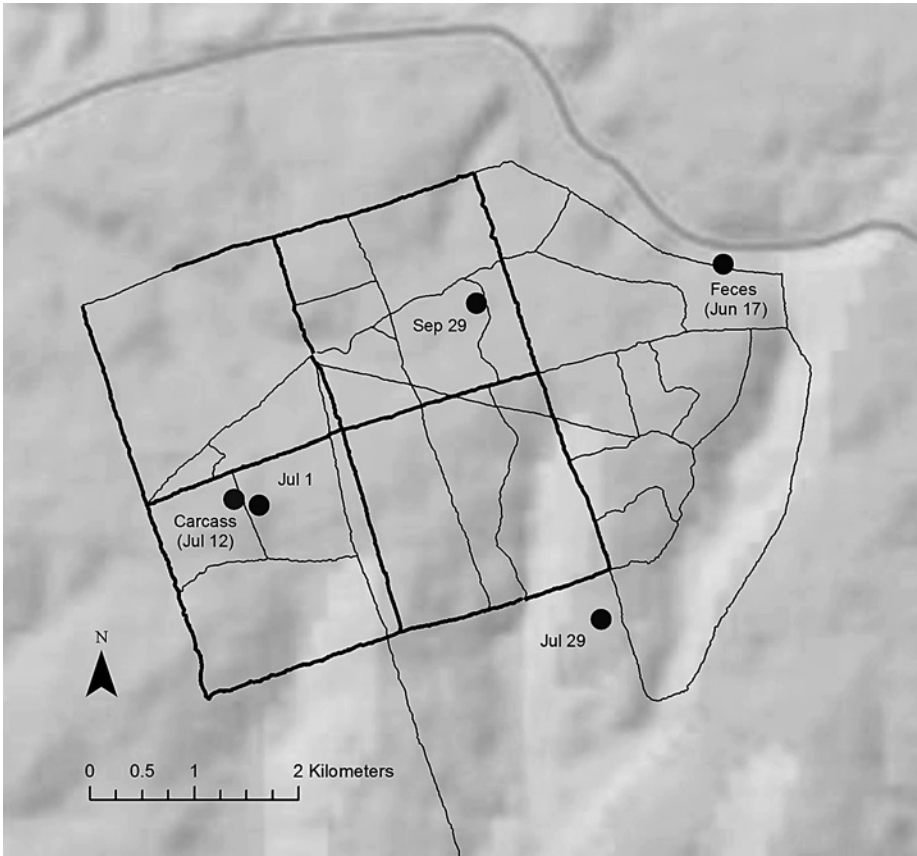
Fig. 1. Map of the Iyema trail system showing the locations of direct and indirect observations of meat consumption. The grid highlighted with bold lines shows the trails used for the mammal censuses.

searching the study area. We recorded party composition, activities, and GPS location during 15-min scan samples. All social behavior or rare events, including meat eating, were recorded ad libitum. All meat-eating events were observed by a pair of researchers and a local guide(s). We scored sharing events using definitions based on Boesch and Boesch [1989] (Table 2).

We conducted censuses to assess the abundance of potential diurnal mammalian prey following the methodology from monkey censuses at N'dele [McGraw, 1994; Waller and White, 2016]. The main grid of the trail system forms 6 unique, nonoverlapping transects, each 4 km in length, except for one transect that was only 3 km in length due to an impassable swamp (Fig. 1). We discarded censuses that were invalidated by rain or other interruptions resulting in 24 complete censuses (93 km total). Censuses were conducted between 06.00 and 12.00 h by a primary observer and a local guide. When monkey species were observed within a 20-m radius of the transect, we collected geospatial information and determined the number of individuals pres-

Table 1. Estimated mean abundance of duiker and monkey species at Iyema based on census data

