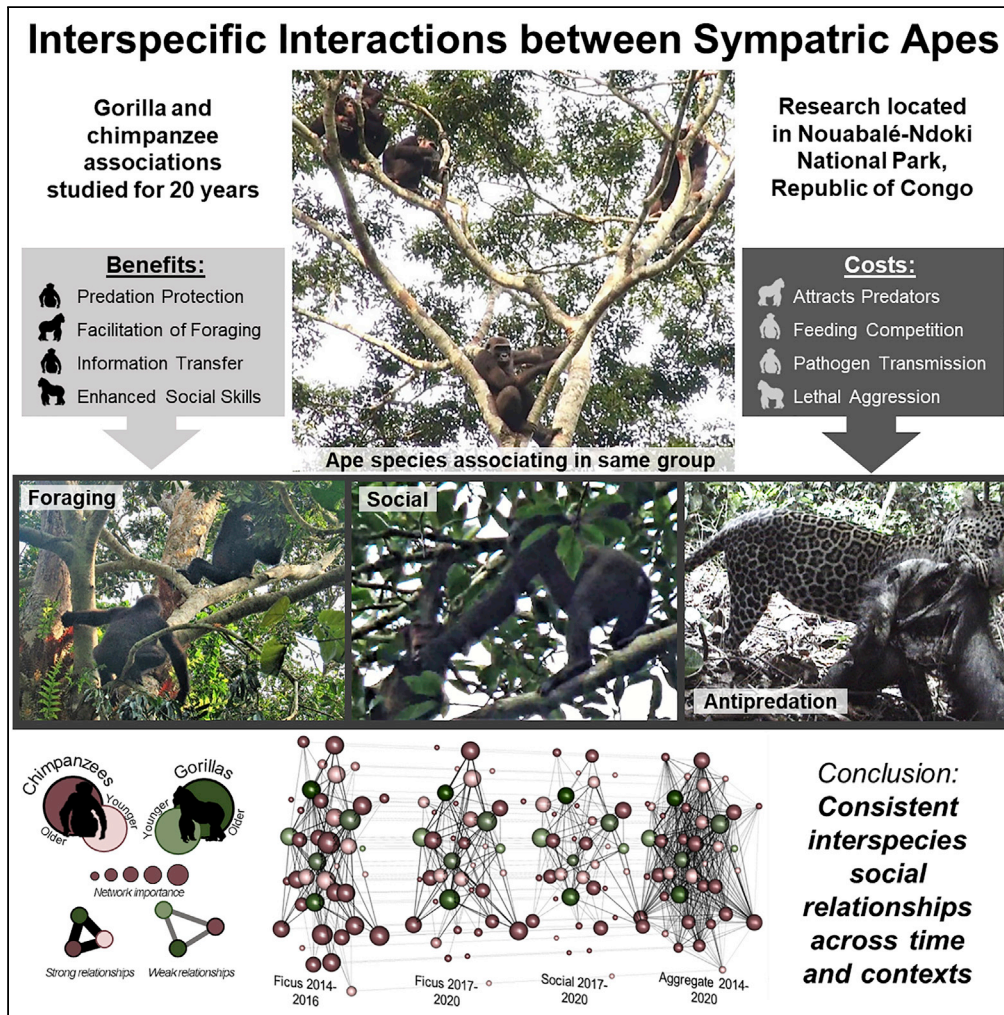


Article

Interspecific interactions between sympatric apes



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Highlights

First evidence of social relationships between chimpanzees and gorillas is reported

Social ties between chimpanzees and gorillas persisted over years and across contexts

Ape species engaged in a wide range of interactions, from play to aggression

Coexisting great apes may inform us about interactions between some early hominins



Article

Interspecific interactions between sympatric apes

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SUMMARY

Gorillas reside in sympatry with chimpanzees over the majority of their range. Compiling all known reports of overlap between apes and augmenting these with observations made over twenty years in the Ndoki Forest, we examine the potential predation-related, foraging, and social contexts of interspecific associations between gorillas and chimpanzees. We reveal a greater diversity of interactions than previously recognized, which range from play to lethal aggression. Furthermore, there are indications that interactions between ape species may serve multiple functions. Interactions between gorillas and chimpanzees were most common during foraging activities, but they also overlapped in several other contexts. From a social perspective, we provide evidence of consistent relationships between particular chimpanzee-gorilla dyads. In addition to providing new insights into extant primate community dynamics, the diversity of interactions between apes points to an entirely new field of study in early human origins as early hominins also likely had opportunities to associate.

INTRODUCTION

Primate communities may be comprised of ten or more species, with local compositions and interactions determined by abiotic and biotic factors operating at variable spatial scales (Callaway and Walker, 1997; Leibold et al., 2004; Chase and Myers, 2011). The organization of these communities has typically been attributed to bottom-up forces, wherein populations are regulated by resource limitations (Lotka, 1925; Volterra, 1926). Interspecific associations can generally be defined as two or more species in such close proximity that they can be regarded as members of the same social unit, during which they may engage in both direct and indirect interactions characterized by territoriality, aggressive behavior, agonism, or competition over shared resources (Levins, 1979; Armstrong and McGehee, 1980). From a traditional perspective, sympatric species that occupy similar ecological niches would be expected to intensely compete and eventually exclude each other from communities (Volterra, 1926; Gause, 1934; Hardin, 1960). However, recent research across an array of species has revealed complex combinations of both resource competition and facilitation (Schoener, 1983; Callaway and Walker, 1997). It has been shown that a species can actually enhance the survival, growth, or fitness of another species by providing protection from predation, accumulating nutrients consumed by the other species, or even by mitigating disturbance (Hunter and Aarssen, 1988; Wilson and Agnew, 1992; Bertness and Callaway, 1994; Callaway and Walker, 1997; Callaway et al., 2002).

Theoretical expectations suggest that predator avoidance and/or enhanced foraging may be potential benefits of mixed-species associations, while costs may include increased feeding competition or parasitism (Terborgh, 2015) (Figure 1). Associating with another species facing similar predators could improve the probability of predator detection (Kenward, 1978), lead to predator confusion (Cott, 1940; Edmunds, 1974), increase dilution effects (Hamilton, 1971), or enhance the ability to more effectively deter predators (Curio, 1978). Furthermore, the benefits of locating food more efficiently through another species' knowledge of food availability and/or their differential ability to access particular food sources may defray the potential costs of interspecific associations (Wolters and Zuberbühler, 2003; Pinheiro et al., 2011). There are also potential social benefits of interspecific grouping which may include establishing tolerant relationships (Struhsaker, 1981), grooming services (Struhsaker, 1981), alloparental care (Stensland et al., 2003), and reproductive advantages of increasing group size without increasing breeding competition (Dunbar, 1993; Buchanan-Smith, 1999; Farmer et al., 2006). Furthermore, it should be noted that these potential functions

