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Chimpanzee (*Pan troglodytes schweinfurthii*) grouping patterns in an open and dry savanna landscape, Issa Valley, western Tanzania

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ABSTRACT

Fission-fusion societies are social systems in which individuals belonging to the same community are rarely all together but rather spend most of their time in temporary parties. This flexible social organization is assumed to be an adaptation that balances advantages and costs of group living in a fluid way as resources and constraints shift through space and time. It has been argued that this flexibility freed hominins from the foraging constraints caused by living in large groups. Given their close genetic relationship to humans and because they represent the classic case of a fission-fusion society, chimpanzees have often been used as referential models to understand human social evolution. Determinants of chimpanzee party size have been widely studied for decades across several communities. However, we lack data from open and dry sites-which closely resemble those reconstructed for Plio-Pleistocene hominins—on communities that potentially face similar environmental constraints as early hominins did. We investigated chimpanzee (Pan troglodytes schweinfurthii) grouping patterns on a recently habituated community living in the savanna-woodland mosaic landscape of the Issa Valley, western Tanzania, by following chimpanzees daily and recording party size every hour. Our results revealed that party size at Issa 1) followed seasonal fluctuations in food availability, 2) increased in the presence of swollen females, and 3) was higher in open vegetation, which potentially presents a high predation risk. Furthermore, we found the Issa community to be highly cohesive compared with the majority of other communities, possibly due to a combination of its small size and potential threats characterizing its home range. Our study fills a gap in our knowledge of chimpanzee sociality by exploring grouping pattern determinants in an East African understudied biome and highlights what elements of early hominin social behavior may have evolved in Late Pliocene landscapes.

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1. Introduction

Despite nearly six decades of field research, gaps remain in our understanding of chimpanzees, particularly when it comes to communities inhabiting savanna woodlands (Marchant et al., 2020). By focusing on wetter, more forested habitats, we may miss key behavioral diversity only exhibited under certain environments, impairing our understanding of the species (Kalan et al., 2020). Research on the social behavior of savanna woodland chimpanzees has numerous implications, such as broadening our view of chimpanzee behavior by revealing how adaptable and flexible the species can be and yielding important insights into

* Corresponding author. *E-mail address:* giuliano.camille@gmail.com (C. Giuliano). hominin evolution. By studying chimpanzee grouping patterns on a newly habituated community in the savanna woodland landscape of Issa Valley, we expand our knowledge of chimpanzee sociality and provide hypotheses to the paleoanthropological scientific community who could build on these results to infer how early hominin social behavior may have evolved in dry and open landscapes.

1.1. Fission-fusion societies and chimpanzee party size

The term fission-fusion was first introduced to describe social systems where group size varies by the splitting (fission) or merging (fusion) of subgroups (Kummer, 1971). While many groupliving mammals occasionally split into smaller units, some species such as bottlenose dolphins (*Tursiops truncatus*; Connor et al., 2000), spotted hyenas (*Crocuta crocuta*; Holekamp et al., 1997),







African elephants (*Loxodonta africana*; Wittemyer et al., 2005), spider monkeys (*Ateles* spp.; Klein and Klein, 1971), chimpanzees (*Pan troglodytes*; Nishida, 1968), and bonobos (*Pan paniscus*; Kano, 1982) fission and fuse on a regular basis, with subgroup size and composition fluctuating by day or even hour (Aureli et al., 2008). This social organization is thought to have evolved as an adaptation that balances costs (e.g., food competition) and benefits (e.g., reduced predation risk) of group living in a fluid way as resources and constraints shift over space and time (Bertram, 1978; Terborgh and Janson, 1986; Dunbar, 1988; Sueur et al., 2011).

Chimpanzees, which rely mainly on ripe fruit (Wrangham et al., 1998), a resource characterized by its spatiotemporal fluctuations in distribution (Chapman et al., 1999), might struggle to maintain viable communities if they did not temporarily fission into small subgroups (Lehmann et al., 2007a). Although individual chimpanzees belong to a community in which all members associate, they split into smaller groups (hereafter, parties) while the entire community rarely aggregates (Sugiyama, 1968). Examining factors that regulate chimpanzee party size is important because it informs on what constraints a community might be facing (e.g., resource fluctuations) and how individuals socially respond to them (Terborgh and Janson, 1986; Schulke and Ostner, 2012).

Two measures of chimpanzee party size are frequently discussed in the literature (Table 1): 1) absolute party size (APS), which is the number of individuals in a party, and 2) relative party size (RPS), which is the percentage of the community that composes the party (APS/community size \times 100; Boesch, 1996) and is often used as a proxy for community cohesion (Furuichi, 2009). Researchers have varied in their operational definition of chimpanzee 'party' over the last half century (Table 1) and definitions impact party size calculations (Chapman et al., 1993; Hashimoto et al., 2001). For example, 'nomadic' APS (all individuals observed over the course of a day) provides a 40% larger estimate than APS calculated at 15-min intervals (Chapman et al., 1994). Methodological discrepancies are difficult to overcome given the specificities of each chimpanzee study site (vegetation, terrain, number of observers, degree of habituation, etc.), making intersite comparisons difficult and limiting our ability to universally assess party-size determinants.

1.2. Chimpanzee party size determinants

Despite methodological heterogeneity, variation in chimpanzee APS has been explained by temporal variation in food availability

Table 1

Comparison of mean absolute party size (APS), mean relative party size (RPS), and methods of calculation used in different studies based on direct observations.