	Species	Mean encounter rate across transects ± SE, individuals/km
Duiker	*Cephalophus dorsalis*	0.06 (0.02)
	Cephalophus silvicultor	0.04 (0.02)
	Cephalophus weynsi	0.16 (0.03)
	Philantomba monticola	0.04 (0.03)
Monkey	*Cercopithecus ascanius*	0.65 (0.15)
	Cercopithecus wolfi	0.69 (0.15)
	Colobus angolensis	0.09 (0.05)
	Lophocebus aterrimus	0.43 (0.06)

ent. We recorded any trace of nonprimate mammals on the census path, or sightings and auditory encounters within 20 m in either direction. As the majority of encounters with nonprimate mammals were auditory, we could only record the minimum number of individuals, thus the values are likely underestimates. Terrestrial mammals such as red river hogs (*Potamochoerus porcus*) and duikers (*Cephalophus* spp., *Philantomba monticola*) are easily identified by their alarm calls and distinct movements when they flee if startled [Lwanga, 2006].

Given that species' abundance may vary across the landscape, we calculated mean abundance for each transect and then calculated total abundance from the mean of all 7 transects. We did not calculate densities as our data violate a number of assumptions for density calculations [see Lwanga, 2006]. We only included species that are known or likely to be consumed by bonobos. Additional mammals are present at the field site, some of which also constitute available prey species (see Appendix).

We observed bonobos consuming meat on three occasions (July 1, July 29, September 29) and saw bonobos fleeing a carcass upon encounter for a fourth event (July 12). A fifth event was inferred from duiker hair found in 2 fecal samples in a single nest party (June 17). This translates to 0.6 events per month (0.028 events/observation hour) excluding indirect cases and 1 event per month (0.017 events/observation hour) with both direct and indirect cases. In all events with a carcass, we identified the species as Weyn's duiker (*Cephalophus weynsi*). This species was the most abundant duiker at Iyema (Table 1). Three species of monkeys were highly abundant and occurred at similar rates; Angolan colobus (*C. a. angolensis*) was present but much less common. Two identifiable species of rodents were also detected during transects, both at low frequencies.

Table 2 summarizes carcass ownership and social behavior observed during meat-eating events. Adult females had primary control of the carcass during the July 1 and July 29 events while an adult male had control for the third (September 29). Sharing was observed on the July 1 and July 29 events. Visibility was too limited to observe meat sharing in the third event (September 29), but sharing was inferred from evidence of meat in the feces of at least 2 members of the party. We describe in detail the observations where visibility allowed us to observe the majority of the events (July 1 and July 29). We use age-sex classes to identify individuals involved, but these are not necessarily the same individuals across events.

Table 2. Summary of social behavior during meat-eating events

Date and how hunting party was located	Owner[a,b]	Participant[a]	Begging by participant[b]	Sharing with participant[b]	Approximate number of sharing events	Agonism from owner to participant	Agonism from participant to owner	Sexual interaction with owner
July 1, 2017 – audio encounter at start of hunt	AF	AM	yes	co-feed active passive	2 0 12	mild resistance (swatting away hands)	attempted carcass thefts, grabbing owner in process	yes
		SM	yes	co-feed active passive	1 0 4	mild resistance (swatting away hands)	none	no
July 29, 2017 – tracking the party prior to hunt	AF#1	AF#2	no	co-feed active passive	0 0 0	none	successful carcass theft	no
		AF#3	no	co-feed active passive	0 0 0	none	none	no
		AM	no	co-feed active passive	0 0 3	resisted carcass theft	attempted carcass theft	no
		SM	yes	co-feed active passive	0 3 12	frequent, ranged from swatting away to hitting in the face (slaps and punches)	none	yes
	AF#2	AF#1	no	co-feed active passive	2 1 0	none	none	no
		AF#3	no	co-feed active passive	2 0 1	none	none	no
		AM	no	co-feed active passive	0 0 1	pulled carcass away from AM while AF#1 still had control preventing the attempted theft by AM	none	no
		SM	yes	co-feed active passive	0 0 2	mild resistance (swatting away hands)	none	no
September 29, 2017[c] – following party from nesting site	AM	AF#1	yes	none observed		hits another individual, but could not identify recipient	none observed	no
		AF#2	no	none observed		see above	none observed	yes