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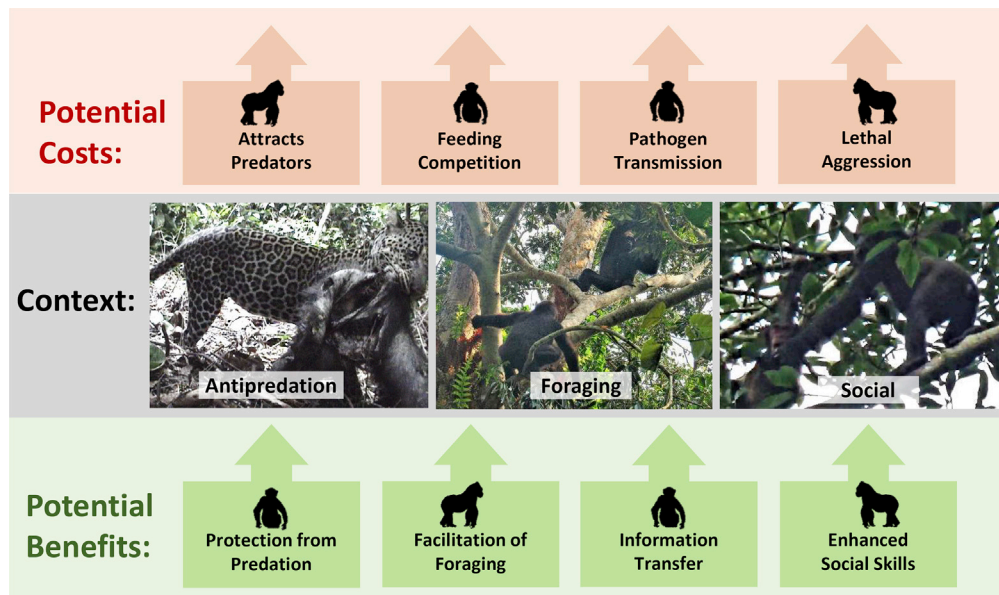


Figure 1. Costs and benefits of interspecific interactions between great apes

The contexts of interspecific associations are predation-related, foraging, and social. The potential benefits of interspecific associations are listed, as well as the deterrents of chimpanzee and gorilla association. It should be noted that these are not mutually exclusive and that interspecific interactions occur in several contexts and may serve multiple functions.

need not be mutually exclusive (Wolters and Zuberbühler, 2003) and that one primate species may benefit more than another (Cords, 1990) or at another's cost (Boinski, 1989).

The potential benefits of interspecific associations among monkeys have been relatively well documented (Table 1). However, comparable assessments of sympatric great apes are lacking despite the fact that gorillas (*Gorilla* spp.) and chimpanzees (*Pan troglodytes*) reside in sympatry over the majority of their range (Table 2 and Figure 2). It is challenging to observe interspecific interactions of these species as there are few sites where both species have been habituated to the presence of researchers. In the few studies that have considered gorilla and chimpanzee sympatry, potential anti-predation advantages have generally been considered irrelevant because it was assumed that the large body sizes of great apes were sufficient to deter predation. However, documented leopard attacks provide evidence to the contrary (Boesch, 1991; Fay et al., 1995). Increased size of interspecific groups could reduce the risk of predation without the increased feeding and mating competition associated with larger groups of conspecifics. Furthermore, recent reports of chimpanzees killing immature gorillas (Southern et al., 2021) prompted us to predict that vulnerable gorillas would avoid close interaction with adult chimpanzees if they posed a risk.

Interactions between sympatric great apes have most commonly been characterized as strategies to avoid competition or as direct competition over food sources (Tutin and Fernandez, 1985, 1993; Kuroda, 1992; Yamagiwa et al., 1996a, 1996b; Basabose and Yamagiwa, 2002). Based on the nest site choice of sympatric apes in east Africa, it was concluded that chimpanzees avoided nesting in trees bearing fruits eaten by mountain gorillas, *Gorilla beringei* (Basabose and Yamagiwa, 2002). Scientists observed contest competition between chimpanzees and mountain gorillas in the Bwindi forests of Uganda (Stanford and Nkuruungi 2003). The counterparts of mountain gorillas in western Africa, lowland gorillas (*Gorilla gorilla*) are more frugivorous than eastern gorillas (*Gorilla beringei*) and thus one might expect them to show a higher degree of overlap with chimpanzees than their eastern counterparts who incorporate less fruit in their diet. There is some evidence that foraging western lowland gorillas and chimpanzees converge during times of fruit abundance and diverge during fruit scarcity (Tutin and Fernandez, 1993; Tutin et al., 1996). Sharing of tree crowns by ape species was observed during foraging in the central African forests of Ndoki (Suzuki, 1992; Yamagiwa et al., 1996a, 1996b). In contrast, scientists reported two observations of lethal attacks of chimpanzees on immature gorillas in Gabon (Southern et al., 2021). Apes may also alter their habitat use, activity patterns, diet selection, or foraging strategies to avoid interspecific overlap through either

Table 1. Overview of the contexts (which may be related to functions) and benefits of interspecific associations among monkeys

	Context/Function	Benefit	Reference
New World Monkeys			
Golden-headed lion tamarin (<i>Leontopithecus chrysomelas</i>); Wied's marmoset (<i>Callithrix kuhlii</i>)	F, A	Both	Oliveira and Dietz, 2011 ; Rocha et al., 2015
Squirrel monkey (<i>Saimiri sciureus</i>); Tufted capuchin (<i>Cebus apella</i>); Bearded saki (<i>Chiropotes satanas</i> , <i>C. utahickae</i>); Howler monkey (<i>Alouatta belzubi</i>); Tamarin (<i>Sanguinus niger</i>); Owl monkey (<i>Aotus azarae</i>); Titi monkey (<i>Callicebus moloch</i>)	F	All	Pinheiro et al., 2011
Golden-headed lion tamarin (<i>Leontopithecus chrysomelas</i>); Wied's marmoset (<i>Callithrix kuhlii</i>)	F, A	Both	Oliveira and Dietz, 2011 ; Rocha et al., 2015
Squirrel monkey (<i>Saimiri sciureus</i>); Tufted capuchin (<i>Cebus apella</i>); Bearded saki (<i>Chiropotes satanas</i> , <i>C. utahickae</i>); Howler monkey (<i>Alouatta belzubi</i>); Tamarin (<i>Sanguinus niger</i>); Owl monkey (<i>Aotus azarae</i>); Titi monkey (<i>Callicebus moloch</i>)	F	All	Pinheiro et al., 2011
Squirrel monkey (<i>Saimiri oerstedii</i>); White-faced capuchin (<i>Cebus capucinus</i>)	A	Cebus only*	Boinski, 1989
Callitrichines review (various: <i>Sanguinus fuscicollis avilapiresi</i> ; <i>S. f. fuscicollis</i> ; <i>S. f. nigrifrons</i> ; <i>S. f. weddelli</i> ; <i>S. f. melanoleucus</i> ; <i>S. mystax</i> ; <i>S. m. pileatus</i> ; <i>S. m. mystax</i> ; <i>S. imperator subgriseus</i> ; <i>S. labiatus</i> ; <i>Callithrix emiliae</i> ; <i>C. goeldii</i>)	F, A	All*	Heymann and Buchanan-Smith, 2000
Old World Monkeys			
Diana monkey (<i>Cercocebus aethiops sabaesus</i>); Olive colobus (<i>Procolobus verus</i>)	(A)	Both	Whitesides, 1989
Diana monkey (<i>Cercopithecus diana</i>); Campbell's monkey (<i>Cercopithecus campbelli</i>)	F, A, S	Both	Wolters and Zuberbühler, 2003
Diana monkey (<i>Cercopithecus diana</i>); Red colobus (<i>Piliocolobus badius</i>)	A	Both	Holenweg et al., 1996 ; Bshary and Noe, 1997
Grey-cheeked mangabey (<i>Lophocebus albigena</i>); Blue monkey (<i>Ceropithecus mitis</i>); Redtailed monkey (<i>Ceropithecus ascanius</i>); Black-and-white colobus (<i>Colobus guereza</i>); Red colobus (<i>Piliocolobus badius</i>)	(F, A)	All	Chapman and Chapman, 1996
Grey-cheeked mangabey (<i>Lophocebus albigena</i>); Redtailed monkey (<i>Cercopithecus ascanius</i>)	(F, A)	Both	Waser, 1982
Grey-cheeked mangabey (<i>Lophocebus albigena</i>); Redtailed monkey (<i>Cercopithecus ascanius</i>)	(A)	Both	Bryer et al., 2013
Redtailed monkey (<i>Cercopithecus ascanius</i>); Blue monkey (<i>Cercopithecus mitis</i>)	F, A	Both*	Cords, 1990