Community	Habitat	Community size APS		RPS	Method	Source		
		w/o dep. ^a	with dep.	w/o dep.	with dep.			
Assirik	Savanna	~16	~24		5.3	_	All individuals present upon first contact	Tutin et al. (1983)
Assirik	Savanna	_	~28	4.0	—	_	All independents present upon first contact	Hunt and McGrew (2002)
Bossou	Forest	13	20	4.0	_	30.8	All independents encountered in a single day (nomadic party)	Sakura (1994)
Bossou	Forest	9	14	5.0	_	55.6	All independents, 5-min scan	Hockings et al. (2012)
Bossou	Forest	10	13	_	6.8	52.3	All individuals, 15-min scan	Bryson-Morrison et al. (2017)
Budongo (Sonso)	Forest	_	46	_	5.0	10.9	All individuals, 30-min scans	Newton-Fisher et al. (2000)
Budongo (Sonso)	Forest	31	43	_	5.6	13.0	All individuals traveling together in a sub-group	Wallis (2002)
Budongo (Sonso)	Forest	36	71	7.3	—	20.4	All independents, continuous (record only when change in the party)	Villioth (2018)
Budongo (Waibira)	Forest	46	88	4.4	_	9.5	All independents, continuous (record only when change in the party)	Villioth (2018)
Fongoli	Savanna	17	35	_	15.0	42.9	All individuals encountered in a single day (nomadic	Pruetz and Bertolani (2009)
Gashaka-Gumti	Forest	—	35	-	4.1	11.7	Max. individuals (infants excluded) visible during an encounter	Sommer et al. (2004)
Gombe	Forest	28	43	_	11.9	27.7	All individuals traveling together in a sub-group	Wallis (2002)
Gombe	Forest		57	_	5.6	9.8	All individuals, continuous (record only when change in the party)	Goodall (1986)
Issa	Savanna	18	26	5.6	_	30.3	All independents seen in 1 h (acoustic party)	This study
Kahuzi-Biega	Forest	14	22		4.4	20.1	All individuals in foraging parties	Basabose (2004)
Kalinzu	Forest	45	_	59	_	13.0	All independents seen in 1 h (acoustic party)	Hashimoto et al. (2001)
Kibale (Kanyawara) ^b	Forest	27	_	51	_	18.8	All independents 15-min scan	Chapman et al. (1995)
		_	—	5.1	_	18.9	All independents, continuous (record only when change in the party)	
		_	_	7.1	_	26.4	All independents seen in 1 h (acoustic party)	
Kibale (Kanyawara)	Forest	30	55	7.0	_	23.3	All independents, 15-min scan	Pokempner (2009)
Kibale (Ngogo)	Forest	101	145	6.7	—	6.6	All independents, 30-min scan (only parties with ≥ 1 female included)	Wakefield (2008)
Kibale (Ngogo)	Forest	95	140	10.3	_	10.8	All independents present upon first contact	Mitani et al. (2002)
Mahale (M-Group)	Forest	45	85	_	24.6	28.9	All individuals encountered in a single day	Matsumoto-Oda et al. (1998)
Mahale (M-Group) ^b	Forest	31	44	4.0	_	12.1	All independents, 1-min scan (face-to-face party)	Itoh and Nishida (2007)
(_	_	15.5	_	47.0	All independents encountered in a single day (nomadic party)	
Semliki	Savanna	_	>29	4.8	_	_	All independents present upon first contact	Hunt and McGrew (2002)
Taï (North)	Forest	_	76		8.0	10.5	All individuals, continuous (record only when change in the party)	Boesch et al. (1996)
Taï (North)	Forest	36	70	3.5	_	9.6	All independents seen in 1 h (acoustic party)	Doran et al. (1997)
Taï (North)	Forest	17	31	5.5	_	32.4	All independents, 15-min scan	Anderson et al. (2002)
Taï (South)	Forest	25	39	5.2	_	20.8	All independents, continuous (record only when change in the party)	Wittiger and Boesch (2013)

^a dep. = dependent individuals i.e., infants and juveniles.

^b More than one method was used to calculate party size in the same study.

across communities (Nishida, 1979; Chapman, 1990; Anderson et al., 2002; Korstjens et al., 2006; Lehmann et al., 2007a), with individuals splitting into small parties when food is scarce as a way of reducing feeding competition and aggregating in larger parties during periods of food abundance. Other studies, in some cases based on data from these same communities, reported no effect of food availability on APS (see Table 2). This inconsistency could result from a curvilinear relationship between food availability and APS (Newton-Fisher et al., 2000). That is, as global food availability increases, the constraints of limited food supply weaken, until it has almost no influence on APS. At Ngogo (Kibale, Uganda) for example, where food productivity is considered to be high all year (Wakefield, 2008), APS was not influenced by food availability (Wakefield, 2008), potentially because it did not reach low enough levels to limit party size (Hashimoto et al., 2001). For this reason, seasonal periods of food scarcity (more than global food availability) may shape chimpanzee grouping behavior. Along with food, the availability of surface water for drinking likely has an impact on chimpanzee APS and overall daily activities (McGrew et al., 1981). At sites where water is seasonally scarce, chimpanzees prefer to feed close to water (Lindshield et al., 2017) and may aggregate in larger parties at the few water sources remaining during the dry season (Tutin et al., 1983; Pruetz and Bertolani, 2009).

In addition to resource availability, the presence of sexually receptive females is consistently associated with greater APS across communities (Table 2). Female chimpanzees reproduce only every 5–6 years (Tutin and McGinnis, 1981; Nishida et al., 1990; Boesch and Boesch-Achermann, 2000) and are thus a limiting resource for males that aggregate around them during periods of sexual receptivity (Deschner et al., 2003). Female chimpanzees are most sexually receptive when they exhibit a maximal anogenital

swelling, which lasts for approximately 10–12 days (Goodall, 1986; Wallis, 1997), although they do attract males also when swellings are not at their maximal size (Tutin and McGinnis, 1981; Hasegawa and Hiraiwa-Hasegawa, 1983).

Additionally, predation is an important force that has long been discussed to shape primate group size (Alexander, 1974; van Schaik and Hörstermann, 1994) and understanding how individuals manage the risk of predation is a central issue in the study of primate grouping patterns (Aureli et al., 2008). The perception of predation risk by prey varies spatially, peaking in locations where predators experience increased hunting success (Willems and Hill, 2009). The landscape of fear hypothesis proposes that prey respond to spatially heterogenous risk by adapting their antipredatory behavior to the context of each location (Coleman and Hill, 2014). Increasing group size is an efficient antipredator strategy because larger groups exhibit enhanced vigilance, benefit from the dilution effect, and offer better defense mechanisms in case of a predator attack (Dunbar, 1988). As an illustration of this phenomenon, spider monkeys (Ateles belzebuth) increase APS when visiting mineral licks, probably because they face high predation risk in these areas (Link and Di Fiore, 2013).

Unfortunately, the effect of predation on chimpanzee APS remains largely understudied (but see Boesch, 1991), likely due to the rarity and difficulty of observing predation events on chimpanzees. Despite their relatively large body mass, chimpanzees suffer predation from leopards (*Panthera pardus*: Boesch, 1991; Zuberbühler and Jenny, 2002; Henschel et al., 2005; Nakazawa et al., 2013) and lions (*Panthera leo*: Tsukahara, 1993; Nishida, 2012). Wild dogs (*Lycaon pictus*) and hyenas are other potential predators (Stewart and Pruetz, 2013; McLester et al., 2016). In one of the only attempts to examine the impact of predation on chimpanzee party