[a] We use age-sex classes to identify different individuals involved in each event. However, these are not necessarily the same individuals across events. Age/sex definitions: AF, adult female; AM, adult male; JF, juvenile female; SM, subadult male. [b] Behavior definitions: owner, the individual who is holding and in control of the carcass; participant, individual present in party and interacting with the owner, but not in control of carcass; begging, participant sits in close proximity to the possessor and peers and/or reaches out hand to possessor; passive sharing, possessor tolerates participant taking piece of meat or exudate, typically only small scraps from the carcass without apparent resistance from the owner; active sharing, owner gives a piece of meat to participant by directly handing or spitting out a piece of meat for participant; cofeed, owner and participant concurrently feed on carcass without apparent aggression or resistance; theft, participant forcefully takes all or part of the carcass from the owner. [c] Visibility was poor for this event which occurred terrestrially.

Event of July 1, 2017

We contacted a party of bonobos before dawn but lost them after we were charged by red river hogs who were at the nest site eating bonobo feces. We searched the area to recontact the party and made audio contact with bonobos at 6:55 after hearing a duiker distress call and bonobo screams. We made visual contact 5 min

later when an adult female (AF) bonobo climbed a tree carrying a duiker, still alive and vocalizing. The AF was followed by an adult male (AM) and subadult male (SM), the rest of the party remained on the ground and moved off a short time later. At 7:14 we located the bonobos in the tree. The AF had control of the carcass. She consumed the eyeballs first and then moved to the abdomen. The AF maintained ownership of the carcass for 71 min. Both males repeatedly begged for meat by reaching out their hands to the female and/or peering. Both males also repeatedly tried to access the carcass with their hands nonaggressively. However, the SM was much more persistent and intense in his begging than the AM. Both were successful at occasionally taking small pinches of meat or exudate, with the adult more successful than the subadult. However, the female often resisted by brushing away their hands. At 8:25, the AM unsuccessfully attempted to copulate with the AF, followed by an attempt to forcibly take the carcass from her. She resisted and moved away with the carcass. At 8:34, the AM approached the AF; she turned her back to him and hunched over the carcass. He grabbed her trying to forcibly turn her towards him, but she resisted. This continued off and on for 5 min. The AM gained control of the carcass briefly, but then co-fed with the AF for the next 8 min, after which the AF took the remaining entrails and moved away leaving the AM with the skin. The SM continued to beg from the AM who allowed him to chew on a hoof of the duiker. At 9:00 the AF returned and approached the AM who avoided her and moved about 2 m away. At 9:02 the AF approached the AM again, and he moved out of sight. At 9:06 we found the AM with the AF and SM near him. At 9:07 the AF and AM co-fed for 3 min, then the AF took a piece of meat to eat while remaining in proximity to the AM. The SM proceeded to beg from both the AM and AF, and the AF passively shared a piece of meat with him. At 9:11 the AF finished her piece of meat and returned to co-feeding with the AM for 3 min, after which the AM dropped the carcass and transferred control to the AF. The AF allowed the SM to co-feed, but by this time, only skin remained. At 9:19, the AM approached and gained control of the carcass, but we could not see whether the AF gave it to him or he took it. At 9:22 the party descended and left the carcass on the ground as they moved away.