"Context/Potential Function": F = foraging efficiency, A = anti-predation, S = social advantages (if listed within parentheses, context-dependent functional advantages were reported). "Benefit" defines which species (or all) were reported to benefit from the mixed species associations. Other species may have been studied in these listed investigations (e.g., [Waser, 1982](#); [Whitesides, 1989](#)); however, only species discussed with possible functional advantages to mixed species associations are listed here. *Note: [Heymann and Buchanan-Smith \(2000\)](#) review the literature on polyspecific callitrichine troops, reporting very low costs to mix-species association of this taxa; [Boinski \(1989\)](#) reports *C. capucinus* to be the primary benefactor (anti-predation) of their sustained association with *S. oerstedii* who may experience a plausible reduction of foraging efficiency; [Cords \(1990\)](#) reports that *C. mitis* appear to be the primary benefactors in some instances while both species experience only minor costs due to mixed-species associations.

spatial or temporal niche partitioning ([Schoener, 1983](#); [Mitchell et al., 1990](#); [Ziv et al., 1993](#); [Eccard and Ylonen, 2003](#)).

Given this evidence, consistent observations of great ape overlap likely represents active choice over avoidance or simply chance encounters. Although not yet detailed in the literature, there are potential

Table 2. Reports of interspecific association between sympatric chimpanzees and gorillas

Ape Taxa, Study Site Location	Period	Interspecific Interactions			
		Foraging	Spatial Intersection	Agonism	Not Known
<i>G. g. gorilla, P. t. troglodytes</i>					
Goulougo, Rep. Congo ^a	1999–2020	148	117		20
Mondika, Rep. Congo ^b	1999–2020	+			
Ndoki, Rep. Congo ^c	1989–1992	4	2		
Rio Muni, Equat. Guinea ^d	1966–1968	–	1		
Lope, Gabon ^e	1984–1993	?			
Loango, Gabon ^f	2005–2019	2		2	7
Ndakan, C.A.R. ^g	1986–1990	+			
<i>G. b. beringei, P. t. schweinfurthii</i>					
Bwindi, Uganda ^h	1996–2005	5			
Kahuzi, Dem. Congo ⁱ	1994–2002	3	7		

Foraging includes both covefeeding and feeding in proximity. Spatial intersection included chimpanzees and gorillas being observed within 50m of each other, but with no apparent interaction. At Loango, two particular interactions between chimpanzees and gorillas involved lethal aggression and so were categorized as agonism. Social interactions among sympatric apes in Goulougo were observed in various contexts.

+ observed, but number of occurrences not available; – not observed; ? information not available.

^aThis study.

^bMorgan, pers comm.

^cKuroda, 1992, Nishihara, 1992, Kuroda et al., 1996.

^dJones and Sabater Pi, 1971.

^eTutin and Fernandez, 1985, Tutin and Fernandez, 1993.

^fHead et al., 2011, Southern et al., 2021.

^gFay, personal comm.

^hStanford and Nkurunungi, 2003.

ⁱYamagiwa et al., 1996a, 1996b, Basabose and Yamagiwa, 2002, Yamagiwa and Basabose, 2006, Yamagiwa and Basabose, 2009.

social benefits of mixed-species associations and social relationships between great ape species. In addition to establishing tolerant relationships and gaining services (such as grooming or alloparental care), the potential for information transmission should also not be overlooked as both chimpanzees and gorillas are capable of social learning. Interspecific associations and social interactions may provide pathways for the spread of behaviors and innovations between ape societies. However, a potential trade-off of social contact between closely related species is the spread of infectious diseases. This study will contribute to the long-term monitoring of social contacts between sympatric apes to provide quantifiable metrics on potential cross-species pathways of disease transmission which is a conservation concern for these endangered species.

Study aims

In this study, we compile previously published observations of interactions between sympatric great apes and augment this with new longitudinal studies of identified apes in the Goulougo Triangle to examine the contexts and potential functions of these interspecific associations. More specifically, we categorized these interspecific associations as covefeeding (foraging on the same food source, such as within the same tree crown), feeding in proximity (feeding within 50m, but not on the same food source), spatial intersection (within 50m, but not foraging or interacting), or social interaction (aggression, play, or sexual encounters between members of different species). In this study, we predict that if interspecific ape groups aid in avoiding predation, then we would expect both ape species to recognize the alarm call of the other species and that smaller chimpanzee parties would frequently associate with gorillas for protection from predators. We also predict that more vulnerable chimpanzee parties, such as those comprised of a single individual or a mother with a dependent offspring might be more likely to associate with gorillas than parties comprised of a greater number of adult chimpanzees, particularly parties with large numbers

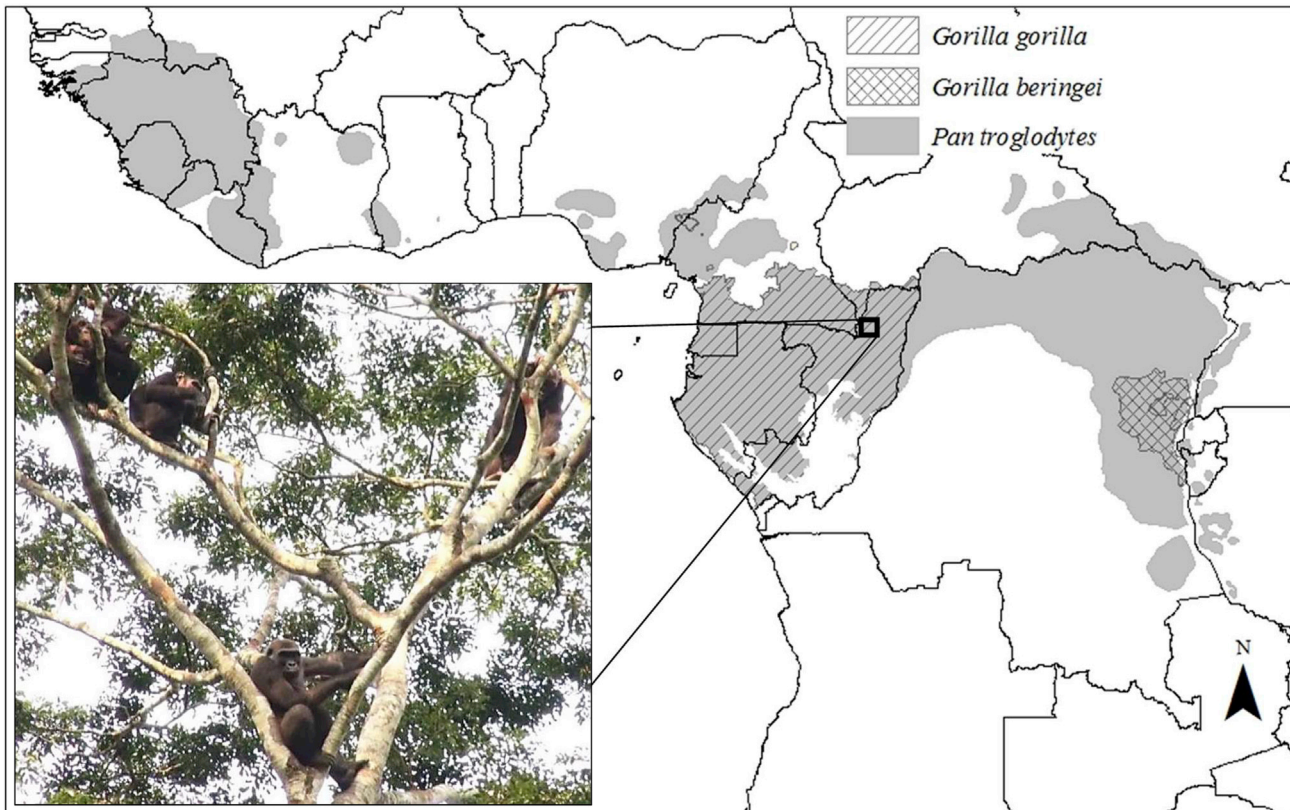


Figure 2. Species distribution and range overlap of wild chimpanzees and gorillas