Table 2

Factors tested for their impact on absolute party size at various field	d sites
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Community	Food availability ^a	Swollen females	Other	Source
Assirik	Rainfall NS ^b	Swollen females + ^c	Activity (largest when traveling)	Tutin et al. (1983)
			Vegetation (largest in open)	
Bossou		Swollen females +	Presence of danger +	Sakura (1994)
Bossou	Fruit availability NS	Swollen females +		Hockings et al. (2012)
Budongo (Sonso)	Food abundance NS		Patch size +	Newton-Fisher et al. (2000)
	Fruit abundance NS			
Budongo (Sonso)		Swollen females +		Wallis (2002)
Fongoli	Rainfall +			Pruetz and Bertolani (2009)
Gashaka-Gumti	Rainfall NS	Swollen females +		Sommer et al. (2004)
Gombe		Swollen females +		Wallis (2002)
Kahuzi-Biega	Fruit abundance NS			Basabose (2004)
	Fruit distribution +			
Kalinzu (M group)	Fruit abundance NS	Swollen females +		Hashimoto et al. (2001)
	Fruit distribution NS			
Kibale (Kanyawara)	Fruit abundance +			Chapman et al. (1995)
	Fruit distribution +			
Kibale (Ngogo)	Fruit availability NS	Swollen females +		Wakefield (2008)
Kibale (Ngogo)	Food availability + Rainfall NS	Swollen females +		Mitani et al. (2002)
Mahale (M-Group)	Fruit abundance +	Swollen females +		Matsumoto-Oda et al. (1998)
Mahale (M-Group)	Fruiting plant density +		Tree patch size +	Itoh and Nishida (2007)
Seringbara (Guinea)	Fruit availability +	Swollen females +		van Leeuwen et al. (2020b)
Taï (North)	Fruit availability +		Predation pressure -	Boesch (1991)
Taï (North)	Fruit availability +	Swollen females +	Activity NS	Boesch (1996)
			DBH +	
			Hunting rate +	
Taï (North)	Rainfall +			Doran et al. (1997)
Taï (North)	Fruit abundance NS	Swollen females +	Activity of focal animal (largest when meat eating)	Anderson et al. (2002)
	Fruit distribution NS		Day time (largest early morning and late afternoon)	
Taï (East and South)	Fruit availability NS	Swollen females +	Group defense score + Territorial activity +	Samuni et al. (2020)

^a Different estimations of food availability have been used depending on the study. We included rainfall as a variable in this column as it is often used as a proxy for food availability.

^b NS = nonsignificant (p > 0.05) correlation between party size and the mentioned variable.

c + = positive correlation between party size and the mentioned variable.

size, Boesch (1991) found that Taï chimpanzees in the Ivory Coast surprisingly decreased APS in response to increased predation pressure (defined as the number of leopard encounters per month). The author suggested that, in the very dense Taï forest, large parties may be very noisy and easily detectable by leopards, making smaller parties one antipredator strategy in this habitat.

While predation from carnivores likely influences chimpanzee APS in ways that have not been systematically studied, humans, as well as neighboring chimpanzee communities, also affect grouping patterns. Similar to predator attacks, human-ape confrontations (Boesch and Boesch-Achermann, 2000) as well as chimpanzee intergroup conflicts (Wilson et al., 2014) may lead to severe injuries and/or death in chimpanzees. In general, carnivores, humans, and neighboring communities may all be perceived as danger for chimpanzees and may elicit similar grouping pattern responses. For instance, chimpanzees at Bossou (Guinea) and at Fongoli (Sénégal) enter anthropogenic areas (such as roads and cultivated fields) in larger parties (Sakura, 1994; Hockings et al., 2012; Lindshield et al., 2017). In the case of intercommunity encounters, larger parties are favorable, with most intercommunity killings occurring when attackers overwhelmingly outnumber their victims (Wilson et al., 2014). As an illustration of this, Taï chimpanzees form larger parties during months when individuals participate in territorial activities (i.e., border patrol and intergroup encounters, Samuni et al., 2020) and at Kanyawara (Kibale, Uganda), APS was larger when parties were close to the home range edges as compared with core areas (Wilson, 2001).

1.3. Chimpanzees as referential models for early hominin behavior

Understanding how spatiotemporal fluctuations in various biotic and abiotic factors shape chimpanzee grouping patterns sheds light on what challenges a community might experience (intergroup encounters, predation, variation in resource availability, etc.) and also has bearing on reconstructions of hominin evolution (Grueter et al., 2012). Given their close genetic relationship to humans (Cheng et al., 2005) and morphological similarity to australopithecines (e.g., Berger and Tobias, 1996), common chimpanzees are frequently used as referential models to understand human evolution (e.g., Wrangham, 1987; Moore, 1996, DeSilva, 2009; Prang et al., 2021 but see Sayers and Lovejoy, 2008). Various authors have argued that ancestral hominin species were most likely characterized by a chimpanzee-like fission-fusion society with a polygynandrous mating system, large numbers of bonded males, and immigrant females (Wrangham, 1987; Chapais, 2010; van Schaik, 2016).

Most studies of wild chimpanzees to date have focused on forest-dwelling populations (Boesch, 2009), whereas extant chimpanzees live across a gradient of habitats from tropical rainforests to open and dry, savannas (van Leeuwen et al., 2020a). Investigation of the latter allows us to ask questions that are more ecologically relevant to Plio-Pleistocene hominin evolution, which largely occurred in similarly open and dry savanna-mosaic environments (Davies et al., 2020). A major climatic shift occurred during the late Pliocene (~3.0–2.6 Ma) resulting in a concomitant transition from closed canopy forests toward more open and dry habitats (Robinson et al., 2017). Specifically, reconstructions of post climatic shifts in Plio-Pleistocene environments describe a combination of woodlands, bushlands, riparian forests, and seasonal flood plains that were characterized by high seasonality in rainfall (Reed and Fish, 2005; Cerling et al., 2011), a landscape very similar to that of some extant chimpanzee communities, such as Issa (Tanzania) and Fongoli. Constraints associated with a heterogenous and seasonal environment were a major challenge faced by Plio-Pleistocene hominins (Foley, 1993; Cerling et al., 2011), and it has been

hypothesized that their adaptation and response to such constraints formed the basis for the divergence of the hominin lineage (Potts, 2013). Understanding the grouping strategies of one of our closest living relatives potentially facing similar environmental constraints as early hominins did can help us better identify the patterns involved in human evolutionary adaptations to these environments.

1.4. Savanna woodlands as current habitats for chimpanzees

Chimpanzee habitats have long been dichotomized as being either savanna or forest dwelling (reviewed in the study by van Leeuwen et al., 2020a). The former (also described as open and dry landscapes) have historically been classified as savannas despite often comprising a heterogenous mosaic of woodlands, grasslands, swamps, and closed-canopy evergreen forests (Bourliere and Hadley, 1983). These sites are regularly described as marginal for chimpanzees compared with more forested sites (Kortlandt, 1983; Moore, 1992; Pruetz and Bertolani, 2009) as they tend to receive less than 1360 mm of annual rainfall (van Leeuwen et al., 2020a) and exhibit long dry seasons (defined as the number of consecutive months having less than 100 mm of rainfall; Hunt and McGrew, 2002) that result in dramatic seasonal fluctuations in food and water availability (e.g., Pruetz, 2006). Forest-dwelling chimpanzees also face seasonality, but the magnitude of seasonal variation in climate and food availability is comparatively moderate (Wessling et al., 2018a). Drier areas (hereafter referred to as 'savanna' sites) also have lower forest cover (<12.5%; van Leeuwen et al., 2020a) with lower tree diversity (Crowther et al., 2015) and thus fewer chimpanzee feeding trees (in number and species diversity) than forested environments (Isbell and Young, 1996; Potts and Lwanga, 2014; Wessling et al., 2020). In a comparative study between Fongoli and Taï chimpanzees, Wessling et al. (2018a) found that total food availability was lower year-round at Fongoli, but ripe fruit availability was higher. Finally, predation pressure and risk is proposed to be higher in savanna sites because they host greater predator diversity and fewer escape opportunities than forests (Tutin et al., 1983).