Event of July 29, 2017

We contacted a party of bonobos while finishing census transect just off the census route and followed them on the ground for about 1 h until we lost visual contact. We continued tracking them until we found 5 bonobos sitting in a tree. The party consisted of an adult female (AF#1), an adult female (AF#2) with an infant, another adult female (AF#3) with an infant, an adult male (AM), and a subadult male (SM). At 11:49 we observed AF#1 consuming a duiker. The eyes and most of the entrails were gone, and she was pulling small pieces of meat off the inside of the ribs. AF#1 maintained control of the carcass for 174 min until 13:43 when AF#2 gained ownership. While AF#1 had control of the carcass, both males remained in proximity to AF#1 and repeatedly begged from her. However, the SM was much more persistent and intense in his begging and was more successful compared to the AM who begged infrequently and was rarely successful in obtaining meat. In addition, during the period that AF#1 controlled the carcass we observed the following behaviors: at-

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tempted carcass theft by the AM, increasingly frequent and intense harassment of AF#1 by the SM, AF#1 responded by growing more aggressive in her resistance to him, pushing away his hand, pulling the carcass away from him, and hitting him. The SM copulated with AF#1 three times. The AM groomed her twice; however, there was no exchange of meat preceding or following the grooming bouts. At 13:30 AF#2 approached AF#1, and at 13:34, the AM and AF#2 each grabbed onto the carcass and pulled it towards themselves while AF#1 tried to maintain control resulting in a three-way "tug-of-war" that lasted for 9 min. This culminated at 13:43 when AF#2 gained control of the carcass and moved off with it towards AF#3 followed by AF#1. While AF#2 had ownership of the carcass, all three females co-fed for about 8 min during which the SM occasionally got pieces of meat. The three females stopped co-feeding after AF#2 had hit the SM in response to his begging. AF#2 was the sole consumer of the carcass until 14:26 when AF#2 and AF#1 resumed co-feeding for 4 min. Starting at 14:38, all party members piled around the carcass, and it was difficult to determine ownership and meat acquisition. At 14:40, AF#1 hit the SM after he had begged from the pile, after which he continued to make attempts to get meat. At 14:56, AF#2 descended with the carcass in her mouth while the rest of the group followed her.

This study contributes to the emerging view that bonobo meat eating and sharing occurs in some populations within the range of variation in chimpanzees [Moore et al., 2017]. The rate from both this study and Fruth and Hohmann [2018] are within the range of some well-studied chimpanzee populations, notably where red colobus are rare to absent (e.g., Budongo at 0.5–2 times/month [Hobaiter et al., 2017]; Ugalla at 5 events over multiple years [Ramirez-Amaya et al. 2015]), albeit on the lower end of the chimpanzee range [Watts and Mitani, 2002].

However, comparison across sites and species is complicated because of differences in methodology, habituation levels, and reporting. Since the Iyema bonobos were not fully habituated, our observed rate is likely a low estimate [Hobaiter et al., 2017]. Conversely, if we were more likely to encounter loud hunting parties, we could overestimate meat consumption. However, we found the bonobos from calls in only one event, we were already tracking the group when they hunted the other times. Additionally, despite being the same localized population (within an approx. 3-km radius of the camp), it is possible our observations include more than one community. Further, chimpanzee meat-eating rates vary seasonally and often include "binge" periods of red colobus hunting when fruit is abundant and parties are large [Stanford et al., 1994; Watts and Mitani, 2002]. However, opportunistic "snatch and grab" hunting of solitary terrestrial animals, such as duikers, is less dependent on party size and thus less likely to increase with food abundance and/or party size. Four of the 5 events in our sample occurred during the dry season when fruit abundance was low (unpublished phenology data). Thus, while we were not witnessing the type of "binge" seen in chimpanzees, we cannot rule out that meat consumption may have been high as a means of nutritional supplementation [Takahata et al., 1984]. Finally, observations of rare events often go unreported due to concerns of small sample sizes.

Duikers were the only type of prey in our sample, and in the cases where we were able to identify the species, all were Weyn's duiker, the most abundant duiker species at Iyema (Table 1). This encounter frequency may explain why this species was preferred due to their higher density or higher encounter rate. Previous fecal washing

at Iyema revealed the consumption of a tree hyrax and an unidentified bird in addition to duikers [Cobden, 2012]. No monkey remains were found, and our Congolese guides also have seen no evidence of the Iyema bonobos consuming monkeys despite their high abundance. Thus, prey availability does not fully explain observed prey preferences at Iyema.