Both western lowland gorillas (*Gorilla gorilla*) and mountain gorillas (*Gorilla beringei*) reside in sympatry with chimpanzees (*Pan troglodytes*) throughout most of their ranges. Inset shows members of the Moto chimpanzee community and Loya gorilla group cofeeding in the crown of a *Treculia africana* tree in the Goualougo Triangle, Republic of Congo.

of adult males. If chimpanzees threaten the survival of vulnerable gorillas, then we would expect to see attempted capture of gorilla infants by chimpanzees or avoidance by gorillas with infants of groups of chimpanzees, particularly groups with adult male chimpanzees. If mutual attraction to food sources is a driving force in associations between species, then we would expect overlap between apes to coincide with the availability of particular foods. It is also possible that one species may capitalize on the other's knowledge of rare and asynchronously available foods (such as figs). If either ape species is gaining social benefits, then we would expect to detect consistent social contacts and relationships between species. In reviewing all reported interactions between sympatric apes, we consider the detection of overlap events at different sites and the frequency of interspecific associations in various contexts (e.g., foraging, spatial intersection, agonism). It is clear that the present study overcomes two key challenges that are associated with the study of sympatric great ape social interactions: 1) both species are habituated to the presence of researchers and 2) members of the great ape groups are individually identifiable by researchers. With regard to the biological importance of interspecific interactions, they directly link to fitness via reduction of predation risk and enhanced foraging potential which is essential to understanding the present and past primate communities.

RESULTS

In our review of published reports, we found a total of 33 documented interspecific interactions (and two other unpublished interactions) at eight sites, representing studies conducted from 1966 to 2020 (Table 2). While conducting daily follows of chimpanzees and gorillas from 1999 to 2020 in the Goualougo Triangle, we observed an additional 285 interspecific associations between great apes. More specifically, research teams tasked with following chimpanzees in the Moto Community located in the Goualougo Triangle study area observed 206 interspecific associations with gorillas between July 1999 and February 2020. In 2013, a gorilla group within the Moto chimpanzee territory was habituated to humans and teams following the

gorilla group observed 62 interspecific associations between February 2013 and February 2020. On 17 occasions, both field teams were present during interspecific associations. Duration of association between chimpanzees and gorillas ranged from 1 min to more than 8 h, with a mean of 67.9 min (median = 32.5, $n = 78$ cases in which full duration was observed). Importantly, our reported encounters represent minimal frequencies of occurrence as it was not possible to simultaneously follow all chimpanzee parties or conduct ape follows every day throughout the study period.

Ape associations and predation

The anti-predation hypothesis predicts that apes would attend and respond to the alarm calls of the other species and that smaller groups would seek association with other species to increase vigilance and overall subgroup size. Both species were observed responding to the alarm vocalizations of the other species. Responses included increasing vigilance by orienting toward the origin of the call and visually monitoring the response of other apes in the subgroup. We did not observe gorillas or chimpanzees emitting alarm calls in response to the arrival of the other ape species to a subgroup. No predation attempts between the ape species were observed in this study, but chimpanzees at Loango have been observed killing infant gorillas on two occasions (Southern et al., 2021). However, we did observe bidirectional aggressive threats and contact agonism between apes in the Goulougo Triangle. We also noted behavioral mechanisms which may mitigate such predation attempts, such as adult female gorillas retrieving their young infants who approached and attempted to initiate play with young chimpanzees. However, several play bouts between a subadult male chimpanzee and juvenile male gorilla were observed. Contrary to staying in close proximity to the silverback as protection from predation, juvenile and subadult gorillas regularly traveled more than 300 m from their group to join a chimpanzee party.

Counter to predictions of reducing vulnerability by increasing numbers, we found that the initial chimpanzee parties in association with gorillas were larger than parties consisting only of chimpanzees (Table 3). The anti-predation hypothesis predicts that lone individuals would more frequently associate with gorillas than other types of chimpanzee parties, but we found that interspecific associations occurred in all types of chimpanzee parties. Interspecific relationships were strongest between gorillas and adult female chimpanzees with dependents (Figure 3), followed by gorilla associations with mature male chimpanzees, and then mature chimpanzee females without infants.

While gathering in large nesting groups could serve to reduce the risk of predation at night, previous research has shown that gorillas and chimpanzees have distinct habitat preferences for nesting which could preclude association in this context (Morgan et al., 2006; Sanz et al., 2007). In our transect surveys of ape nests, we observed that only 2.4% of all fresh chimpanzee nest sites/groups (5 of 206 total sites) were within 50m of a gorilla nest site. A slightly higher percentage of fresh gorilla nest sites (6.7%, 7 of 105 sites) were found within 50m of chimpanzee nest groups.

Ape associations in foraging-related contexts

The enhanced foraging hypothesis predicts that interspecific associations between apes would coincide with particular foods. Supporting this assertion, these gorillas and chimpanzees are most often associated in contexts where both species were feeding either on the same food source (cofeeding) or on different foods but in close proximity. Cofeeding at the same food source (e.g., same tree) represented 34% of interspecific associations, with another 18% of observations involving apes foraging in close spatial proximity but on different foods. At least 20 different plant species were targeted by apes during cofeeding events in this study (Table 4), which greatly expands our knowledge of the diversity of resources shared during interspecific associations. Despite the extreme rarity of *Ficus* spp. in this region, figs were consumed during 64% of the observed cofeeding events.

To assess whether one species was potentially benefiting from the knowledge of the other species, we examined the temporal pattern of interspecific associations at cofeeding events when we followed the gorilla group two days prior to, during, and for two days after cofeeding events with chimpanzees. A total of 10 cofeeding events met this criterion, with five of the trees representing species with synchronized fruiting and the other five being asynchronous *Ficus* resources (figs). At four of the synchronous resources, the gorilla group was observed feeding at the trees on days prior to the cofeeding event and continued to feed on these trees for two days after, suggesting that their presence at the trees was independent of chimpanzees. In contrast, gorillas were not observed visiting any of the five *Ficus*

Table 3. The size of chimpanzee parties when alone and in association with gorillas

Chimpanzee Party Type	Chimpanzee Parties		Number of Chimpanzees in Interspecific Associations	
	Party Size	Percent of Parties	Chimpanzees in Interspecific Association	Percent of Interspecific Associations
Mixed Age/Sex Party	8.66 ± 4.03	54%	12.71 ± 4.71	59%
Adults Party	4.67 ± 1.85	17%	5.86 ± 2.57	10%
Females Party	4.19 ± 1.71	12%	5.63 ± 2.22	14%
Males Party	2.61 ± 0.84	3%	3.00 ± 0	3%
Mother and Offspring	2.30 ± 0.50	5%	2.00 ± 0	7%
Lone Individual	1.00	5%	1.00	3%
Undetermined	2.48 ± 0.74	3%	2.00 ± 0	3%

Chimpanzee parties consisted of all individuals travelling, feeding, resting, or socializing within 50m of one another (adopted from Wrangham et al., 1992 and Wilson et al., 2001). Interspecific associations can generally be defined as two or more species in such close proximity that they can be regarded as members of the same group. We have applied this definition to identify interspecific associations.

locations on the two days prior to the cofeeding event and visitation to figs was rare on the days after cofeeding. During ape follows, we also observed the gorilla group immediately change their travel direction to head toward chimpanzee vocalizations originating from the canopy of *Ficus* with ripe figs. Chimpanzees did not exhibit any similar behaviors that would indicate they were attracted to food sources by gorillas.