Early studies of chimpanzees living in these landscapes hypothesized that they would show variation in their sociality compared with forest-dwelling communities as a response to the 'extreme' environment (Suzuki, 1969; Izawa, 1970; Kano, 1971; Kortlandt, 1983; Tutin et al., 1983; Moore, 1996). They may be more cohesive (i.e., larger RPS) than forest-dwelling communities as a way to cope with predation (Tutin et al., 1983). The first (and only to date) results that described APS and RPS in a savanna community came from Fongoli, where Pruetz and Bertolani (2009) found that both APS and RPS were higher than what has been reported in other communities, which may be a savanna adaptation. In that study, the authors defined party as all individuals observed on a given day (i.e., nomadic party size), which is demonstrated to overestimate APS compared with other methods (Chapman et al., 1994). However, even after reducing their estimates by 40% (as suggested by Chapman et al., 1994), RPS at Fongoli (26%) was still larger than most reported values from other communities (Table 2). Unfortunately, no thorough examination of factors (e.g., fluctuations in food and water availability, predation risk, etc.) potentially influencing party size at this site was made and only seasonal trends (dry vs. wet season) were reported.

It may not just be habitat that influences RPS. Studies from the forest-dwelling communities of Taï and Bossou revealed that chimpanzees were also highly cohesive (Boesch, 1996; Anderson et al., 2002; Hockings et al., 2012; Wittiger and Boesch, 2013; Bryson-Morrison et al., 2017), especially when compared with the East African chimpanzee (*Pan troglodytes schweinfurthii*)

communities of Gombe and Mahale (Tanzania) and Budongo (Uganda). Rather than cohesion being a response to the local habitat, it was suggested that increased cohesion could be specific to the western subspecies (*Pan troglodytes verus*; Boesch, 1996) and that West African communities may be intermediate between the high degree of cohesion observed in bonobos (*P. paniscus*) and lower degree seen in East African chimpanzees (e.g., Yamakoshi, 2004).

1.5. Study aims, research questions, and hypotheses

We lack data from additional savanna sites and especially from East African communities to disentangle the drivers of community cohesiveness and identify if a clear distinction between forest versus savanna and/or eastern versus western (species) grouping patterns can be made. Furthermore, investigation into chimpanzees that experience an open and dry landscape can shed light on how early hominins may have adapted to similar constraints. For instance, savanna sites are more likely to show great seasonal fluctuations in resources, such as water, that are likely to influence grouping patterns in ways that have not yet been explored. Finally, if grouping patterns are a response to predation, we stand to gain most by asking these questions in places where predators have not been extirpated, as they have largely been in Fongoli (Stewart and Pruetz, 2013).

To that end, in the current study we examined grouping patterns of a chimpanzee community living in the Issa Valley, located ~100 km east of the eastern shore of Lake Tanganyika, western Tanzania (see Fig. 1 for study site map). The Issa landscape is a combination of heterogenous vegetation where forest represents only 7% of vegetation cover. The region receives lower annual rainfall than the majority of chimpanzee sites and is characterized by an extensive dry season (see Methods for detailed site characteristics). We addressed the following questions:

- (1) What are the factors shaping chimpanzee APS at Issa?
- (2) How does RPS in the Issa community compare to other chimpanzee communities?

We hypothesized that APS would be significantly influenced by four key predictors: food availability, the presence of sexually receptive females, vegetation structure, and water availability. Considering the seasonality in rainfall and potential associated fluctuations in food availability at Issa, we expected that APS would be positively correlated with food availability with significantly smaller parties during periods of low food availability. We also expected the presence of swollen females to play a significant role in explaining APS at Issa, with larger parties in the presence of swollen females, similar to other communities. Given the presence of predators (see later part of the article) and the heterogeneity of the vegetation at Issa, we expected chimpanzees to adjust their APS to perceived predation risk in the different vegetation structures. We expected parties to be significantly larger in open vegetation as a strategy to confront potentially higher predation risk in areas that offer fewer escape routes than in closed vegetation. We further expected water availability to have an impact on APS at Issa with significantly larger parties during periods of low water availability owing to individuals aggregating around water sources. Finally, we expected that the Issa community will be highly cohesive (i.e., high mean RPS) similar to what has been described at Fongoli, and in contrast to forested sites, rather than expecting less cohesion at Issa owing to previously hypothesized subspecies differences in sociality.

2. Materials and methods

2.1. The Issa study site

The Issa study site is comprised of five major valleys separated by steep mountains and flat plateaus ranging from 1150 m to 1800 m above sea level (Piel et al., 2017). Vegetation is dominated by deciduous miombo woodland, named for the dominant tree genera of *Brachystegia* and *Julbernardia*, interspersed by thin strips of evergreen riparian forest (7% landcover), small patches of seasonally inundated grasslands, and rocky outcrops. There are two distinct seasons at Issa: a wet season starting in November and an extended 6-month dry season from May until the end of October. Precipitation at Issa averages 1220 mm per annum, and the annual mean temperature is 23 °C (Piel et al., 2017). Although direct measures of predator density have not been made, Issa chimpanzees are one of only two known chimpanzee communities that live sympatrically with leopards, lions, hyenas, and wild dogs (Tutin et al., 1981; McLester et al., 2016; Piel et al., 2018.



Figure 1. Chimpanzee (*Pan troglodytes*) distribution (in yellow), with Issa (in Tanzania) study area (black callout boxes). Modified from the study by Humle et al. (2016). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

2.2. The Issa community

We collected data on the Issa community between May 2018 and May 2019. When data collection began, the Issa community was comprised of 26 individual chimpanzees: eight adult females, seven adult males, three subadult males, five juveniles, and three infants. Given that the community was fully habituated only in the beginning of 2018 (when individual males and females could be followed from morning to nightly nest and from within <15 m), we do not have birth records and exact age information of community members; we thus estimated ages and classified them into the following categories: adult: >11 years, adolescent: 8-11 years, juvenile: 4-7 years, infant: 0-4 years (following Sugiyama, 1999). One subadult female joined the community in October 2018, one adult female disappeared in January 2019, and an adult female gave birth in March 2019. The Issa community home range was 36 km² at the time of study (based on minimum convex polygon methods; Giuliano, unpublished data).