Curiously, eyes were consumed first or very early during consumption both times we observed the event from the beginning of the kill. Typically, intestines are consumed first in bonobos [Fruth and Hohmann, 2002] whereas prey age appears to influence which part is first consumed in several chimpanzee populations [e.g., Gilby and Wawrzyniak, 2018]. With additional data from both bonobos and chimpanzees, we encourage future analyses to consider interindividual or population differences in preferred prey parts.

Interactions between individuals during the consumption of duikers ranged from peaceful co-feeding to frequent aggression. This is in contrast to other sites where bonobos are reported to consume and share meat peacefully, even with extra-group individuals [e.g., White, 1994; Hirata et al., 2010; Fruth and Hohmann, 2018; but see Goldstone et al., 2016]. Consistent with other bonobo research, most sharing was passive whereas active sharing was relatively infrequent [Fruth and Hohmann, 2002; Jaeggi et al., 2010]. While our data are insufficient at this time to test any hypotheses for the function of sharing, our observations that the most frequent and intense begging came from subadult males is consistent with the assessing relationships hypothesis [Goldstone et al., 2016].

As expected, 2 of the 3 directly observed hunts at Iyema involved female control of the carcass. However, 1 event involved male control of the carcass, and in both instances of female control, males attempted (mostly unsuccessfully) to forcibly take the carcass from the female. Male ownership of carcasses has been reported at other sites as well (LuiKotale [Fruth and Hohmann, 2018]; Wamba [Ihobe, 1992]; Iyondji [Sakamaki et al., 2016]; and N'dele [White, 1994]) and thus should not be underestimated. Yet, frequent female control of carcasses and ability to thwart theft attempts from males is still a notable difference from chimpanzees where female control is rare and females often lose control of meat to males even if they make the kill [Wakefield, pers. observation; Gilby et al., 2017; Hobaiter et al. 2017; but see Pruetz et al., 2015; Samuni et al., 2018b].

This study contributes further information on *Pan* meat eating and on social behavior during meat eating, including aggression and meat sharing. We echo the need to be cautious in generalizing about *Pan* meat eating patterns by population or species, given the intraspecific variation in both bonobos (reviewed here) and chimpanzees [e.g., Pruetz et al., 2015; Samuni et al., 2018b]. While there are patterned similarities (e.g., community level prey preferences, begging behavior) and differences (e.g., sex biases in carcass ownership) between chimpanzees and bonobos in vertebrate consumption, it is now becoming clear that the full range of variation in both species leads to overlapping but not identical behavioral spectrums.

Appendix

Other Mammals Present at Iyema, DRC
In addition to the listed species, we encountered a number of unidentified cusimanse, mongoose, and rodent species.

Order	Species
Artiodactyla	*Cephalophus dorsalis*
	Cephalophus silvicultor
	Cephalophus weynsi
	Philantomba monticola
	Potamochoerus porcus
Carnivora	*Civettictis civetta*
	Genetta maculata
	Genetta servalina
	Panthera pardus
	Poiana richardsoni
	Profelis aurata
Pholidota	*Phataginus tetradactyla*
	Phataginus tricuspis
Primates	*Allenopithecus nigroviridis*
	Cercopithecus ascanius
	Cercopithecus neglectus
	Cercopithecus wolfi
	Colobus angolensis
	Galago demidovii
	Galago thomasi
	Lophocebus aterrimus
	Perodicticus potto
Rodentia	*Anomalurus* sp.
	Atherurus africanus
	Funisciurus congicus
	Protoxerus stangeri

Statement of Ethics

All of the research reported here was noninvasive and complied with all standards set forth by the University of Oregon Institutional Animal Care and Use Committee (IACUC) (#12-09). Our research complied with all legal and ethical requirements of the DRC and was approved by the ICCN (#0358/ICCN/DG/CWB/2017).

Disclosure Statement

The authors have no conflicts of interest to declare.

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