Social relationships between ape species

The beneficial sociality hypothesis predicts that species are attracted to mixed-species associations by the social benefits of interactions with and/or forming a relationship with an individual(s) of another species. Network statistics were used to assess the strength of social associations (calculated as simple ratio indexes) between individually identifiable gorillas and chimpanzees. We confirmed that the observed distribution of gorilla and chimpanzee association rates significantly differed from those that would be expected by randomly permuted network datasets (2014-2020 observed mean ± s.d. = 0.16 ± 0.17, random = 0.15 ± 0.15; $p < 0.001$, 1000 permutations (Manly, 1995; Bejder et al., 1998; Whitehead, 1999; Stensland et al., 2003; Whitehead, 2008)). Furthermore, we found that particular dyads were associated on multiple occasions and across different contexts (cofeeding, resting, traveling, socializing) over a period of at least six years (Figure 3). We confirmed the consistency of these associations using a subset of the multidimensional network that contained those individuals active in all layers (mean edge overlap = 71.07%; Spearman correlation analysis; see STAR Methods). All layers were highly correlated (*Ficus* 2014 to 2016 – *Ficus* 2017 to 2020: $r_s = 0.93$; *Ficus* 2014 to 2016 – social 2017 to 2020: $r_s = 0.82$; *Ficus* 2017 to 2020 – social 2017 to 2020: $r_s = 0.82$).

In accordance with conventional definitions, we refer to repeated patterns of both associations and interactions between individually identifiable chimpanzees and gorillas as social relationships (Figure 4) (Sueur et al., 2011; Farine and Whitehead, 2015). Although on average chimpanzees had more total social ties (degree, chimpanzee: 30.67 ± 8.58 , $n = 36$; gorilla: 27.6 ± 1.34 , $n = 5$) and displayed higher levels of social integration (eigenvector centrality, chimpanzee: 0.48 ± 0.32 , $n = 36$; gorilla: 0.14 ± 0.03 , $n = 5$) than gorillas when feeding on figs, the range of network measures for all the individual gorillas in this context was within the range of chimpanzees. The silverback male had the lowest eigenvector centrality score among the gorillas in this context, whereas the younger male gorillas had the highest measures of connectedness and social integration. This was confirmed by average dyadic simple ratio index associations of gorillas from 2017 to 2020 which showed that the younger males (Kao = 0.29 ± 0.17 , Modiaye = 0.26 ± 0.16 , Eteko = 0.22 ± 0.16) had stronger collective ties to chimpanzees and engaged in more social relationships with chimpanzees than the silverback (0.21 ± 0.12) or female (0.24 ± 0.16) and infant (0.21 ± 0.10). In accordance with differences in network ties between chimpanzee-gorilla dyads, we observed that some individuals repeatedly sought particular social partners over time.

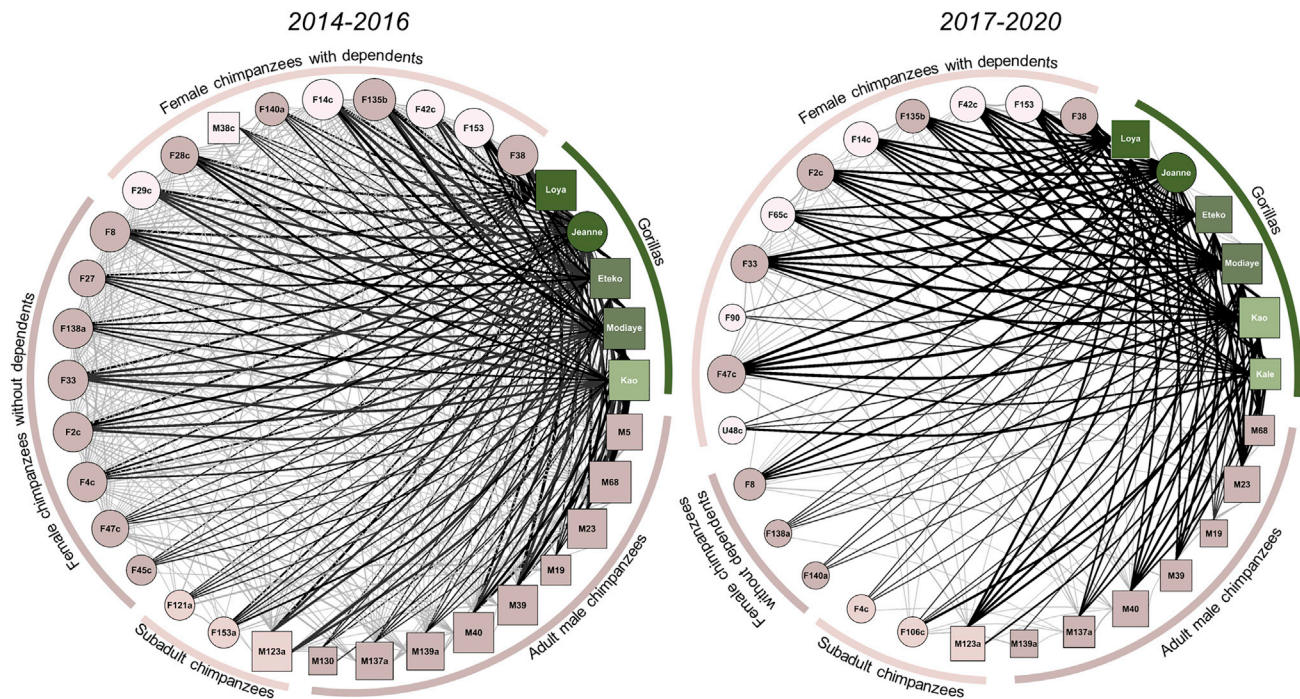


Figure 3. Networks of dyadic associations between chimpanzees and gorillas across time periods

Chimpanzees (rose-colored nodes) and gorillas (green-colored nodes) maintained a selective set of relationships with particular individuals. Also, gorillas associated twice as much with chimpanzee females that had dependent offspring (0.37 ± 0.14) compared to either chimpanzee males (0.18 ± 0.09) or females without dependents (0.12 ± 0.07). Female apes are represented by circles and males as squares. All nodes are shaded darker with age and scaled in size to represent eigenvector centrality. Strong relationships are represented by thicker and darker lines.

We observed a range of social interactions between chimpanzees and gorillas in the Ndoki Forest, ranging from affiliative to aggressive encounters. Interspecific aggression was bidirectional and most frequently consisted of threats. During this study in the Goulougo Triangle, contact aggression was rare and never escalated to the types of lethal attacks documented in Loango, Gabon (Southern et al., 2021). Affiliative interactions included play with individuals of both species engaged in chasing, wrestling, play biting, and play hitting. An interspecific sexual interaction was observed in which a juvenile male gorilla repeatedly dorsally mounted and thrust his groin into contact with the anogenital region of an immature female chimpanzee. We also observed gesturing between species to initiate social interactions. Intriguingly, chimpanzees exhibited chest-beating which is a behavior characteristic of gorillas. Although most interactions involved a chimpanzee-gorilla pair, we also observed polyadic interactions.