2.3. Data collection

Food availability We calculated a food availability index (FAIe) based on the 10 most important plant food items in the Issa chimpanzee diet (see Supplementary Online Material [SOM] for methodological details and SOM Table S1 for a list of preferred food items). We chose to focus only on the most frequently consumed items because some rarely consumed species are overly represented in the Issa landscape (e.g., Brachystegia microphylla: basal area: 2.8 m² per ha versus 0.26% of total diet), which would have overestimated food availability during months when these species are in season. From 2013 to 2019, we botanically sampled 306 20 \times 20-m plots across the study site (n = 204 forest plots; n = 100 woodland plots; n = 2 swampplots). Plots were randomly sampled inside each vegetation category, that is, forest, woodland, and swamp. We identified all stems >10 cm to species level and recorded the number of stems for each plant species and diameter at breast height (DBH) of each stem. We calculated a mean DBH for each species. We obtained species density estimates in each vegetation category and extrapolated species density (D_s) over the study area based on the percentage cover of each vegetation category, that is, evergreen forest 7%, woodland 85%, and swamp 8% cover (data extracted from satellite image analysis). We followed Basabose (2004) and calculated global basal area (BA_s) for each species s

using the formula: $BA_s = \left(\frac{1}{2} \times DBH_s\right)$

$$(\text{DBH}_{s})^{2} \times \pi \times D_{s}$$
. On a monthly

basis, we monitored phenological changes in the top ten feeding items on 288 trees inside the chimpanzee territory using phenological trails. We scored the percent abundance (0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%) of each item in the crown of individual trees. We followed Knott (2005) suggestion and included item nutritional value in our calculation of monthly FAIe by collecting, drying, weighing, and assessing gross energy in each item using a bomb calorimeter (see SOM Table S1 for details). We calculated FAIe based on the top ten feeding items using the following formula:

$$FAIe_m = \sum_{1}^{10} P_{ism} \times BA_{si} \times M_i \times E_i$$

where P_{im} denotes the mean abundance of item *i* on species *s* in month *m*, *BA*_{*si*} represents the total basal area per hectare (ha) for the species *s* to which the item *i* belongs, M_i represents the average

dry mass for item i, and E_i represents the average energy per gram of dry mass for item i.

<u>Water availability</u> We used the water availability index (WAI) described in the study by Wessling et al. (2018b), and each month monitored the depths (at the deepest point) of eight water sources that can be considered representative of water availability in the Issa community home range. The WAI for each month was calculated using the following equation:

$$WAI_m = \sum_{1}^{8} \frac{Depth_{im}}{Depth_{max[i]}}$$

where ($Depth_{im}$) denotes the depth of source *i* for month *m* and $Depth_{max[i]}$ the maximum observed depth for source *i*. The WAI ranges from zero (no standing ground water available) to one (maximum standing water available).

Party follows We looked for and followed chimpanzee parties on average 20 days/month and attempted nest-to-nest follows. We performed group follows and recorded APS, defined as the number of adult and subadult individuals that were seen every hour (Chapman et al., 1995; Doran, 1997). For each 1-hour party. we documented the number of sexually receptive females present in the party. We defined sexually receptive females as females that exhibited an anogenital swelling, regardless of the swelling size (following Wallis, 2002; van Leeuwen et al., 2020b) because given the very recent habituation of the chimpanzees at the time, we did not have data on intracycle and interindividual variation and so could not define with certainty full anogenital swellings. We assigned parties a score of 0 or 1 depending on the presence or absence of at least one swollen female. We classified vegetation structure into two categories-open (comprised of woodland and grasslands) and closed (riparian evergreen forest)—and recorded the vegetation structure in which the party was followed for each 1-hour scan. If a party was dispersed across the two vegetation structures, we recorded the vegetation structure in which the majority of individuals were found. Over the study period, we gathered 816 1-hour scans for which all these data were available.

2.4. Data analyses

We performed all statistical analyses in R v. 3.4.0 (R Core Team, 2017) and set the significance level alpha at 0.05.

Party size model To investigate the factors influencing APS, we fit a generalized linear mixed model (GLMM; Baayen, 2008) using the function 'glmer' of the package 'lme4' (Bates et al., 2015) with Poisson error structure. In this model, we tested the effects of 1) FAIe, 2) the presence of swollen females, 3) vegetation structure, and 4) WAI, on the response variable: 1-hour-APS (n = 816). In addition, we included an interaction between the FAIe and the presence of swollen females to test the influence of the presence of swollen females on APS depending on food availability. To account for seasonality in APS, we included a seasonal term as a control predictor represented by both sine and cosine of Julian date (divided by 365.25 and then multiplied by 2π ; Stolwijk et al., 1999; Wessling et al., 2018b) to which the data correspond. This seasonal term assumes regular periodicity in a single annual cycle. We also added time of day as a control predictor to account for any potential diurnal effects on APS. We included observer identities (n = 24) as a random effect. Because consecutive scans were likely to occur under more similar social or ecological conditions, the response variable (APS) was likely to show temporal autocorrelation unexplained by the fixed effects included in the model. This may lead to a violation of the

assumption of independent residuals (i.e., neighboring residuals being more similar than more distant ones). Therefore, we incorporated a temporal autocorrelation term into the APS model by first running the model as described earlier (with all fixed and random effects included) to retrieve the residuals. We then calculated a temporal 'autocorrelation term' for each data point, which was the weighted mean of all other residuals, with the weight equaling the inverse number of minutes between each respective data point and the residuals (as described in the study by, e.g., Furtbauer et al., 2011). The weighting function followed a normal distribution. We then included the 'autocorrelation term' as an additional control factor into the model.

We checked for the assumptions of normally distributed and homogenous residuals by visually inspecting q-q plots and the residuals plotted against fitted values and found no violations. We checked for model stability by excluding each level of the random effect one at a time and comparing the estimates derived from these data sets with those derived for the full data set and found that the model was sufficiently stable. Variance inflation factors were derived using the 'vif' function of the 'car' package (Fox and Weisberg, 2011) based on a standard linear model excluding the random effect, and no collinearity issues were found. Before interpreting the results of the model, we first determined the significance of the full model (including all predictors and the random effect) as compared with the corresponding null model (including only the control predictors and the random effects) with a likelihood ratio test (Dobson, 2002) using the R function 'anova.' We measured the statistical significance of each predictor using likelihood ratio tests comparing the full model with the respective reduced model (full model without the predictor). Because the interaction between the FAIe and the presence of swollen females was not significant, we removed it and re-ran the model without the interaction term.

<u>Mean absolute party size and relative party size</u> We first calculated the annual mean for daily APS (daily mean of 1-hour-APS values) and then computed an annual mean for daily RPS (daily APS/community size [only independent individuals] \times 100; Boesch, 1996). This second measure gave us a proxy for community cohesion, that is, the average proportion of the community that was found together. Both calculations were derived from data collected between June 2018 and May 2019. We compared these values to other long-term study sites where these data are available.

3. Results

3.1. Predictors of absolute party size

Absolute party size showed pronounced fluctuations (mean \pm SD = 6.6 \pm 4.3, range = 1–19) during the study period, with a monthly minimum of 1.5 (SD = 0.7) in May 2018 and a maximum of 9.7 (SD = 3.9) in September 2018 (Fig. 2). Monthly FAIe varied substantially as well (mean \pm SD = 336,832 \pm 456,750, range = 2493–1538781). We observed a peak in food availability in November 2018, and there were two periods of very low food availability: May–July 2018 and January–March 2019 (Fig. 2). The WAI (mean \pm SD = 0.7 \pm 0.2, range = 0.2–0.9) was highest in February 2019 and lowest at the end of the dry season in October 2018 (Fig. 2). Although water was scarce and/or stagnant in some areas of the home range in October, it remained available and flowing at the majority of the points where we measured the WAI.

The APS full null model comparison was significant (likelihood ratio test: $\chi^2 = 373.8$, df = 4, p < 0.001). We found that APS significantly increased with food availability (Table 3) and with the presence of swollen females (Table 3; Fig. 3). Moreover, we found larger parties in open vegetation (Table 3; Fig. 3). However, APS was not influenced by water availability (Table 3).

3.2. Mean absolute party size and relative party size

Issa chimpanzee annual averages of daily APS and RPS were 5.5 (SD = 3.55) and 30.3% (SD = 19.3), respectively, during the study period.

4. Discussion

In this study, we investigated APS and RPS in chimpanzees from the Issa Valley. Our study is the first to test the impact of water availability and vegetation structure on chimpanzee party size and



Figure 2. Fluctuations in Issa chimpanzee monthly absolute party size (APS; black dots are monthly means, bars represent monthly standard deviations), top 10 food availability index (FAIe; in yellow), and water availability index (WAI; in blue) during the study period (May 2018–May 2019). Absolute party size is significantly (*p* < 0.001) correlated with the FAIe but not with the WAI. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

Table 3

Generalized linear mixed model testing the effect of monthly food availability index, the presence of swollen females, vegetation structure, and monthly water availability index on absolute party size.^{a,b}

Term	Coded level	Estimate ± SE	χ^2	<i>p</i> -value
(Intercept)		1.287 ± 0.068	_	-
Test predictors				
Food availability index (FAIe) ^c		0.160 ± 0.028	33.890	<0.001
Swollen females ^d	Presence	0.571 ± 0.035	274.500	<0.001
Vegetation structure ^d	Open	0.063 ± 0.030	4.239	0.039
Water availability index (WAI) ^c		0.036 ± 0.045	0.650	0.420
Control predictors				
Temporal autocorrelation term		0.305 ± 0.014	487.760	<0.001
Cosine (Julian date)		0.032 ± 0.041	1.570	0.456 ^e
Sine (Julian date)		-0.060 ± 0.063		
Time of the day ^c		0.824 ± 0.015	30.594	<0.001

^a Results correspond to a reduced model not including the interaction between FAIe and swollen females (see text).

^b n = 816 scans. Statistically significant results (p < 0.05) appear in bold. Observer ID (n = 24) was included as a random factor.

^c Z-transformed to a mean of 0 and a standard deviation of 1. Original means \pm SD of the original variable: FAIe = 498,357 \pm 523,197; WAI: 0.94 \pm 0.35; time of the day = 394.52 \pm 188.69.

d Estimate refers to the comparison between the categories in the table and the reference categories; Swollen females = absence; Vegetation structure = closed.

^e Indicated is the overall test of the significance of season as obtained from comparing the full model with a reduced model lacking the two terms representing season.

to provide an analysis of APS determinants from direct observations of an East African community at a savanna site. Additionally, by investigating RPS at Issa, we are able to shed light on two competing explanations—phylogeny and ecology—on community cohesion. Here we compare our results with findings from other field sites and discuss the implications for hominin evolution.

4.1. Predictors of absolute party size

We found that APS varied monthly and was influenced by food availability, swollen females, and vegetation structure. Absolute party size was positively correlated with food availability, with mean party size dramatically lower from May–July 2018 and again from January–February 2019 (Fig. 2) when food availability was the lowest. Similar to Kanyawara chimpanzees (Kibale; Chapman et al., 1995), M-group (Mahale; Matsumoto-Oda et al., 1998; Itoh and Nishida, 2007), and Taï (Boesch, 1991,

1996), Issa chimpanzees divided into small parties when food was scarce, likely to reduce intragroup feeding competition. Conversely, by reuniting when food was abundant, they were able to gain the benefits of sociality when the costs of doing so were likely minimal. In communities where food may be abundant year-round, APS is not correlated with food availability (e.g., Sonso: Newton-Fisher et al., 2000; Ngogo: Wakefield, 2008; Bossou: Hockings et al., 2012). We could not assess whether food availability at Issa is lower (at least seasonally) than at these sites because intersite comparisons of all feeding species productivity were not possible (due, for example, to intersite differences in diet preferences, in the availability of species on which to feed, as well as difficulties in replicating the same methodology in contrasting landscapes, etc.). However, there are some indications that food availability may be lower at Issa. For example, when looking at Ficus fruit, a staple, important food source for chimpanzees (Wrangham et al., 1993), we noted that Ficus tree density



Figure 3. Chimpanzee absolute party size (APS) at Issa (n = 816 data points) is significantly larger a) in the presence of swollen females (p < 0.001) and b) in open vegetation (p = 0.039). Shown are medians (horizontal lines), quartiles (boxes), and percentiles (2.5% and 97.5%; vertical lines).

at Issa was much lower (0.33 stems/ha; Giuliano, unpublished data) than at Ngogo (4.1 stems/ha; Emery Thompson et al., 2007). Our results suggest that food at Issa might not be as abundant as in certain communities (e.g., Ngogo) and that chimpanzees may use flexibility in their grouping patterns to adapt to the seasonal fluctuations in food availability. Intersite comparisons of food productivity (e.g., Chapman et al., 1999), particularly between starkly contrasting landscapes with disparate vegetation profiles and food species, may shed light on the causes of population-level variability in the relationship between food availability and chimpanzee party size.