DISCUSSION

In this study, we reveal a greater diversity of interactions than previously documented among sympatric apes, including social relationships between members of different species that persisted over years. Furthermore, we found that interspecific associations between great apes occur in several different contexts and thus may have multiple functions. Supporting the anti-predation hypothesis, both species appropriately responded to the alarm calls of the other species which could increase the detection of potential threats. We have also observed apes approach, investigate, and retreat from recently killed victims of predation that were the other ape species. However, larger chimpanzee parties associated with gorillas more often than smaller parties which are counter to the antipredation hypothesis and could result in increased feeding competition. Some observations could be interpreted either way, such as those of individual gorillas leaving the protection of their group's silverback to join a chimpanzee party that was more than a hundred meters away. The majority of associations between gorillas and chimpanzees occurred in foraging contexts and we observed cofeeding at many more types of food sources than previously documented. In contrast to predictions of competition between species, nearly all interspecific associations were tolerant or affiliative. Aggression was observed between gorillas and chimpanzees, but did not escalate to killing as reported from Loango, Gabon (Southern et al., 2021). The aim of our study was to broaden

Table 4. Food sources targeted by chimpanzees and gorillas during cofeeding events

Family	Species of Plant	Lifeform	Size Class of Trees	Food Part Eaten during Cofeeding	Observed Cofeeding Events
Apocynaceae	<i>Landolphia</i> sp.	liane		fruit	1
Calophyllaceae	<i>Mammea africana</i>	tree	small, medium	fruit	2
Cannabaceae	<i>Celtis tessmannii</i>	tree	large	fruit	1
Fabaceae	<i>Angylocalyx pynaertii</i>	tree	small, medium	fruit	1
	<i>Dialium pachyphyllum</i>	tree	small	fruit	1
	<i>Pterocarpus soyauxii</i>	tree	small, medium, large	fruit	1
	<i>Tetrapleura tetraptera</i>	tree	medium, large	fruit	1
Irvingiaceae	<i>Klainedoxa gabonensis</i>	tree	large	fruit	4
Loganiaceae	<i>Strychnos</i> sp.	liane		fruit	1
Malvaceae	<i>Ceiba pentandra</i>	tree	small	fruit	2
Moraceae	<i>Antiaris toxicaria</i>	tree	large	fruit	1
	<i>Ficus burretiana</i>	hemi-epiphyte, strangler		fig	1
	<i>Ficus elasticoides</i>	hemi-epiphyte, strangler		fig	33
	<i>Ficus exasperata</i>	hemi-epiphyte, strangler		fig	1
	<i>Ficus recurvata</i>	strangler		fig	12
	<i>Ficus wildemania</i>	hemi-epiphyte, strangler		fig	2
	<i>Ficus</i> spp.	hemi-epiphyte, strangler		fruit	13
	<i>Treulia africana</i>	tree	medium	seeds, fruit	7
Rubiaceae	<i>Nauclea diderrichii</i>	tree	medium	fruit	1
Sapindaceae	<i>Pancovia laurentii</i>	tree	small, medium, large	fruit	4
	<i>Zanha golungensis</i>	tree	medium, large	fruit	1
Sapotaceae	<i>Chrysophyllum lacourtianum</i>	tree	medium, large	fruit	4
Unknown	Unidentified			fruit	1
	Unidentified			flowers	1

Cofeeding events involved at least one member of both species feeding at the same food source (e.g., in the same tree crown). Lifeform describes plant morphology of the species cofed upon by sympatric apes (see [Ndolo Ebika et al., 2018](#) for the lifeforms of *Ficus* spp.). Size classes of trees are small (10-30 cm diameter at breast height, DBH), medium (30-80 cm DBH), and large (>80 cm DBH).

perspectives about interspecific interactions that occur within primate communities, particularly those among sympatric great apes, which can be used to inform reconstructions of the contacts and exchanges between early hominin species.

It has been hypothesized that differences in body size may allow closely related species to coexist, as has been shown in rodents ([Brown, 1975](#)) and birds ([Lack, 1971](#); [Cody, 1974](#); [Diamond, 1975](#)). Larger-bodied species are predicted to win contests and exploit food sources more effectively than smaller species ([Ecard and Ylonen, 2003](#); [Zeng and Lu, 2009](#)). This has been proposed in Gabon where elephants excluded sympatric apes from particular foods ([Head et al., 2012](#)). Although Head et al did not examine the relationship between sympatric great apes, they argue that the distribution and abundance of food are more important than the degree of dietary overlap between competing large-bodied mammals. In contrast to predictions of competition between species, we found that members of the gorilla group were integrated within a social network with the chimpanzees that included repeated association and interactions.

The majority of associations occurred at a variety of *Ficus* spp. ([Kuroda et al., 1996](#); [Stanford, 2008](#)) which is similar to reports of ape cofeeding on figs at other sites. Figs are asynchronous and found at extremely low densities across the region. Although further research is warranted on the temporal patterning of interspecific associations at particular food resources, we suggest that gorillas may exploit chimpanzee knowledge of the location of ripe figs. Based on our observations in the Goulougo Triangle, large parties of chimpanzees would often broadcast their location while feeding on figs which gorillas

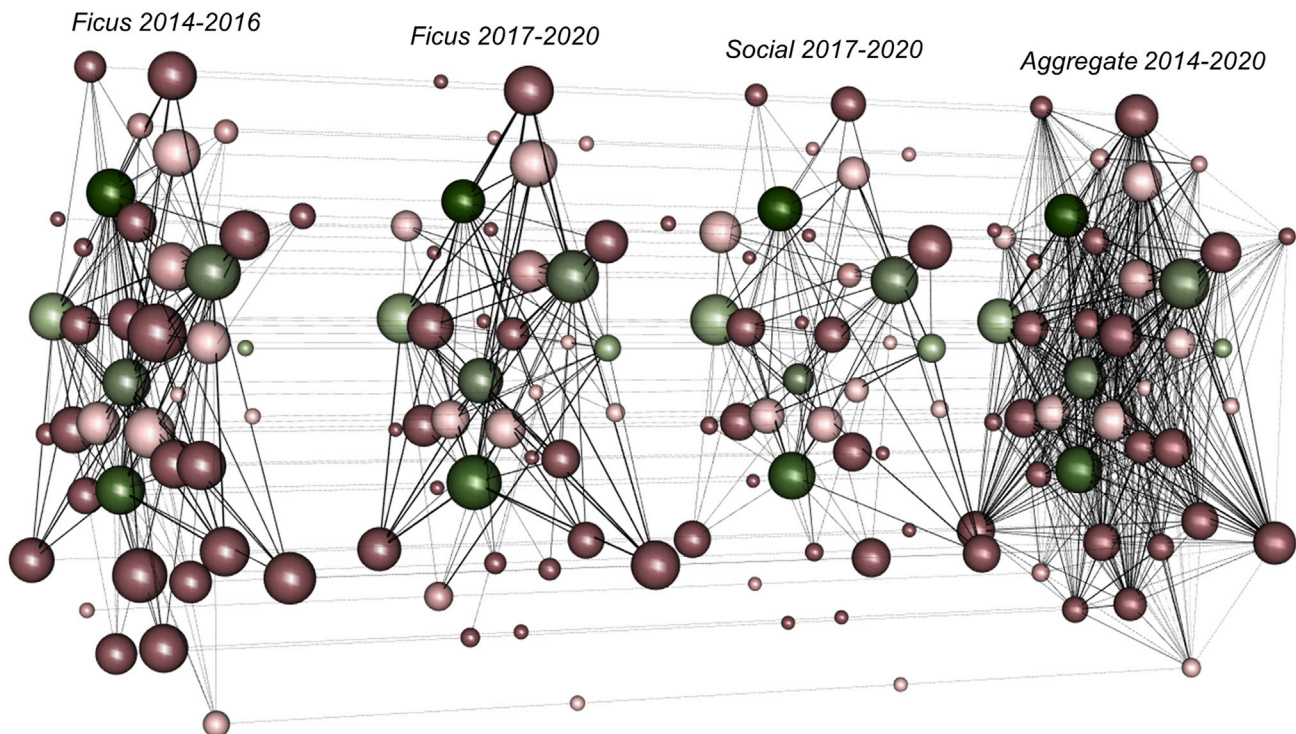


Figure 4. Multidimensional social network of interspecific relationships across contexts and time