The presence of swollen females also had a positive effect on APS. This relationship has been described for numerous communities (see Table 2). Owing to the very long interbirth interval that characterizes chimpanzees (i.e., 5–6 years; Sugiyama, 1994; Wallis, 1997), females are sexually receptive during only 6.4% of their adult life (refer to the study by Furuichi, 2006 for detailed calculation), which offers very few opportunities for males to reproduce. Because sexually receptive females are a limited resource (at Issa and elsewhere), males aggregate around them and compete for mating opportunities. It is advantageous for Issa males to join parties with swollen females as it has been shown at other field sites (see Table 2). We could not define full anogenital swellings with certainty and had to consider all females that exhibited an anogenital swelling (regardless of swelling size) to be sexually receptive. However, studies at other sites revealed that males are more attracted to fully swollen females than partially swollen ones (e.g., Deschner et al., 2004) and parous females over nulliparous (Muller et al., 2006). Also, even within the traditionally defined maximum swelling period, slight variations of swelling size occur, and male behavior closely follows these subtle changes (Deschner et al., 2004). In the future, data on individual Issa female swelling patterns will allow us to refine our understanding of the relationship between female swelling size and party size at Issa. Although periodicity in the occurrence of sexual swellings within the community was beyond the scope of this study, female swellings at Issa seem to be highly seasonal (Giuliano, unpublished data) and may themselves be influenced by food availability and/or diet quality as is the case in other communities (Wallis, 2002; Anderson et al., 2006; Emery Thompson and Wrangham, 2008). Preliminary results at Issa (Giuliano, unpublished data) suggest that female sexual swellings might be positively correlated with the ingestion of leaves (and particularly young leaves of Pterocarpus tinctorius). Future investigation of the diet of cycling females and detailed phytochemical analysis of Pt. tinctorius (among others) may provide a better understanding of the determinants of seasonality in female reproductive ecology at Issa and, indirectly, grouping patterns and their fluctuations.

We found that vegetation structure had an impact on APS with parties in open vegetation being larger than those in closed vegetation. This is consistent with studies on chimpanzees from Mt. Assirik (Tutin et al., 1983), but also on another primate species, that is, spider monkeys from western Amazonia (Link and Di Fiore, 2013) that exhibit larger subgroup size in open vegetation. Issa chimpanzees regularly traveled between closed and open vegetation and spent more than 50% of their time in the latter (Giuliano, unpublished data). The predators at Issa are known to use both closed and open vegetation. We do not have data on predators' hunting success across vegetation at Issa and thus are unable to calculate a direct measure of predation risk. Instead, we used vegetation structure as a proxy for estimating this risk with open areas considered higher risk for chimpanzees. Although woodland trees constitute temporary refuges, lower canopy connection in open vegetation likely reduces escape routes for chimpanzees from predators (Stewart and Pruetz, 2013) and thus results in a landscape of fear (Coleman and Hill, 2014). The predator avoidance hypotheses suggest that collective predator detection, defense against predators, and dilution of predation risk should increase with larger subgroup size (Wrangham, 1986). Assuming that open areas are associated with a higher predation risk, our results suggest that, at Issa, larger parties in open vegetation might be one antipredation strategy. This contrasts with patterns observed in the Taï forest where chimpanzees decrease APS as a response to high predation pressure (Boesch, 1991). Such difference may be due to the very dense nature of the Taï forest, which reduces early predator detection and makes large parties more conspicuous when moving through the vegetation (Boesch, 1991).

Our results provide grounds for future finer scale analyses into the spatial distribution of predation risk at Issa. For example, while predator relative abundance could be extracted from camera trap footage (Gerber et al., 2010), future work could also assess vigilance rates and travel speed as indirect metrics of fear perception (Laundré et al., 2010). Furthermore, the presence of predators inside the territory of Issa chimpanzees may vary temporally and affect chimpanzee party size inconsistently throughout the year. Subsequent studies that systematically and accurately account for spatiotemporal patterns of large carnivore presence may confirm the hypothesis of increased perceived predation risk in open vegetation and resolve the role of large party sizes as an antipredation strategy at Issa.

Similar to party size, chimpanzee party composition may vary with party location. Male chimpanzees at Bossou, for instance, are more willing to enter crop fields than are females (Hockings et al., 2012) and lone or mother parties at Mt. Assirik were less frequently observed in open areas than other types of parties (Tutin et al., 1983). Future investigation of Issa chimpanzee party composition with respect to vegetation structure and predation risk will complement our findings on party size.

While predation risk may shape APS at Issa, risk may also come from anthropogenic sources. Humans (often accompanied by domestic dogs) are known to use the area for logging, cattle herding, and poaching (Piel et al., 2015). A recent encounter with domestic dogs resulted in the death of two Issa community members (a chimpanzee mother and her infant; Piel and Stewart, 2019). If Issa chimpanzees perceive humans (and their domestic dogs) as a threat, we would expect grouping patterns to reflect that, with larger parties near areas with the highest rates of human encounters. There are no villages within 10 km of the Issa chimpanzee home range, but there are known paths used by humans and there are seasons where humans seem to occur more frequently within the area (Giuliano, pers. observ.). Subsequent studies could address chimpanzee grouping patterns in response to spatiotemporal variations in human presence. An alternative explanation as to why subgroup size at Issa is greater in open areas than in closed areas is methodological. Owing to reduced visibility in closed forest, party size could have been underestimated. However, to minimize risk of underestimating party size, a minimum of two researchers (often placed at two extremities of the party) synchronized data on party size and composition through two-way radios.

Finally, although water availability has been suggested to play an important role in shaping grouping patterns at sites described as savannas, such as Mt. Assirik (Tutin et al., 1983) and Fongoli (Pruetz and Bertolani, 2009), it did not significantly impact APS at Issa where water remained flowing and available during the entire study period. The Senegalese sites are drier and hotter than Issa (van Leeuwen et al., 2020a) and characterized by periods of water scarcity with only a few sparsely dispersed waterholes remaining in the late dry season (McGrew et al., 1981; Pruetz, 2006), which may force chimpanzees to aggregate around these sources. Although sites with low forest cover such as Issa are always described as dry and challenging for chimpanzees in term of water acquisition, our results suggest that water availability did not impact grouping behavior at Issa, even in the late dry season. These findings support the suggestion of van Leeuwen et al. (2020a) to refine our description of chimpanzee sites along with the environmental variables that characterize them rather than just assuming that savanna sites necessarily impose greater challenges (such as dehydration) than forest sites.

4.2. Community size and cohesion

Although APS showed large fluctuations and was lower on average during months of low food availability, we found that the annual mean was similar to other sites and that the Issa community was more cohesive overall (measured by mean RPS; 30.3%) compared with the majority of communities studied elsewhere (Table 1). High RPS was also reported at Fongoli (42.9%; Pruetz and Bertolani, 2009; or 26.0% after methodological bias correction), Taï (32.4%; Anderson et al., 2002), and Bossou (52.3%; Bryson-Morrison et al., 2017). Two studies conducted in M-group at Mahale (Matsumoto-Oda et al., 1998; Itoh and Nishida, 2007) also revealed high mean RPS (28.9% and 47.0%; see Table 1), but these values resulted from the use of a method known to overestimate party size (i.e., nomadic party) and were lower when using another method (i.e., 1-min scan: 12.1%, Itoh and Nishida, 2007). Our results provide the first evidence of increased community cohesion in an East African community and counter the hypothesis that high cohesion is specific to the western subspecies (P. t. verus).

While average APS is roughly similar across all chimpanzee communities, demography, and especially community size, may strongly influence cohesion (Lehmann and Boesch, 2004). The communities that exhibit the highest RPS values have in common a small community size (Issa = 26; Fongoli = 35; Taï North = 31; Bossou < 20) compared with other communities (e.g., Kanyawara = 55; Ngogo = 145; Sonso = 71; Mahale = 85; Table 1). Difference in community size may be explained by intersite variability in total food availability, for instance (Potts et al., 2011), but future studies should investigate in more detail the influences of community size at Issa and elsewhere.

Regardless of high RPS being a possible mathematical artifact of small community size, there are potential benefits for individuals spending more time together, independent of community size. For example, this allows for the development of very strong social bonds (through grooming for instance; Lehmann et al., 2007b). Individuals that are strongly bonded can also more easily rely on each other (Dunbar, 1991; Hemelrijk and Ek, 1991; Wittig et al., 2014), which may increase the effectiveness of defensive behavior against threats, either neighboring communities or predators. Among other species, crested macaques (Macaca nigra) and dwarf mongooses (Helogale parvula), for instance, individuals respond more strongly to recruitment alarm calls (i.e., calls eliciting cooperative mobbing behavior) if they share strong social bonds with the caller (Micheletta et al., 2012; Kern and Radford, 2016). Also, male chimpanzees prefer to patrol with partners with whom they have developed strong social bonds and on whom they can rely during agonistic intergroup encounters (Watts and Mitani, 2001). Additionally, modern humans are well known to intensify social bonds in risky situations, such as between soldiers in active warzones where relationship strength is argued to play an important role in combat effectiveness (Wong et al., 2003).

Although the formation of large communities among mammals provides defense mechanisms against danger (Krause and Ruxton, 2002), a small community size could also be an efficient strategy to face threats through the facilitation of strong social bonds. Social relationships among primates require complex cognitive capacities such as individual recognition or record of previous interactions with a given partner (Barrett et al., 2000), and they become exponentially demanding with increasing group size (Dunbar and Shultz, 2007). A study on Trinidadian guppies (Poecilia reticulata) revealed that under high perceived predation risk, individuals formed smaller shoals and developed stable and more differentiated social ties, interpreted as the consequence of a conflict between forming stable social relationships and larger social groups (Heathcote et al., 2017). The authors suggested that, in species where social bonds have a functional role in antipredatory response, there is a trade-off between group size and relationship quality between group members (Heathcote et al., 2017). Accordingly, the small community size (and high RPS at Issa and elsewhere) could be an advantage in defense against dangers (predators, neighboring communities, or humans), a hypothesis that remains to be directly tested. In the current study, we could not calculate an intergroup encounter rate or a predator density and compare them to other sites to test whether they are higher than elsewhere. Data collected in the coming years, at Issa and across communities of varying sizes, on predation pressure and intergroup encounter rates may elucidate the influence of these variables on chimpanzee grouping behavior and especially on high cohesion in small communities.

4.3. Implications for hominin evolution

Large carnivore diversity was greater in Africa's past than it is today, and Plio-Pleistocene hominins coexisted with large predators such as Acinonyx, Chasmaporthetes, Parahyaena, Pliocrocuta, Megantereon, and Dinofelis (Turner and Anton, 1997; Werdelin and Lewis, 2005). Associations of fossil hominins with remains of these carnivores indicate sympatry for millions of years (6.0–1.8 Ma) in habitats reconstructed as a mixture of woodlands and open grasslands (Cooke, 1991; Keyser, 1991; Brain, 1994; Brantingham, 1998a), and several authors agree that predation was a serious threat for early hominins (e.g., Treves and Naughton-Treves, 1999; Lee-Thorp et al., 2000). Predation has shaped human evolution (Brain, 1981; Isbell, 1994; Brantingham, 1998b), whereas hominin antipredator behavior remains a puzzle. Some have suggested that material culture such as fire and weaponry were the main deterrents used to reduce predation pressure (Kortlandt, 1980; Brain, 1981). However, others have proposed that a social adaptation to high predation pressure preceded any elaboration of material culture (Treves and Palmqvist, 2007). While chimpanzees are sometimes used as referential models for hominins because of their genetic and morphological similarities with humans (Cheng et al., 2005), most studies to date have relied on data from forest-dwelling communities, where local environmental conditions differ from the likely environment in which early hominins evolved. These conditions have important bearing on how we interpret the implications for hominins.

Our study does not dispute the pattern found at Taï, with inversely related party size and predation pressure; instead, we offer a different antipredator scenario for what might be driving grouping patterns in chimpanzees, especially those that spend large proportions of their time in open vegetation. We propose that one possible antipredator strategy for hominins could have been to establish small, cohesive communities that form (when food availability allows) larger parties in open areas where individuals are vulnerable to terrestrial carnivore predation. This agrees with the hypothesis developed by Treves and Palmqvist (2007), who predicted that early hominin foraging parties would have adopted a more cohesive social organization with groups formed of trusted and familiar members who cooperate in antipredator behavior. The ability to develop increasingly complex, strong, and stable social bonds in response to very high predation pressure while covering a highly heterogenous and seasonal open territory might have catalyzed hominin-chimpanzee differentiation (Grueter et al., 2012; Grove and Dunbar, 2015). Derived features of human sociality such as language, intense cooperation, prosociality, and cultural transmission might have followed (Dunbar, 1996) and allowed hominins to colonize nearly all parts of the world (Grove et al., 2012). This theory remains to be tested, and other studies on chimpanzees living in open environments, particularly their social strategies in the face of predators (and other sources of danger), may improve not only our understanding of the drivers of chimpanzee behavioral variability (Kalan et al., 2020) but also hominin social evolution.

5. Conclusions

Our model suggested that APS at Issa 1) follows seasonal fluctuations in food availability, 2) increases in the presence of swollen females, and 3) is higher in open areas, which are potentially risky. We found the Issa community to be highly cohesive compared with other communities, possibly due to a combination of its small size and the potential threats (neighboring communities, predators) characterizing its home range. Comparison of chimpanzees in widely differing habitats can shed light on the sources and functions of variability in chimpanzee behavior. Our study fills a gap in our knowledge of chimpanzee sociality by exploring the determinants of grouping patterns in an understudied biome in East Africa and highlights the elements of early hominin social behavior that may have evolved in late Pliocene landscapes. We stress the need for additional data from other communities, but especially those with rich predator guilds in open landscapes, to further test some of these ideas.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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C. Giuliano, F.A. Stewart and A.K. Piel

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C. Giuliano, F.A. Stewart and A.K. Piel

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