The graphs show gorillas (green-colored nodes) and chimpanzees (rose-colored nodes) encountered in parties together while cofeeding on *Ficus* from 2014 to 2016, cofeeding on *Ficus* from 2017 to 2020, in other social contexts from 2017 to 2020, and aggregated across all contexts from 2014 to 2020. Node size is scaled to layer-specific eigenvector centrality (larger nodes indicate greater network importance) and shaded darker with age. Edge widths are scaled to the strengths of gorilla-chimpanzee dyadic relationships (thicker lines indicate stronger relationships). Horizontal lines across these network layers connect nodes that represent the same individual across all contexts. Overall, the integrated structure of these networks across time and contexts highlights the consistency in relationships between chimpanzees and gorillas.

responded to by changing their travel orientation toward the food resource. Other loci of association consisted of large trees that produce fruits (e.g., *Chrysophyllum lacourtianum*, *Pancovia laurentii*) that are available for weeks compared to the relatively brief period of figs (3-4 days). On some occasions, part of the gorilla group would climb into the tree crown to feed with chimpanzees while others remained on the ground and fed upon fallen fruit. Further research on the availability of preferred foods across habitats is needed to improve our understanding of how competition and niche partitioning vary across ape populations.

Additional study of how relationships between socially acquainted gorillas and chimpanzees change with time and across contexts would also provide clarity on the construction, maintenance, and limits of interspecies tolerance. On several occasions at food sources, we observed young gorillas and chimpanzees seeking out particular partners to engage in bouts of play which may afford unique developmental opportunities to extend their social, physical, and cognitive competencies (Palagi, 2018). Subadults were observed to engage in interspecific play, but these social dynamics seemed to shift as they matured to adulthood. Additionally, interactions between apes may also take on different severity depending on where they occur in the species' respective home ranges. Both species have core areas that are surrounded by peripheral zones which are visited less frequently and tend to have more aggressive interactions than core areas (Watts and Mitani, 2001; Morrison et al., 2020a, 2020b). For example, most of our observations of interspecific interactions occurred within the core area of the chimpanzee community range which is where the gorilla group resides. This is in contrast to observations of lethal killing in the periphery of a chimpanzee community range (Southern et al., 2021). Different groups of sympatric apes may have other types of home range overlap that influence their interactions. Future studies that spatially position interspecies interactions and outcomes within the contexts of the apes' home ranges will shed light on the dynamics of territoriality and perceptions of risk in certain regions of their ranges. Further, determining the shared

strategies of gorillas and chimpanzees holds the promise of revealing a greater depth of their social awareness than previously imagined.

Facilitated by social network connections, interspecific disease transmission is an unintended consequence of association and affiliative behavior. Cross-species transmission of infectious diseases has been known to occur between gorillas and chimpanzees, but the exact pathways and mechanisms of disease spillover remain speculative (Walsh et al., 2007). We observed several potential modes of pathogen transmission besides direct physical contact between individuals during play, aggression, and sexual interactions. Gorillas were observed feeding on fruit mesocarps that had been fed upon and discarded by chimpanzees. Also, gorillas were observed foraging on fruits and figs in the leaf litter under areas where chimpanzees had foraged, urinated, and defecated. Overlaying cofeeding events with food availability data could be useful in modeling potential areas of disease spillover events. Given that so many of the chimpanzee-gorilla interactions were observed in a feeding context, it is possible that detailed analyses of the diets and feeding adaptations in contemporaneous populations of fossil hominins (Henry et al., 2012; Ledogar et al., 2016; Martin et al., 2021) may also reveal previously unimagined insights into the paleobiology of our early relatives and ancestors.

There has been a long history in paleoanthropology of assuming that hominin species would competitively exclude each other from using the same resources in the same area (Gauss, 1934), to the point that it was once even hypothesized that only one hominin species could exist at any given time (Mayr, 1950; Wolpoff, 1971). The fossil record ultimately proved that hypothesis to be false (Leakey and Walker, 1976) and now behavioral data provide an African ape model for interspecies hominin interactions. With respect to later hominins, paleogenetics has confirmed sexual interactions between various such species. If observations of non-human apes are informative about the behaviors of archaic and early modern humans, then our study suggests these interactions would have most likely occurred in tolerant social contexts and were not contested by conspecifics.

Our review of interspecific associations between extant great apes indicates that they occur in several different contexts and may serve multiple functions, with broad implications for ape health and culture. It also provides a variety of advantages that are relevant to understanding the behavioral patterns of both present and past primate assemblages. Indeed, multiple hominin species are known to have contemporaneously occupied the same geographic regions, implying that they had opportunities to interact with each other. In eastern Africa, *Paranthropus boisei* and multiple species of early *Homo* are found in the Turkana Basin between roughly 2.0 and 1.5 million years ago (Ma) (Wood and Leakey, 2011). Hominin fossils are distributed in an expansive area around Lake Turkana, and there is some evidence that resident hominin species may have partitioned their environment (Behrensmeier, 1978; Shipman and Harris, 1988; Reed, 1997), so it is difficult to assess how frequently interspecific associations might have occurred. However, in South Africa at ~2.0 Ma, species of three hominin genera (*Australopithecus sediba*, *P. robustus*, and early *Homo*) occupy a landscape no larger than the Goualougo Triangle research area (Herries et al., 2020). Although sympatry among these taxa cannot be demonstrated conclusively, at a minimum they would have had adjacent ranges whose boundaries might have shifted over time (allowing their fossils to be deposited in the same small area). Thus, these hominins were likely either sympatric or parapatric, implying some opportunity for interaction and transmission of information. Although direct evidence of interspecies interactions in the early hominin fossil record will probably remain elusive, our findings point toward a research program modeling the nature and likelihood of such interactions given what is known about paleoecology, geography, adaptation, and the density of fossil sampling. In short, we can no longer assume that these interactions did not occur.

We show that extant chimpanzees and gorillas do not so completely partition their habitats to preclude regular interaction and the formation of lasting social relationships. This is interesting given that the chimpanzee, gorilla, and hominin clades diverged from each other during the Miocene when climatic conditions were becoming cooler and drier, which presumably would have placed ancestral ape populations under increasing ecological stress (e.g., Harrison, 2010). One might have expected that the divergence of these populations would have been hampered by associative behaviors, especially during the period prior to the evolution of reproductive isolation. It is worth considering whether evolutionary processes might have driven the divergence of these clades without eliminating some level of

behavioral interaction, or if the interactions seen among gorillas and chimpanzees today are evolutionarily novel. Unfortunately, anthropogenic disturbances and degradation are removing the environments and resources that draw them together, jeopardizing the future of these apes and with them the opportunity to further understand the relationships between and knowledge shared by our closest living relatives (Kühl et al., 2019).

Limitations of the study

While this study provides the first comprehensive review of interspecific interactions among sympatric great apes, many of the groups included in previous reports were not habituated to human presence which is likely to have limited the behaviors observed. This research would also benefit from the inclusion of multiple groups of gorillas and chimpanzees at each site to assess variation in responses.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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AUTHOR CONTRIBUTIONS

Conceptualization: CS, DM; Methodology: CS, DM, CEA, JMM, FE; Investigation: CS, DM, SB, CEA, JMM, FE, GM, SK, DN, DRKB; Visualization: CS, DM, JMM, SB, JAF; Funding acquisition: CS, DM; Project administration: CS, DM, CEA, SB, JMM, FE, GM, SK, DN, DRKB; Supervision: CS, DM, CEA, SB; Writing – original draft: CS, DM, DS; Writing – review & editing: CS, DM, DS, JAF, SB.

DECLARATION OF INTERESTS

The authors declare no competing interests in relation to this work.

INCLUSION AND DIVERSITY

We worked to ensure sex balance in the selection of non-human subjects. One or more of the authors of this paper self-identifies as an underrepresented ethnic minority in science. One or more of the authors of this paper self-identifies as a member of the LGBTQ+ community. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list. The author list of this

paper includes contributors from the location where the research was conducted who participated in the data collection, design, analysis, and/or interpretation of the work.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Report of interspecific association between sympatric chimpanzees and gorillas	Kuroda (1992)	
Report of interspecific association between sympatric chimpanzees and gorillas	Kuroda et al. (1996)	
Report of interspecific association between sympatric chimpanzees and gorillas	Nishihara (1992)	
Report of interspecific association between sympatric chimpanzees and gorillas	Jones and Sabater Pi (1971)	
Report of interspecific association between sympatric chimpanzees and gorillas	Southern et al. (2021)	https://doi.org/10.1038/s41598-021-93829-x
Report of interspecific association between sympatric chimpanzees and gorillas	Stanford and Nkurunungi (2003)	https://doi.org/10.1023/A:1024689008159
Report of interspecific association between sympatric chimpanzees and gorillas	Yamagiwa et al. (1996b)	
Report of interspecific association between sympatric chimpanzees and gorillas	Yamagiwa and Basabose (2006)	https://doi.org/10.1007/s10329-005-0147-7
Report of interspecific association between sympatric chimpanzees and gorillas	Yamagiwa and Basabose (2009)	https://doi.org/10.1002/ajpa.21102
Report of interspecific association between sympatric chimpanzees and gorillas	Basabose and Yamagiwa (2002)	https://doi.org/10.1023/A:1013879427335
Network data from this study	Interspecific Interactions between Sympatric Apes	https://openscholarship.wustl.edu/data/100

RESOURCE AVAILABILITY

Lead contact

Requests for additional information should be directed to the lead contact, Crickette Sanz (csanz@wustl.edu).

Materials availability

This study did not generate new unique reagents.

Data and code availability

No custom codes were generated for this research, as publicly available software and packages were used to conduct the analyses. Data sets have been posted in Washington University's Open Scholarship repository (<https://openscholarship.wustl.edu/data/100>) and are accessible to other researchers for the purposes of reproducing or extending the analysis.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

This research was conducted in the Goulougo Triangle which is located in the southern portion of the Nouabalé-Ndoki National Park (2°05'–3°03'N; 16°51'–16°56'E), Republic of Congo. Direct observations of chimpanzees in the Goulougo Triangle have been ongoing since February 1999. The Moto chimpanzee community consisted of 71 individuals at the time of this study, including 12 adult males and 24 adult females. Systematic information on encounters with gorillas have been recorded during daily chimpanzee follows since the beginning of the study. In 2013, we initiated habituation of a group of western lowland gorillas within the Moto chimpanzee community range. The Loya gorilla group consisted of 7 individuals

during the time of this study, including a dominant male silverback and two adult females. During daily follows of the Loya group, we recorded information on interspecific interactions with chimpanzees. To ensure temporal independence of our observations, only one intergroup encounter per day was included in the analysis, unless the analysis involved different individual apes. Ape nests and groups of nests (often referred to as nest sites) were also surveyed during this study.

Our study adhered to the legal requirements of the Republic of Congo where the research was conducted. The research was approved by the Nouabalé-Ndoki Foundation and the Wildlife Conservation Society's Congo Program. We also received endorsement to conduct this research from the Institutional Animal Care and Use Committee of Washington University in St. Louis. We also complied with ethics guidelines of the Association for the Study of Animal Behaviour (ASAB) and Animal Behavior Society.

METHOD DETAILS

The Goulougo Triangle study area is part of the Sangha River Trinational Protected Area Complex which is comprised of 7,000 km² of contiguous forest spanning national parks and reserves across Republic of Congo, Cameroon, and Central African Republic. The study area encompasses 380 km² of lowland forest with altitudes ranging between 330 m and 600 m. The climate can be described as transitional between the Congo-equatorial and sub-equatorial climatic zones. The diurnal primate community includes western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) which are found at overall density estimates of 2.34 gorillas/km² and 1.53 chimpanzees/km² in the Goulougo Triangle (Morgan et al., 2006).

Data collection protocols and definitions

Interspecific associations can generally be defined as two or more species in such close proximity that they can be regarded as members of the same group. The size and composition of chimpanzee parties may change several times throughout a day, but can be operationalized as all individuals travelling, feeding, resting, or socializing within 50m of one another (adopted from (Wrangham et al., 1992; Wilson et al., 2001)). Thus, we have applied this definition to identify interspecific associations among chimpanzees and gorillas.

Interspecific associations were categorized as cofeeding, feeding in proximity, spatial intersections, or social interactions. *Cofeeding* was defined as at least one member of both species feeding at the same food source (e.g., in the same tree crown). *Feeding in proximity* occurred when apes were feeding within 50m of each other, but not on the same food source. *Spatial intersections* involved chimpanzees and gorillas being observed within 50m of each other, but with no apparent interaction. Social interactions observed during interspecific events were described, and subsequently categorized as aggressive, playful, or sexual.

QUANTIFICATION AND STATISTICAL ANALYSIS

Associations

Simple ratio index social associations between individual chimpanzees and gorillas were calculated in SOCPROG (Whitehead, 2009). We used an established matrix randomization procedure (as described by (Manly 1995; Bejder et al., 1998; Whitehead 1999; Stensland et al., 2003; Whitehead 2008)) to test the observed distribution of chimpanzee and gorilla associations against the expected random distributions after 1000 permutations in SOCPROG.

Social network analysis

To assess the potential integration and centrality of individual gorillas and chimpanzees in mixed-species associations, we constructed a social network using group scan observations recorded during interspecific associations (within 50m) at *Ficus* spp. We used network statistics to assess the strength of social associations between individuals in the network (Whitehead 2008; Borgatti et al., 2013). The measure of *degree* is the sum of each node's weighted ties with all other nodes. *Eigenvector centrality* is a measure of the connectedness of an individual, as well as the connectedness all of those with whom the individual is connected; often interpreted to indicate social integration (De Domenico et al., 2015; Finn et al., 2019; Sosa et al., 2021). Degree and eigenvector centrality calculations were performed with the "degree()" and

"eigen_centrality()" codes via iGraph 1.3.0 in R 4.1.3 (Bonacich 1987; Csardi and Nepusz 2006; R Core Team 2021).

Temporal patterning of interspecific interactions at particular food resources

Based on the assumption that asynchronous species (such as figs) are more difficult to locate than synchronously fruiting trees, we compared Loya gorilla group's foraging patterns before, during, and after cofeeding events with chimpanzees at asynchronous and synchronous resources.